

Evol Ecol (2011) 25:681–693
 DOI 10.1007/s10682-010-9412-3

ORIGINAL PAPER

Change in individual growth rate and its link to gill-net fishing in two sympatric whitefish species

Sébastien Nusslé · Amanda Bréchon · Claus Wedekind

Received: 7 March 2010 / Accepted: 14 July 2010 / Published online: 23 July 2010
 © Springer Science+Business Media B.V. 2010

Abstract Size-selective fishing is expected to affect traits such as individual growth rate, but the relationship between the fishery-linked selection differentials and the corresponding phenotypic changes is not well understood. We analysed a 25-year monitoring survey of sympatric populations of the two Alpine whitefish *Coregonus albellus* and *C. fatioi*. We determined the fishing-induced selection differentials on growth rates, the actual change of growth rates over time, and potential indicators of reproductive strategies that may change over time. We found marked declines in adult growth rate and significant selection differentials that may partly explain the observed declines. However, when comparing the two sympatric species, the selection differentials on adult growth were stronger in *C. albellus* while the decline in adult growth rate seemed more pronounced in *C. fatioi*. Moreover, the selection differential on juvenile growth was significant in *C. albellus* but not in *C. fatioi*, while a significant reduction in juvenile growth over the last 25 years was only found in *C. fatioi*. Our results suggest that size-selective fishing affects the genetics for individual growth in these whitefish, and that the link between selection differentials and phenotypic changes is influenced by species-specific factors.

Keywords Rapid evolution · Artificial selection · Salmonid · *Coregonus* · Selection differential · Lake Brienz (Switzerland)

Electronic supplementary material The online version of this article (doi:[10.1007/s10682-010-9412-3](https://doi.org/10.1007/s10682-010-9412-3)) contains supplementary material, which is available to authorized users.

S. Nusslé (✉) · A. Bréchon · C. Wedekind
 Department of Ecology and Evolution, Biophore, University of Lausanne,
 1015 Lausanne, Switzerland
 e-mail: Sebastien.Nussle@unil.ch

A. Bréchon
 e-mail: Amanda.Brechon@unil.ch

C. Wedekind
 e-mail: Claus.Wedekind@unil.ch

Introduction

Fishing-induced mortality can be very high and often exceeds natural mortality significantly (Rijnsdorp 1993; Mertz and Myers 1998; Jackson et al. 2001). Fishing is typically size-selective (Myers and Hoenig 1997; Fukuwaka and Morita 2008), and since significant heritabilities have been reported for traits that could be size-related in many fish [up to $h^2 = 0.5$, see (Theriault et al. 2007; Carlson and Seamons 2008)], size-selective fishing is expected to induce rapid evolutionary changes (Palumbi 2001; Smith and Bernatchez 2008; Darimont et al. 2009). Traits such as age or size at maturation (Heino et al. 2002; Grift et al. 2003; Sharpe and Hendry 2009), average reproductive effort (Yoneda and Wright 2004; Thomas et al. 2009), or individual growth rates (Handford et al. 1977; Ricker 1981; Swain et al. 2007; Thomas and Eckmann 2007; Nusslé et al. 2009) are likely to evolve in response to size-selective fishing. Such fishing has therefore been termed a ‘large-scale experiment in life-history evolution’ (Rijnsdorp 1993; Law 2000; Stokes and Law 2000), and studies on fishery-induced evolution have increased in numbers during the last decade (see Jørgensen et al. (2007) for a review of phenotypic change attributed to fishery-induced selection).

Despite this increased interest in recent years, it is still largely unclear how much of the frequently observed change in individual growth rate is due to harvesting and how much to other environmental factors that have changed over time. For example, many freshwater systems have seen a change in phosphorus concentration and hence of biomass production over the last few decades (Müller et al. 2007a, b). Such changes in phosphorus concentration could contribute to changes in growth rates of many fish (Gerdeaux et al. 2006; Müller et al. 2007b; Thomas and Eckmann 2007). Separating the effects of fishery- versus environmentally-induced changes on individual growth rates is usually difficult (Heino et al. 2008) because phenotypic plasticity is important in fish (Thorpe 1998; Crozier et al. 2008). Even if genetic changes can be documented over time, monitoring data alone cannot conclusively demonstrate the causal link between such genetic changes and particular changes in the environment (Hutchings and Fraser 2008). However, a critical step forward in estimating the importance of evolution for phenotypic changes is to measure the strength of selection, namely the selection differential (Law 2000, 2007; Smith and Bernatchez 2008).

Alpine whitefish (*Coregonus* sp., Salmonidae) may be valuable models for studying human impacts on evolution of fish (Müller et al. 2007b; Thomas and Eckmann 2007; Nusslé et al. 2009; Thomas et al. 2009). Populations of Alpine whitefish are comparatively well-defined because they are usually confined to individual lakes, and genetic analyses suggest that there is often little gene flow between populations (Douglas 1998; Vonlanthen 2009; Bittner et al. 2010). Fishery on Alpine whitefish has generally been regulated and monitored for several decades. A typical pattern is that the fishing pressure on Alpine whitefish has been fairly constant and high during the last decades, i.e. most fish were harvested in their first years of life and old individuals are now scarce (Müller et al. 2007b; Nusslé et al. 2009). We analysed a 25-year long monitoring program to determine the selection differentials and the phenotypic changes over several generations of two sympatric Alpine whitefish species. We found significant selection differentials and a significant growth decrease in both species. Differences between the species suggest that fishing-induced evolution is to some degree species-specific.

Methods

We studied whitefish of Lake Brienz, Switzerland (46.43°N, 7.58°E; surface area = 29.8 km², elevation = 564 m, maximum depth = 261 m). Lake Brienz is one of the few Alpine lakes that was largely unaffected by the general eutrophication prior and up to the 1970s. Its relatively low phosphorus concentrations have even decreased since then (Fig. 1a), so that the lake can now be called “ultra-oligotrophic” (Müller et al. 2007a). A monitoring program, collecting 25 whitefish from ordinary fishery catches every month, has been conducted by the Fishery Inspectorate of the Bern Canton since 1984. Each individual is sexed (by dissection) and total body length and body weight are measured to the nearest mm and g, respectively. Gillrakers are counted for species identification (Müller 2003) and scale samples are taken (above the lateral line between the adipose and dorsal fin) for age and growth determination. The gillnets used by fisheries were set to 35–40 mm mesh size (as measured when stretched) for bottom nets and 38 mm for floating nets prior to 1992. In response to the observed growth decrease and the declining yield (Fig. 1a), the minimal legal mesh size was reduced to 30 mm for bottom nets in 1993, and for floating nets in 1996. The fishing pressure is not determined in detail, but fishermen seem to largely adapt their effort to the availability of the fish (C. Küng, Fishery Inspectorate Bern, Personal Communication). The number of fishermen declined from four until 1998 to three until 2005. During the last 5 years, only two fishermen remained.

Two groups of whitefish were sampled, the slow-growing “small-type” whitefish Brienzlig (*Coregonus albellus* Fatio) and the fast-growing “large-type” whitefish which are mostly, if not exclusively, Albock (*C. fatioi* Kottelat). The taxonomy of Alpine whitefish is often unclear and controversial. This is also true for the different whitefish of Lake Brienz although they can clearly be grouped according to life history, morphology, and genetics (Kottelat and Freyhof 2007; Bittner 2009; Vonlanthen 2009). While Bittner (2009), for example, call the various whitefish of Lake Brienz “forms” of *C. lavaretus*, Kottelat and Freyhof (2007) distinguish them as species. We do not attempt to solve this ongoing discussion here but use Kottelat and Freyhof’s (2007) guide to name the two most abundant whitefish groups of Lake Brienz (see also the discussion in Fraser and Bernatchez (2001) on defining conservation units). There is a third and probably a fourth other whitefish species in Lake Brienz (Douglas 1998; Kottelat and Freyhof 2007) that are both difficult to distinguish from *C. fatioi* on the basis of phenotypic characteristics only, but these other species are comparatively rare and numerically not important for fishery (Müller et al. 2007b). Moreover, because we confined our scale measurements (see below) and all further analyses to fish that were caught in December and January only ($N_{\text{total}} = 1,106$, $N_{\text{Brienzlig}} = 727$, $N_{\text{Albock}} = 379$), i.e. around the spawning time of the winter-spawning *C. albellus* and *C. fatioi*, we assume that large-type whitefish that are not *C. fatioi* are not present or rare in our samples and will therefore not significantly affect our analyses. *C. albellus* is a pelagic species with relatively dense gillrakers, indicating fish that are more efficient when feeding on zooplankton and *C. fatioi* has less gillrakers indicating fish that are thought to be more efficient on benthic food (Link and Hoff 1998).

For each individual fish we determined the average scale radius and all annulus radii, i.e. the distances from the nucleus to the subsequent annuli, using an ocular micrometer and two different scales per fish. We back-calculated the length at previous ages according to the method of Finstad (2003). This method is based on a multiple regression including the size of the scale, the age and length of the fish. This takes into account that scale growth might not be linearly related to fish growth as slower growing fish may have proportionately larger scales than faster growing individuals, or that there might be an

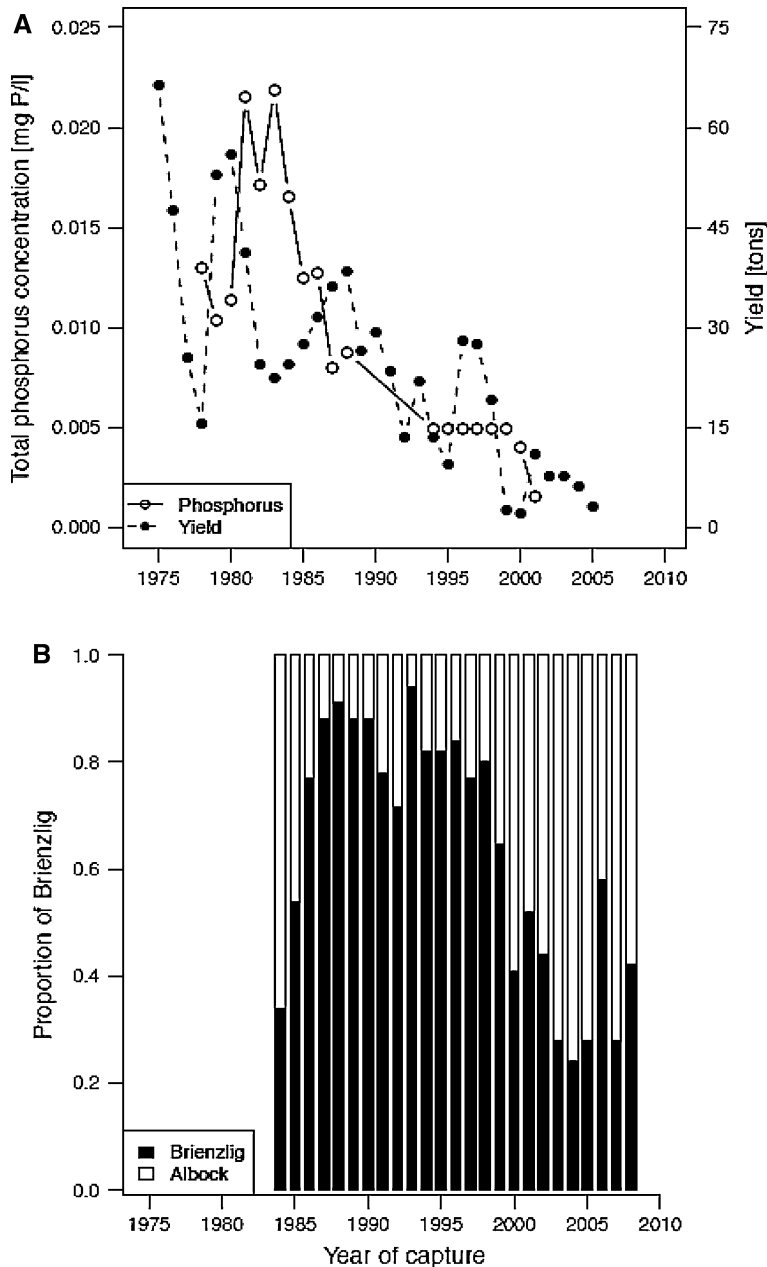


Fig. 1 Total phosphorus concentration, fishery yield, and relative abundances of the two whitefish species. **a** Total phosphorus (mg/l) (empty circles) in Lake Brienz during the last decades, redrawn from (Hoyle 2004) and fishing yield in Lake Brienz in tons (full circles). **b** Proportion of the total number of Brienzlig (black) and Albock (white) caught each year

age-specific growth of the scale irrespective of somatic growth. Then, to test for a potential bias in the back-calculations that could be linked to the age-at-capture, we analysed the residuals of the regression of the back-calculated lengths at capture (based on annuli radii) with the empirical length (based on the growth parameters) (Supplementary Fig. 1).

From the resulting length-at-age back-calculations, we computed the two-parameter logarithmic growth curve for each fish described in Nusslé et al. (2009):

$$L_i(t) = \alpha_{0i} + \alpha_{ti} \log(t) \quad (1)$$

where $L_i(t)$ is the back-calculated length of each fish at age t , α_{0i} is the back-calculated length at age 1, and α_{ti} is the logarithmic growth of the i -th fish. Parameter α_{ti} represents the length increase per time unit on a logarithmic scale. Hence α_0 represents juvenile growth while α_t is a measure of adult growth (Supplementary Fig. 2). The fit of this model was assessed with linear regressions of the back-calculated length (modelled) as a function of the length at capture (observed) (Supplementary Fig. 1). These back-calculated lengths fit well with the observed ones for both the Brienzlig (linear regression: slope = 0.98 ± 0.01 , $r^2 = 0.86$, Supplementary Fig. 1A) and the Albock (slope = 0.93 ± 0.02 , $r^2 = 0.83$, Supplementary Fig. 1B). The adult growth estimation based on all the annuli does not significantly differ from the estimations with a reduced number of annuli (Supplementary Fig. 3), suggesting that our estimation of the selection differentials is not biased in this regard. There is, however, a small but statistically significant effect of the age at capture on the residuals of the linear regression between back-calculated length and observed length for both the Brienzlig (linear regressions: $t_{347} = -3.6$, $p < 0.01$, $r^2 = 0.01$; Supplementary Fig. 1C) and the Albock ($t_{704} = -3.1$, $p < 0.001$, $r^2 = 0.03$; Supplementary Fig. 1D). The back-calculated lengths and the adult growth parameters are hence slightly underestimated for the oldest fish of our sample, but this barely affects our overall estimates of the selection differentials (see below) because the respective r^2 s are rather small (≤ 0.03) and older fish relatively scarce.

We used linear regressions of cohort-averaged growth parameters on year of birth of the fish to detect a potential change in growth parameters over time. In order to compare the two whitefish species, the observed growth changes were standardized to relative growth change (in %). We therefore divided, separately for Brienzlig and Albock, the observed change by the average growth parameters and multiplied this ratio with the respective average generation time. By assuming that average generation time remained constant over the observation period, an average generation time could be estimated separately for small-type and large-type whitefish according to Stearns (1992), assuming that only minor changes in survival and fecundity occurred during the monitoring:

$$\text{Generation time} = \frac{\sum_x x l_x m_x}{\sum_x l_x m_x} \quad (2)$$

where x is the age class of the fish, l_x is the probability of survival to age x , and m_x is the fecundity of age class x . Fecundity was estimated as the probability (p) of being mature at age x times the mean length (L) of the fish in the age class x cubed ($m_x = pL^3$), assuming that fecundity is proportional to the length³ of the fish (Clark and Bernard 1992).

As a potential indicator for resource allocation from growth to reproduction, we estimated the reproductive investment of females as the condition factor Fulton K ($K = 10^5 \cdot \text{fish weight}/\text{fish length}^3$). We also estimated the age at maturation for each fish according to the method of Rijnsdorp and Storbeck (1995) which assumes that growth is maximal and linear when the fish is immature and decreases after the fish becomes mature because some

resources are invested into reproduction instead of growth. We used linear regressions to test for linear trends over time in these two measures.

The selection differential s was determined for each age class within each cohort by comparing the reproducers, i.e. the fish caught in subsequent years and at older age, with all the fish of that particular age class. These estimates of s were then averaged for each cohort as in Nusslé et al. (2009). For each fish, we calculated individual growth parameters based on annuli radii and compared these growth parameters within cohorts. For each comparison between age classes, the estimation of the growth parameters was calculated with the same number of annuli in order to estimate the differences within cohort with the same metric. Analyses of variance of the estimated growth parameter as a function of the number of annuli indicated that effect of age had no effects our estimation of growth parameters (Supplementary Fig. 3). All analyses were run in the open-access statistical software “R” (R Development Core Team 2009). Population means are presented as mean \pm standard deviation. All p -values are two-tailed.

Results

Overall, the samples consisted of 66% Brienlzlig and 34% Albock (354 individuals). The relative prevalence of Brienlzlig varied over the years and generally declined from the 1990s to the 2000s (Fig. 1b). The average generation time, i.e. the average age difference between parents and offspring was estimated to be 3.81 years for the slow-growing Brienlzlig, and 3.59 years for the fast-growing Albock.

Length at age 1 (α_0) did not seem to change over the observational period for Brienlzlig ($t_{23} = -0.5$, $p = 0.62$, Fig. 2a), while a slight but significant linear decrease of $-0.90 \pm 0.32\%$ per generation was observed for Albock ($t_{23} = -2.8$, $p = 0.01$, Fig. 2b). Large decreases in logarithmic growth (α_l) were observed for both species: $-7.71 \pm 1.7\%$ per generation for Brienlzlig ($t_{23} = -4.4$, $p < 0.001$, Fig. 2c) and $-9.72 \pm 1.4\%$ per generation for Albock ($t_{23} = -7.1$, $p < 0.0001$, Fig. 2d).

Selection differentials on parameter α_0 , i.e. the difference in juvenile growth between reproducers and the whole population, were small but significant for Brienlzlig ($-3.9 \pm 1.1\%$, $t_{22} = -3.9$, $p = 0.001$, Fig. 3a) and not significantly different from zero for Albock ($t_{22} = -0.7$, $p = 0.49$, Fig. 3b). These α_0 were also not significantly different between the species ($t_{44} = 1.4$, $p = 0.16$). In contrast, selection differentials for logarithmic growth (α_l) were large and significantly negative for both Brienlzlig ($-17.4 \pm 2.2\%$, $t_{22} = -17.4$, $p < 0.0001$, Fig. 3c) and Albock ($-7.0 \pm 2.4\%$, $t_{23} = -7.0$, $p = 0.008$, Fig. 3d). Moreover, the selection differentials were larger for Brienlzlig than for Albock ($t_{45} = 2.4$, $p = 0.02$).

There seem to be slight changes for both the maturation schedule ($t_{23} = 1.9$, $p = 0.07$, Fig. 4a), and Fulton’s condition factor ($t_{19} = -2.1$, $p = 0.04$, Fig. 4c) in Brienlzlig. In this species, age at maturation increased by $0.23 \pm 0.12\%$ per year (but this apparent increase was not statistically significant), while the condition factor of the females during the winter months decreased by $0.61 \pm 0.29\%$ per year. No such change was found in Albock: neither the maturation schedule ($t_{23} = 0.9$, $p = 0.39$, Fig. 4b) nor Fulton’s condition factor ($t_{20} = -1.5$, $p = 0.38$, Fig. 4d) changed significantly over time.

Discussion

The 25-year long monitoring program revealed significant negative selection differentials for individual growth in the two most common whitefish species of Lake Brien. The

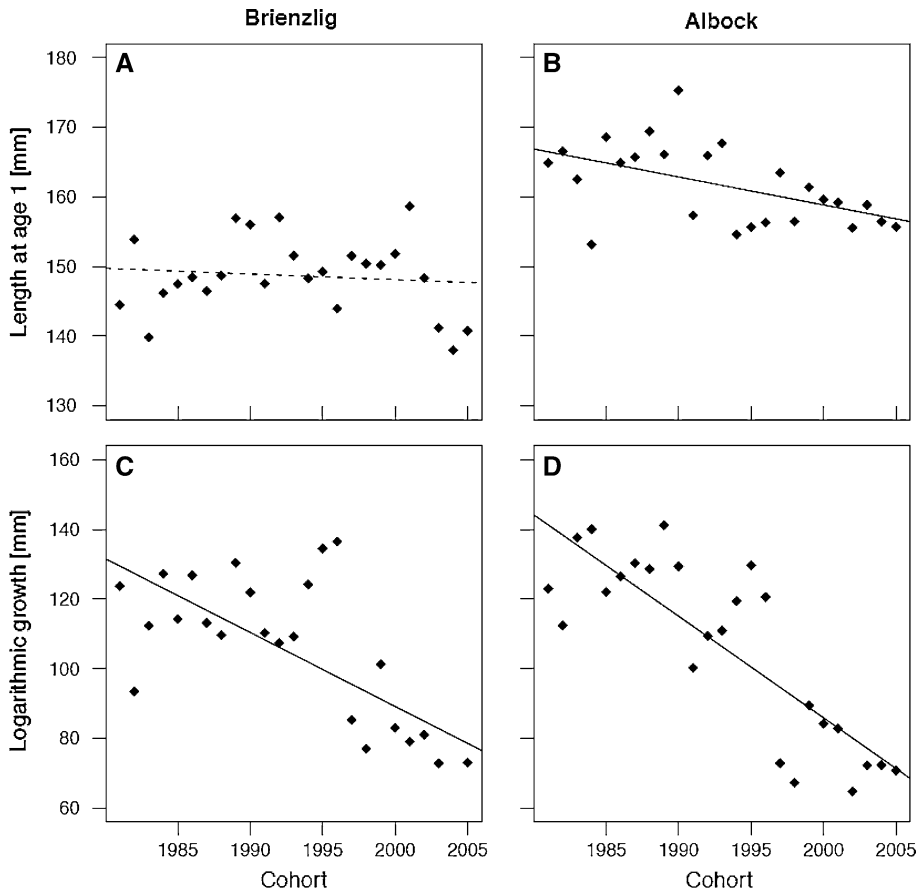


Fig. 2 Growth parameters over time. Growth parameters per cohort: **a, b** average length at age 1 (x_0) and **c, d** average logarithmic growth (x_t). The lines represent regression lines (solid = significant linear relationship, dashed = non-significant)

selection differential for adult growth in the fast-growing Albock seems only slightly higher than the selection differential of $-4.9 \pm 1.2\%$ that was found in a previous study on the Palée (*C. palaea* Fatio), a fast-growing whitefish in Lake Joux, Switzerland (Nusslé et al. 2009). The selection differential for adult growth that was found in the slow-growing Brienzzlig is, however, around 3 times larger than in Albock and Palée. This difference in the strength of selection could be due to different phenotypic responses to environmental changes, differences in the ecological changes of the species-specific ecological niches, or qualitative differences in the fishing pressure, such as potential differences in the gillnet selectivity relative to age classes. The similar mean generation times that we found for Brienzzlig and Albock (3.6 and 3.8 years, respectively) suggest, however, that the overall fishing pressure on these two species is about comparable. If mean generation time is indeed a useful indicator of the fishing pressure on whitefish, both Albock and Brienzzlig seem to be under stronger fishing pressure than the Palée of Lake Joux for which Nusslé et al. (2009) found a mean generation time of 4.7 years.

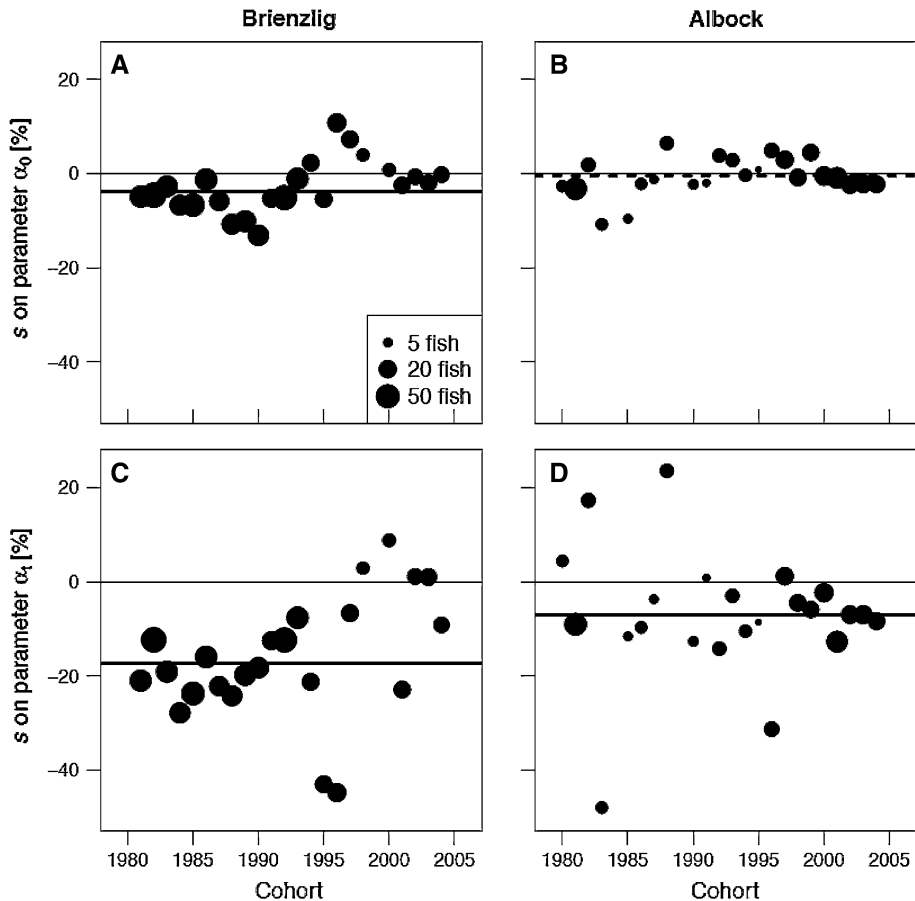


Fig. 3 Selection differentials (s) estimated for each cohort. **a, b** s for length at age 1 (α_0), and **c, d** s for logarithmic growth (α_t). The width of the circle corresponds to the number of fish within each cohort. The cohort is specified by the year of hatching from egg. The lines represent the average selection differential (solid = significantly different from zero, dashed = non-significant)

The selection differential on juvenile growth was not significantly different from zero in the Albock. This is in accordance with the previous findings on the Palée of Lake Joux (Nusslé et al. 2009). In the case of the slow-growing Brienzlig, the selection differential for juvenile growth was significantly different from zero but about 4 times smaller than the selection differential for adult growth. As juvenile growth is typically linked to juvenile survival (Tipping 2008), there might be compensatory mechanisms, or even selection against slow-growers, that could partly explain the pattern we observed here.

We found no or only a slight decline in juvenile growth rate but a marked decline in adult growth rate in both species. The decline in adult growth of both species of Lake Brienz was 2–2.5 times more pronounced than the decline found in the Palée of Lake Joux (Nusslé et al. 2009). This may again indicate differences in fishing intensity (see above) or could be linked to ecological differences between the lakes. For example, the total phosphorus concentration in Lake Joux halved from 30 to 35 mg/m³ in the 1980s to

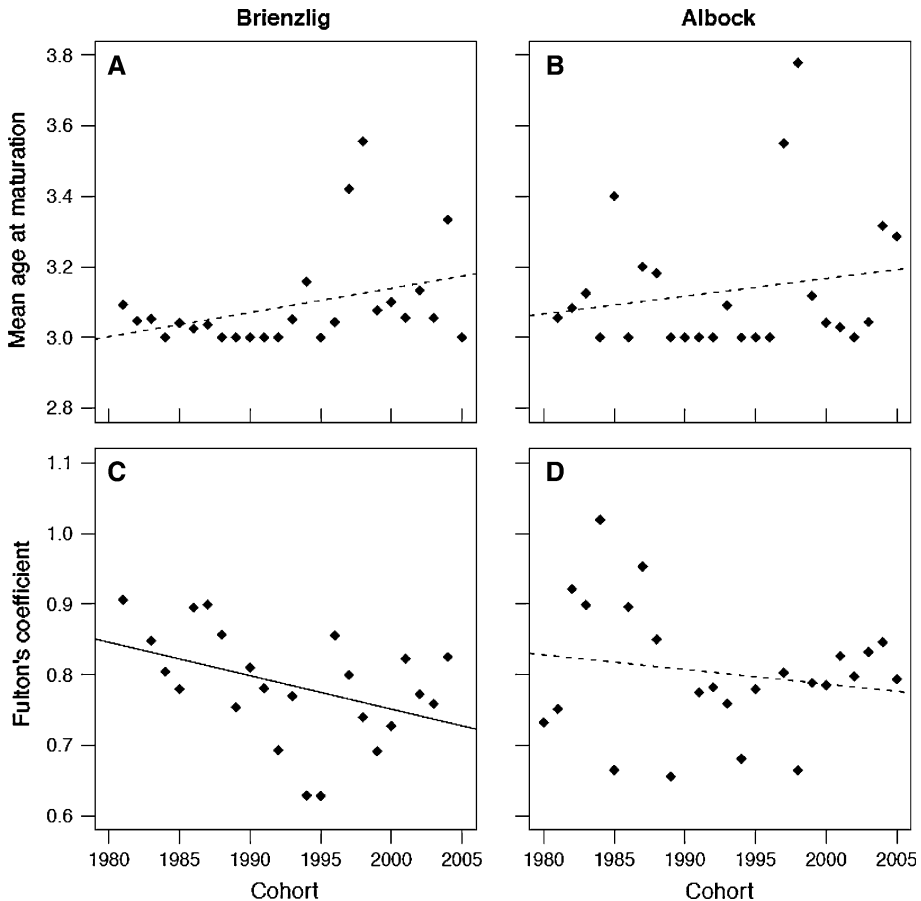


Fig. 4 Resource allocation from growth to reproduction. Indicators of resource allocation from growth to reproduction: **a** the mean age at maturation for each cohort and **b** the Fulton's coefficient of females during December and January. The lines represent regression lines (solid = significant linear relationship, dashed = non-significant)

15–20 mg/m³ today (Lods-Crozet et al. 2006), while in Lake Brienz the corresponding decline was approximately by a factor of 4.

Fishery-induced selection and environmental change can both lead to a decrease in growth, and the relative contributions of genetic variation and phenotypic plasticity to changes in life history traits is mostly unclear (Hilborn 2006; Browman et al. 2008). However, assuming that genetic and environmental factors have additive effects on growth, and that interactions between genotype and environment can be ignored, a first estimate of the evolutionary response to fishery-induced selection R can be derived from the breeder's equation $R = h^2s$ (Falconer and Mackay 1996), where h^2 is the narrow-sense heritability for growth rate. The fraction of change due to fishery-induced selection can then be estimated as h^2s divided by the total observed change in growth. As far as we know, no estimates exist for h^2 in Alpine whitefish. However, estimates of h^2 in other fish, including many other salmonids, range mostly from 0.1 to 0.5 and may be well-represented by $h^2 = 0.3$ (range: 0.1–0.5) (Law 2000; Garcia de Leaniz et al. 2007; Swain et al. 2007;

Theriault et al. 2007; Carlson and Seamons 2008). Our study populations provide measures of selection differentials because the large majority of fish are eventually harvested and old individuals are scarce (Nusslé et al. 2009). The response to selection on adult growth would then be a growth reduction of $5.2 \pm 0.7\%$ per generation for the Brienzlig (range: 1.7–8.7%), and $2.1 \pm 0.7\%$ for Albock (range: 0.7–3.5%). The proportion of the observed decline per generation in adult growth decrease that is due to fishery-induced selection would then be 67.7% (range 22.6–100%) for the Brienzlig and 21.6% (range: 7.2–36%) for the Albock. The corresponding value for the Palée of Lake Joux was 34% (range 11–56%) (Nusslé et al. 2009). All these estimates suggest that fishery-induced evolution plays a significant role in the contemporary evolution in Alpine whitefish.

We would like to stress that these estimates are based on various simplified model assumptions, apart from the fact that the h^2 of our study populations could differ from what is known about salmonids in general. We found a correlation between fishing yield, a potential measure of the density of fish, and the phosphorus concentration in the lake. Both factors are expected to influence fish growth, but in opposite directions: a reduced fish density might typically increase individual growth while a reduced phosphorus concentration might typically decrease it. It is unclear whether and by how much these opposing effects can cancel each other out so that the remaining variation in individual growth would then largely be linked to genetic factors only. In addition, different back-calculation methods could lead to slightly different estimates of the selection differentials. It is possible that our estimates of the selection differentials are somewhat biased if, for example, age-at-capture affects the estimation of the back-calculated lengths. Finally, we know little about possible genetic \times environment interaction effects. All these potential drawbacks illustrate the difficulties encountered when estimating the contribution of genetic and environmental factors on growth in the changing environments of natural populations. However, our first estimates of the genetic effects of fishery-induced selection may at least indicate the range at which we expect that environmental and genetic factors interact. Moreover, the different responses that we observed in the two species suggests that fisheries impact might be species-specific.

The Brienzlig was on average more abundant than the Albock, but the relative contribution of Brienzlig to the total catch varied over the years and declined since the 1990s. This yearly variation could potentially be linked to the lake's total biomass production (i.e. to phosphorus concentrations) or to other ecological factors that changed over the observational period. Alpine whitefish are known to show high variation in the number of gillrakers, which are linked to food preference (Vonlanthen 2009; Bittner et al. 2010). A change in phosphorus concentration is likely to influence the primary production, which in turn may favour selection for one or the other species. The yearly variation in species abundance may also be influenced by the fishing regime on these two species. Indeed, the fishing pressure was not constant throughout the monitoring period as minimal mesh size was reduced in 1993 for bottom nets and in 1996 for floating nets. Our calculated selection differentials could therefore be underestimating the current strength of selection because a larger range of mesh size is currently allowed.

Fishery-induced selection and environmental change can lead to changes in reproductive strategies. We used mean age at maturation and the Fulton's K coefficient as first possible indicators of reproductive strategies (Gadgil and Bossert 1970; Heino et al. 2008). Females with many eggs are expected to be heavier and therefore to have a higher Fulton's coefficient. Our findings suggest that the individual reproductive investment of females did not increase over the years. In addition, the age at maturation did not significantly change over time. Overall, it seems that the resources allocated to growth have not been

re-invested into reproductive strategies over the observational period. The decrease observed in Fulton's coefficient of Brienzzig could be explained by fish being slimmer due to decreased nutrients concentration and/or adaptation to fishing gear (Hard et al. 2008).

A decrease in both adult and juvenile growth can have deleterious consequences for populations. There is now mounting evidence that artificial selection such as harvesting can reduce the average viability of populations (Fenberg and Roy 2008). Several specific consequences may arise from the removal of large fish, and even if these issues are still debated (Carlson et al. 2008), a precautionary approach should be taken when managing evolving fish stocks (Francis and Shotton 1997). First, large and fast-growing individuals may be of higher genetic quality than small and slow-growing individuals (Birkeland and Dayton 2005). A systematic removal of 'high quality' adults could therefore result in an increase of the average genetic load in a population. Second, as large females usually produce larger offspring of higher viability (Trippel 1995; Walsh et al. 2006), a decrease in growth could impair the recruitment and consequently the long-term yield of the population. Third, as females in many species prefer to mate with large males (Wedekind et al. 2007; Hutchings and Rowe 2008; Rudolfson et al. 2008; Jacob et al. 2009; Labonne et al. 2009) increased mortality of large fish could have an impact on sexual selection and therefore on mating behaviour. Fourth, non-random mortality could decrease the genetic diversity of the population and make it more vulnerable to environmental changes or diseases (Jones et al. 2001).

Phenotypic plasticity can lead to reduced individual growth in lakes that experienced reduced biomass production due to reduced phosphorus input. However, our analyses suggest that phenotypic plasticity is not the only possible explanation for the significant reduction in individual growth rates that we observed. The large selection differentials that are imposed by size-selective fishing are likely to change the standing genetic variation for individual growth rates in the two whitefish species we studied here. Such fishery-induced evolution should be taken into account by population managers (Stokes and Law 2000; Ashley et al. 2003; Smith and Bernatchez 2008).

Acknowledgments We thank the Fishery Inspectorate of the Bern Canton for providing the monitoring data, E. Baumgartner for technical help, E. Clark, C. Küng, T. Mehner, R. Müller, M. Pompini, A. Ross-Gillespie, M. dos Santos, R. Stelkens, J. Van Buskirk, and two anonymous reviewers for discussion and/or comments on the manuscript, and the Swiss National Science Foundation for financial support.

References

- Ashley MV, Wilson MF, Pergams ORW, O'Dowd DJ, Gende SM, Brown JS (2003) Evolutionarily enlightened management. *Biol Conserv* 111:115–123
- Birkeland C, Dayton PK (2005) The importance in fishery management of leaving the big ones. *Trends Ecol Evol* 20:356–358
- Bittner D (2009) Gonad deformations in whitefish (*Coregonus spp.*) from Lake Thun, Switzerland. A population genetic and transcriptomic approach. PhD thesis, University of Bern, Bern, Switzerland
- Bittner D, Excoffier L, Largiader CR (2010) Patterns of morphological changes and hybridization between sympatric whitefish morphs (*Coregonus spp.*) in a Swiss lake: a role for eutrophication? *Mol Ecol* 19:2152–2167
- Browman HI, Law R, Marshall CT, Kuparinen A, Merila J, Jørgensen C, Enberg K, Dunlop ES, Arlinghaus R, Boukal DS, Brander K, Ernande B, Gårdmark A, Johnston F, Matsumura S, Pardoe H, Raab K, Silva A, Vainikka A, Dieckmann U, Heino M, Rijnsdorp AD (2008) The role of fisheries-induced evolution. *Science* 320:47–50
- Carlson SM, Seamons TR (2008) A review of quantitative genetic components of fitness in salmonids: implications for adaptation to future change. *Evol Appl* 1:222–238
- Carlson SM, Olsen EM, Vøllestad LA (2008) Seasonal mortality and the effect of body size: a review and an empirical test using individual data on brown trout. *Funct Ecol* 22:663–673

- Clark JH, Bernard DR (1992) Fecundity of humpback whitefish and least cisco in the Chatanika River, Alaska. *T Am Fish Soc* 121:268–273
- Crozier LG, Hendry AP, Lawson PW, Quinn TP, Mantua NJ, Battin J, Shaw RG, Huey RB (2008) Potential responses to climate change in organisms with complex life histories: evolution and plasticity in Pacific salmon. *Evol Appl* 1:252–270
- Darimont CT, Carlson SM, Kinnison MT, Paquet PC, Reimchen TE, Wilmers CC (2009) Human predators outpace other agents of trait change in the wild. *P Natl Acad Sci USA* 106:952–954
- Douglas M (1998) Central Alpine *Coregonus* (*Teleostei*, *Coregonidae*): evolution and conservation of a unique assemblage. PhD thesis, University of Zürich, Zürich, Switzerland
- Falconer DS, Mackay TFC (1996) Introduction to quantitative genetics, 4th edn. Benjamin Cummings, Essex
- Fenberg PB, Roy K (2008) Ecological and evolutionary consequences of size-selective harvesting: how much do we know? *Mol Ecol* 17:209–220
- Finstad AG (2003) Growth backcalculations based on otoliths incorporating an age effect: adding an interaction term. *J Fish Biol* 62:1222–1225
- Francis RICC, Shotton R (1997) “Risk” in fisheries management: a review. *Can J Fish Aquat Sci* 54:1699–1715
- Fraser DJ, Bernatchez L (2001) Adaptive evolutionary conservation: towards a unified concept for defining conservation units. *Mol Ecol* 10:2741–2752
- Fukuwaka M, Morita K (2008) Increase in maturation size after the closure of a high seas gillnet fishery on hatchery-reared chum salmon *Oncorhynchus keta*. *Evol Appl* 1:376–387
- Gadgil M, Bossert WH (1970) Life historical consequences of natural selection. *Am Nat* 104:1
- García de Leaniz C, Fleming IA, Einum S, Verspoor E, Jordan WC, Consuegra S, Aubin-Horth N, Lajus D, Letcher BH, Youngson AF, Webb JH, Vøllestad LA, Villanueva B, Ferguson A, Quinn TP (2007) A critical review of adaptive genetic variation in Atlantic salmon: implications for conservation. *Biol Rev* 82:173–211
- Gerdeaux D, Anneville O, Hefti D (2006) Fishery changes during re-oligotrophication in 11 peri-alpine Swiss and French lakes over the past 30 years. *Acta Oecol* 30:161–167
- Grift RE, Rijnsdorp AD, Barot S, Heino M, Dieckmann U (2003) Fisheries-induced trends in reaction norms for maturation in North Sea plaice. *Mar Ecol Prog Ser* 257:247–257
- Handford P, Bell G, Reimchen T (1977) Gillnet fishery considered as an experiment in artificial selection. *J Fish Res Board Can* 34:954–961
- Hard JJ, Gross MR, Heino M, Hilborn R, Kope RG, Law R, Reynolds JD (2008) Evolutionary consequences of fishing and their implications for salmon. *Evol Appl* 1:388–408
- Heino M, Dieckmann U, Godo OR (2002) Measuring probabilistic reaction norms for age and size at maturation. *Evolution* 56:669–678
- Heino M, Baulier L, Boukal DS, Dunlop ES, Eliassen S, Enberg K, Jørgensen C, Varpe O (2008) Evolution of growth in Gulf of St Lawrence cod? *Proc R Soc Lond B Biol Sci* 275:1111–1112
- Hilborn R (2006) Faith-based fisheries. *Fisheries* 31:554–555
- Hoyle C (2004) Phosphorus cycling in lake Brienz, Switzerland. MSc thesis, Swiss Federal Institute of Technology, Zurich, Kastanienbaum, Switzerland
- Hutchings JA, Fraser DJ (2008) The nature of fisheries- and farming-induced evolution. *Mol Ecol* 17:294–313
- Hutchings JA, Rowe S (2008) Consequences of sexual selection for fisheries-induced evolution: an exploratory analysis. *Evol Appl* 1:129–136
- Jackson JBC, Kirby MX, Berger WH, Bjørndal KA, Botsford LW, Bourque BJ, Bradbury RH, Cooke R, Erlandson J, Estes JA, Hughes TP, Kidwell S, Lange CB, Lenihan HS, Pandolfi JM, Peterson CH, Steneck RS, Tegner MJ, Warner RR (2001) Historical overfishing and the recent collapse of coastal ecosystems. *Science* 293:629–638
- Jacob A, Evanno G, Renai E, Sermier R, Wedekind C (2009) Male body size and breeding tubercles are both linked to intrasexual dominance and reproductive success in the minnow. *Anim Behav* 77:823–829
- Jones MW, McParland TL, Hutchings JA, Danzmann RG (2001) Low genetic variability in lake populations of brook trout (*Salvelinus fontinalis*): a consequence of exploitation? *Conserv Genet* 2:245–256
- Jørgensen C, Enberg K, Dunlop ES, Arlinghaus R, Boukal DS, Brander K, Ernande B, Gärdmark A, Johnston F, Matsumura S, Pardoe H, Raab K, Silva A, Vainikka A, Dieckmann U, Heino M, Rijnsdorp AD (2007) Ecology—managing evolving fish stocks. *Science* 318:1247–1248
- Kottelat M, Freyhof J (2007) Handbook of European freshwater fishes. Kottelat and Freyhof, Cornol
- Labonne J, Augery M, Parade M, Brinkert S, Prevost E, Heland M, Beall E (2009) Female preference for male body size in brown trout, *Salmo trutta*: is big still fashionable? *Anim Behav* 77:129–137
- Law R (2000) Fishing, selection, and phenotypic evolution. *Ices J Mar Sci* 57:659–668

- Law R (2007) Fisheries-induced evolution: present status and future directions. *Mar Ecol Prog Ser* 335:271–277
- Link J, Hoff MH (1998) Relationships of Lake Herring (*Coregonus artedii*) gill raker characteristics to retention probabilities of zooplankton prey. *J Freshwat Ecol* 13:55–65
- Lods-Crozat B, Reymond O, Strawczynski A (2006) Evaluation de la qualité chimique et biologique du lac de Joux (Jura Suisse) entre 1985 et 2004. *Bull Soc Ne Sci Nat* 129:29–47
- Mertz G, Myers RA (1998) A simplified formulation for fish production. *Can J Fish Aquat Sci* 55:478–484
- Müller R (2003) Populationsdynamische Untersuchungen an den Felchen des Brienersees. In: Bericht an das Fischereinspektorat des Kantons Bern. EAWAG, Kastanienbaum, Kastanienbaum, p 81
- Müller B, Finger D, Sturm M, Prasuhn V, Haltmeier T, Bossard P, Hoyle C, Wuest A (2007a) Present and past bio-available phosphorus budget in the ultra-oligotrophic Lake Brienz. *Aquat Sci* 69:227–239
- Müller R, Breitenstein M, Bia MM, Rellstab C, Kirchhofer A (2007b) Bottom-up control of whitefish populations in ultra-oligotrophic Lake Brienz. *Aquat Sci* 69:271–288
- Myers RA, Hoenig JM (1997) Direct estimates of gear selectivity from multiple tagging experiments. *Can J Fish Aquat Sci* 54:1–9
- Nusslé S, Bornand C, Wedekind C (2009) Fishery-induced selection on an Alpine whitefish: quantifying genetic and environmental effects on individual growth rate. *Evol Appl* 2:200–208
- Palumbi SR (2001) Evolution—humans as the world's greatest evolutionary force. *Science* 293:1786–1790
- R Development Core Team (2009) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna
- Ricker WE (1981) Changes in the average size and average age of pacific salmon. *Can J Fish Aquat Sci* 38:1636–1656
- Rijnsdorp A (1993) Fisheries as a large-scale experiment on life-history evolution: disentangling phenotypic and genetic effects in changes in maturation and reproduction of North Sea plaice, *Pleuronectes platessa* L. *Oecologia* 96:391–401
- Rijnsdorp AD, Storbeck F (1995) Determining the onset of sexual maturity from otoliths of individual female North Sea plaice, *Pleuronectes platessa* L. In: Secor DH, Dean JM, Campana SE (eds) Recent developments in fish otolith research. University of South Carolina Press, Columbia, S.C., pp 271–282
- Rudolfson G, Müller R, Urbach D, Wedekind C (2008) Predicting the mating system from phenotypic correlations between life-history and sperm quality traits in the Alpine whitefish *Coregonus zugensis*. *Behav Ecol Sociobiol* 62:561–567
- Sharpe DMT, Hendry AP (2009) Life history change in commercially exploited fish stocks: an analysis of trends across studies. *Evol Appl* 2:260–275
- Smith TB, Bernatchez L (2008) Evolutionary change in human-altered environments. *Mol Ecol* 17:1–8
- Stearns SC (1992) The evolution of life histories. Oxford University Press, New York
- Stokes K, Law R (2000) Fishing as an evolutionary force. *Mar Ecol Prog Ser* 208:307–309
- Swain DP, Sinclair AF, Hanson JM (2007) Evolutionary response to size-selective mortality in an exploited fish population. *Proc R Soc Lond B Biol Sci* 274:1015–1022
- Theriault V, Garant D, Bernatchez L, Dodson JJ (2007) Heritability of life-history tactics and genetic correlation with body size in a natural population of brook charr (*Salvelinus fontinalis*). *J Evol Biol* 20:2266–2277
- Thomas G, Eckmann R (2007) The influence of eutrophication and population biomass on common whitefish (*Coregonus lavaretus*) growth—the Lake Constance example revisited. *Can J Fish Aquat Sci* 64:402–410
- Thomas G, Quoss H, Hartmann J, Eckmann R (2009) Human-induced changes in the reproductive traits of Lake Constance common whitefish (*Coregonus lavaretus*). *J Evol Biol* 22:88–96
- Thorpe JE (1998) Salmonid life-history evolution as a constraint on marine stock enhancement. *Bull Mar Sci* 62:465–475
- Tipping JM (2008) The effect of juvenile length in autumn on 2-year-old male and adult Coho salmon survival rates at three Washington hatcheries. *N Am J Fish Aquacult* 70:111–114
- Trippel EA (1995) Age at maturity as a stress indicator in fisheries. *Bioscience* 45:759–771
- Vonlanthen P (2009) On speciation and its reversal in adaptive radiations. The central European whitefish system. PhD Thesis, University of Bern, Bern, Switzerland
- Walsh MR, Munch SB, Chiba S, Conover DO (2006) Maladaptive changes in multiple traits caused by fishing: impediments to population recovery. *Ecol Lett* 9:142–148
- Wedekind C, Rudolfson G, Jacob A, Urbach D, Müller R (2007) The genetic consequences of hatchery-induced sperm competition in a salmonid. *Biol Conserv* 137:180–188
- Yoneda M, Wright PJ (2004) Temporal and spatial variation in reproductive investment of Atlantic cod *Gadus morhua* in the northern North Sea and Scottish west coast. *Mar Ecol Prog Ser* 276:237–248