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

3  
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10  
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20  
21 Abstract

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

## 1 Introduction

2 Fishing-induced mortality can be very high and often exceeding natural  
3 mortality significantly (Rijnsdorp 1993; Mertz & Myers 1998; Jackson et al. 2001).  
4 Fishing is typically size-selective (Myers & Hoenig 1997; Fukuwaka & Morita 2008),  
5 and since significant heritabilities have been reported for traits that could be size-  
6 related in many fish (up to  $h^2=0.5$ , see Theriault et al. (2007); Carlson & Seamons  
7 (2008)), size-selective fishing is expected to induce rapid evolutionary changes  
8 (Palumbi 2001; Smith & Bernatchez 2008; Darimont et al. 2009). Traits such as age  
9 or size at maturation (Heino et al. 2002; Grift et al. 2003; Sharpe & Hendry 2009),  
10 average reproductive effort (Yoneda & Wright 2004; Thomas et al. 2009), or  
11 individual growth rates (Handford et al. 1977; Ricker 1981; Swain et al. 2007;  
12 Thomas & Eckmann 2007; Nusslé et al. 2009) are likely to evolve in response to size-  
13 selective fishing. Such fishing has therefore been termed a 'large-scale experiment in  
14 life-history evolution' (Rijnsdorp 1993; Law 2000; Stokes & Law 2000), and studies  
15 on fishery-induced evolution have increased in number during the last decade (see  
16 Jorgensen et al. (2007) for a review of phenotypic change attributed to fishery-  
17 induced selection).

18 Despite this increased interest in recent years, it is still largely unclear how  
19 much of the change in individual growth rate that can often be observed is due to  
20 harvesting and how much is due to other environmental factors that have changed  
21 over time. For example, many freshwater systems have seen a change in phosphorous  
22 concentration and hence of biomass production over the last few decades (Müller et  
23 al. 2007a). Such changes in phosphorous concentration could contribute to changes in  
24 growth rates of many fish (Gerdeaux et al. 2006; Müller et al. 2007b; Thomas &  
25 Eckmann 2007). Separating the effects of fishery- versus environmentally-induced  
26 changes on individual growth rates is usually difficult (Heino et al. 2008) because  
27 phenotypic plasticity is important in fish (Thorpe 1998; Crozier et al. 2008) and even  
28 if genetic changes can be documented over time, monitoring data alone cannot  
29 conclusively demonstrate the causal link between such genetic changes and particular  
30 changes in the environment (Hutchings & Fraser 2008). However, a critical step  
31 forward in estimating the importance of evolution for phenotypic changes is to  
32 measure the strength of selection, namely the selection differential (Law 2000; Law  
33 2007; Smith & Bernatchez 2008).

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

49

## 1 Methods

2 We studied whitefish of Lake Brienz, Switzerland (46.43°N, 7.58°E; surface area =  
3 29.8 km<sup>2</sup>, elevation = 564 m, maximum depth = 261 m). Lake Brienz is one of the  
4 few Alpine lakes that was little affected by the general eutrophication until the 1970s.  
5 Its relatively low phosphorus concentrations have even decreased since then (Figure  
6 1A), so that the lake can now be called “ultra-oligotrophic” (Müller et al. 2007a). A  
7 monitoring program, collecting 25 whitefish from ordinary fishery catches every  
8 month, has been conducted by the Fishery Inspectorate of the Bern Canton since  
9 1984. Each individual is sexed (by dissection) and total body length and body weight  
10 are measured to the nearest mm and g, respectively. Gillrakers are counted for species  
11 identification (Müller 2003) and scale samples are taken (above lateral line between  
12 adipose and dorsal fins) for age and growth determination. The gillnets used by  
13 fisheries had been set to 35-40 mm mesh size (as measured when stretched) for  
14 bottom nets and 38 mm for floating nets prior to 1992. In response to the observed  
15 growth decrease and the declining yield (Figure 1A), the minimal legal mesh size was  
16 reduced to 30 mm for bottom nets in 1993, and for floating nets in 1996. The fishing  
17 pressure is not determined in detail, but fishermen seem to largely adapt their effort to  
18 the availability of the fish (C. Küng, Fishery Inspectorate Bern, personal  
19 communication). The number of fishermen declined from four until 1998 to three  
20 until 2005. During the last 5 years, only two fishermen remained.

21 Two groups of whitefish were sampled, the slowly growing “small-type”  
22 whitefish Brienzlig (*Coregonus albellus* Fatjo) and the fast growing “large-type”  
23 whitefish which are mostly, if not exclusively, Albock (*C. fatioi* Kottelat). The  
24 taxonomy of Alpine whitefish is often unclear and controversial. This is also true for  
25 the different whitefish of Lake Brienz although they can clearly be grouped according  
26 to life history, morphology, and genetics (Kottelat & Freyhof 2007; Bittner 2009;  
27 Vonlanthen 2009). While Bittner et al. (2009), for example, calls the various whitefish  
28 of Lake Brienz “forms” of *C. lavaretus*, Kottelat and Freyhof (2007) distinguishes  
29 them as species. We do not attempt to solve this ongoing discussion here but use  
30 Kottelat and Freyhof’s (2007) guide to name the two most abundant whitefish groups  
31 of Lake Brienz (see also the discussion in Fraser and Bernatchez (2001) on defining  
32 conservation units). There is a third and probably a fourth other whitefish species in  
33 Lake Brienz (Douglas 1998; Kottelat & Freyhof 2007) that both are difficult to  
34 distinguish from *C. fatioi* on the basis of phenotypic characteristics only, but these  
35 other species are comparatively rare and numerically not important for fishery (Müller  
36 et al. 2007b). Moreover, because we confined our scale measurements (see below)  
37 and all further analyses to fish that were caught in December and January only ( $N_{\text{total}}$   
38 = 1,106,  $N_{\text{Brienzlig}} = 727$ ,  $N_{\text{Albock}} = 379$ ), i.e. around the spawning time of the winter-  
39 spawning *C. albellus* and *C. fatioi*, we assume that large-type whitefish that are not *C.*  
40 *fatioi* are not present or rare in our samples and will therefore not significantly affect  
41 our analyses.

42 ADD A SHORT DESCRIPTION OF THE ECOLOGY AND LIFE HISTORY  
43 OF THESE TWO SPECIES (IN RESPONSE TO ONE OF THE REVIEWER  
44 COMMENTS).

45 For each individual fish we determined the average scale radius and all  
46 annulus radii, i.e. the distances from the nucleus to the subsequent annuli, using an  
47 ocular micrometer and two different scales per fish. We back-calculated the length at  
48 previous ages according to the method of Finstad (2003). This method is based on a  
49 multiple regression including the size of the scale, the age and length of the fish which  
50 takes into account that scale growth might not be linearly related to fish growth as

1 slower growing fishes may have proportionately larger scales than faster growing  
 2 individuals, or that there might be an age-specific growth of the scale irrespective of  
 3 somatic growth. Then, to test for a potential bias in the back-calculations that could be  
 4 linked to the age-at-capture, we analysed the residuals of the regression of the back-  
 5 calculated lengths at capture (based on annuli radii) with the empirical length (based  
 6 on the growth parameters) (Supplementary figure 1).

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

$$9 \quad L_i(t) = \alpha_{0i} + \alpha_{ii} \log(t) \quad (1)$$

10 where  $L_i(t)$  is the back-calculated length of each fish at age  $t$ ,  $\alpha_{0i}$  is the back-calculated  
 11 length at age 1, and  $\alpha_{ii}$  is the logarithmic growth of the  $i$ -th fish. Parameter  $\alpha_{ii}$   
 12 represents the length increase per time unit on a logarithmic scale. Hence  $\alpha_{0i}$   
 13 represents juvenile growth while  $\alpha_{ii}$  is a measure of adult growth (Supplementary  
 14 figure 2). The fit of this model was assessed with linear regressions of the back-  
 15 calculated length (modelled) as a function of the length at capture (observed)  
 16 (Supplementary figures 1). These back-calculated lengths fit well with the observed  
 17 ones for both the Brienzlig (linear regression: slope =  $0.98 \pm 0.01$ ,  $r^2 = 0.86$ ,  
 18 Supplementary Figure 1A) and the Albock (slope =  $0.93 \pm 0.02$ ,  $r^2 = 0.83$ ,  
 19 Supplementary Figure 1B). The adult growth estimation based on all the annuli does  
 20 not significantly differ from the estimations with a reduced number of annuli  
 21 (Supplementary figure 3), suggesting that our estimation of the selection differentials  
 22 is not biased with this regard. There is a small but statistically significant effect of the  
 23 age at capture on the residuals of the back-calculated/observed length regression for  
 24 both the Brienzlig (linear regressions:  $t_{347} = -3.6$ ,  $p < 0.01$ ,  $r^2 = 0.01$ ; Supplementary  
 25 figure 1C) and the Albock ( $t_{704} = -3.1$ ,  $p < 0.001$ ,  $r^2 = 0.03$ ; Supplementary figure 1D).  
 26 The back-calculated lengths and the adult growth parameters are hence slightly  
 27 underestimated for the oldest fish of our sample, but this may only little affect our  
 28 overall estimates of the selection differentials (see below) because the respective  $r^2$ s  
 29 are rather small ( $\leq 0.03$ ) and older fish are relatively scarce.

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

$$40 \quad \text{Generation time} = \frac{\sum_x x l_x m_x}{\sum_x l_x m_x} \quad (2)$$

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

46 As a potential indicator for resource allocation from growth to reproduction,  
 47 we estimated the reproductive investment of females as the condition factor Fulton  $K$

1 ( $K = 10^5 \cdot \text{fish weight} / \text{fish length}^3$ ). We also estimated the age at maturation for each  
2 fish according to the method of Rijnsdorp and Storbeck (1995) which assumes that  
3 growth is maximal and linear when the fish is immature and decreases after the fish  
4 becomes mature because some resources are invested into reproduction instead of  
5 growth. We used linear regressions to test for linear trends over time in these two  
6 measures.

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

## 20 Results

21 Overall, the samples consisted of 66% Brienzlig and 34% Albock (354  
22 individuals). The relative prevalence of Brienzlig varied over the years and generally  
23 declined from the 1990s to the 2000s (figure 1B). The average generation time, i.e.  
24 the average age difference between parents and offspring was estimated to be 3.81  
25 years for the slowly growing Brienzlig, and 3.59 years for the fast-growing Albock.  
26 Faster growing Brienzlig or Albock are caught earlier in life than slower growing  
27 ones (Brienzlig: **STATS**; Albock: **STATS**), but this link between age-at-catch and  
28 growth does not significantly affect our growth estimates (Supplementary figure 1).

29 Length at age 1 ( $\alpha_0$ ) did not seem to change over the observational period for  
30 Brienzlig ( $t_{23} = -0.5$ ,  $P = 0.62$ , figure 2A), while a slight but significant linear  
31 decrease of  $-0.90 \pm 0.32$  % per generation was observed for Albock ( $t_{23} = -2.8$ ,  $P =$   
32  $0.01$ , figure 2B). Large decreases in logarithmic growth ( $\alpha_t$ ) were observed for both  
33 species:  $-7.71 \pm 1.7\%$  per generation for Brienzlig ( $t_{23} = -4.4$ ,  $P < 0.001$ , figure 2C)  
34 and  $-9.72 \pm 1.4\%$  per generation for Albock ( $t_{23} = -7.1$ ,  $P < 0.0001$ , figure 2D).

35 Selection differentials on parameter  $\alpha_0$ , i.e. the difference in juvenile growth  
36 between reproducers and the whole population, were small but significant for  
37 Brienzlig ( $-3.9 \pm 1.1$  %,  $t_{22} = -3.9$ ,  $P = 0.001$ , figure 3A) and not significantly different  
38 from zero for Albock ( $t_{22} = -0.7$ ,  $P = 0.49$ , figure 3B). These  $\alpha_0$  were also not  
39 significantly different between the species ( $t_{44} = 1.4$ ,  $P = 0.16$ ). In contrast, selection  
40 differentials for logarithmic growth ( $\alpha_t$ ) were large and significantly negative for both  
41 Brienzlig ( $-17.4 \pm 2.2$  %,  $t_{22} = -17.4$ ,  $P < 0.0001$ , figure 3C) and Albock ( $-7.0 \pm 2.4$  %,  $t_{23} = -7.0$ ,  $P = 0.008$ , figure 3D). Moreover, the selection differentials were larger for  
42 Brienzlig than for Albock ( $t_{45} = 2.4$ ,  $P = 0.02$ ).

44 There seem to be slight changes for both the maturation schedule ( $t_{23} = 1.9$ ,  $P = 0.07$ , figure 4A), and Fulton’s condition factor ( $t_{19} = -2.1$ ,  $P = 0.04$ , figure 4C) in  
45 Brienzlig. In this species, age at maturation increased by  $0.23 \pm 0.12\%$  per year (but  
46 this apparent increase was not statistically significant), while the condition factor of  
47 the females during the winter months decreased by  $0.61 \pm 0.29\%$  per year. No such  
48 change was found in Albock: neither the maturation schedule ( $t_{23} = 0.9$ ,  $P = 0.39$ ,

1 figure 4B) nor Fulton's condition factor ( $t_{20} = -1.5$ ,  $P = 0.38$ , figure 4D) changed  
2 significantly over time.

### 3 4 Discussion

5 The 25-year long monitoring program revealed significant negative selection  
6 differentials for individual growth in the two most common whitefish species of Lake  
7 Brienz. The selection differential for adult growth in the fast-growing Albock seems  
8 only slightly higher than the selection differential of  $-4.9 \pm 1.2\%$  that was found in a  
9 previous study on the Palée (*C. palaea* Fatio), a fast-growing whitefish in Lake Joux,  
10 Switzerland (Nusslé et al. 2009). The selection differential for adult growth that was  
11 found in the slowly growing Brienzlig is, however, around 3 times larger than in  
12 Albock and Palée. This difference in the strength of selection could be due to different  
13 phenotypic responses to environment changes, differences in the ecological changes  
14 of the species-specific ecological niches, or qualitative differences in the fishing  
15 pressure like, for example, potential differences in the gillnet selectivity relative to  
16 age classes. The similar mean generation times that we found for Brienzlig and  
17 Albock (3.6 and 3.8 years, respectively) suggest, however, that the overall fishing  
18 pressure on these two species is about comparable. If mean generation time is indeed  
19 a useful indicator of the fishing pressure on whitefish, both Albock and Brienzlig  
20 seem to be under stronger fishing pressure than the Palée of Lake Joux for which  
21 Nusslé et al. (2009) found a mean generation time of 4.7 years.

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

30 We found no or only a slight decline in juvenile growth rate but a marked  
31 decline in adult growth rate in both species. The decline in adult growth of both  
32 species of Lake Brienz was 2 to 2.5 times more pronounced than the decline found in  
33 the Palée of Lake Joux (Nusslé et al. 2009). This may again indicate differences in  
34 fishing intensity (see above) or could be linked to ecological differences between the  
35 lakes. For example, the total phosphorus concentration in Lake Joux only halved from  
36  $30\text{-}35 \text{ mg/m}^3$  in the 1980s to  $15\text{-}20 \text{ mg/m}^3$  today (Lods-Crozet et al. 2006), while in  
37 Lake Brienz the corresponding decline was by about a factor 4.

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

1 Seamons 2008). Our study populations provide measures of selection differentials  
2 because the large majority of fish are eventually harvested and old individuals are  
3 scarce (Nusslé et al. 2009). The response to selection on adult growth would then be a  
4 growth reduction of  $5.2 \pm 0.7$  % per generation for the Brienzlig (range: 1.7% - 8.7%),  
5 and  $2.1 \pm 0.7$  % for Albock (range: 0.7% - 3.5%). The proportion of the observed  
6 decline in adult growth decrease that is due to fishery-induced selection would then be  
7 67 % (range 22% - 100%) for the Brienzlig and 22% (range: 7% - 36%) for the  
8 Albock. The corresponding value for the Palée of Lake Joux was 34% (range 11% -  
9 56%) (Nusslé et al. 2009). All these estimates suggest that fishery-induced evolution  
10 plays a significant role in the contemporary evolution in Alpine whitefish.

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

31 The Brienzlig was on average more abundant than the Albock, but the relative  
32 contribution of Brienzlig to the total catch varied over the years and declined since the  
33 1990s. This yearly variation could potentially be linked to the lake's total biomass  
34 production (i.e. to phosphorus concentrations) or to other ecological factors that  
35 changed over the observational period. Alpine whitefish are known to show high  
36 variation in the gillrakers number, which are linked to food preference (Vonlanthen  
37 2009; Bittner et al. 2010). A change in phosphorus concentration is likely to influence  
38 the primary production, which in turn may favour selection for one or the other  
39 species. The yearly variation in species abundance may also be influenced by the  
40 fishing regime on these two species. Indeed, the fishing pressure was not constant  
41 throughout the monitoring period as minimal mesh size was reduced in 1993 for  
42 bottom nets and in 1996 for floating nets. Our calculated selection differentials could  
43 therefore be underestimating the current strength of selection because a larger range  
44 of mesh size than before is now allowed.

45 Fishery-induced selection and environmental change can lead to changes in  
46 reproductive strategies. We used mean age at maturation and the Fulton's K  
47 coefficient as first possible indicators of reproductive strategies (Gadgil & Bossert  
48 1970; Heino et al. 2008). (Females with many eggs are expected to be heavier and  
49 therefore to have a higher Fulton's coefficient.) Our findings suggest that the  
50 individual reproductive investment of females did not increase over the years. In



1 addition, the age at maturation did not significantly change over time. Overall, it  
2 seems that the resources allocated to growth have not been re-invested into  
3 reproductive strategies over the observational period. The decrease observed in  
4 Fulton's coefficient of Brienzi could be explained by fish being slimmer due to  
5 decreased nutrients concentration and/or adaptation to fishing gears (Hard et al.  
6 2008).

7 A decrease in both adult and juvenile growth can have deleterious  
8 consequences for populations. There is now mounting evidence that artificial  
9 selection such as harvesting can reduce the average viability of populations (Fenberg  
10 & Roy 2008). Several specific consequences may arise from the removal of large fish,  
11 and even if these issues are still debated (Carlson et al. 2008), a precautionary  
12 approach should be taken when managing evolving fish stocks (Francis & Shotton  
13 1997). First, large and fast-growing individuals may be of higher genetic quality than  
14 small and slowly-growing individuals (Birkeland & Dayton 2005). A systematic  
15 removal of 'high quality' adults could therefore result in an increase of the average  
16 genetic load in a population. Second, as large females usually produce larger offspring  
17 of higher viability (Trippel 1995; Walsh et al. 2006), a decrease in growth could  
18 impair the recruitment and consequently the long-term yield of the population. Third,  
19 as females in some species prefer to mate with large males (Hutchings & Rowe  
20 2008)(Jacob et al. 2009; Labonne et al. 2009) and male whitefish often have age-  
21 linked reproductive strategies (Wedekind et al. 2007; Rudolfson et al. 2008),  
22 increased mortality of large fish could have an impact on sexual selection and  
23 therefore on mating behaviour. Fourth, non-random mortality could decrease the  
24 genetic diversity of the population and make it more vulnerable to environmental  
25 changes or diseases (Jones et al. 2001).

26 Phenotypic plasticity can lead to reduced individual growth in lakes that  
27 experienced reduced biomass production due to reduced phosphorus input. However,  
28 our analyses suggest that phenotypic plasticity is not the only possible explanation for  
29 the significant reduction in individual growth rates that we observed. The large  
30 selection differential that are imposed by size-selective fishing are likely to change the  
31 standing genetic variation for individual growth rates in the two whitefish species we  
32 studied here. Such fishery-induced evolution should be taken into account by  
33 population managers (Stokes & Law 2000; Ashley et al. 2003; Smith & Bernatchez  
34 2008).

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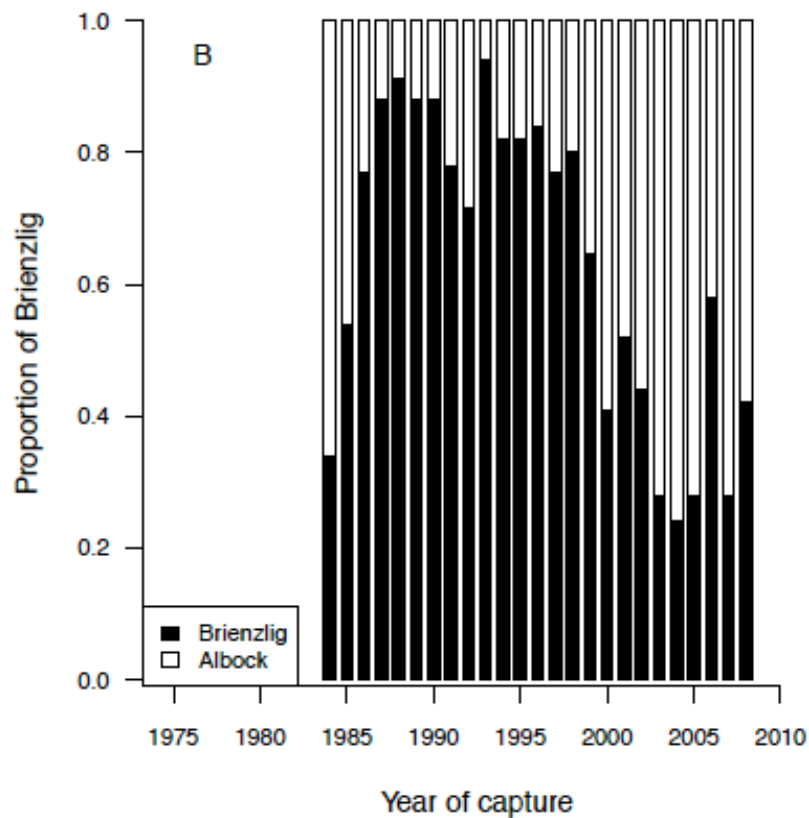
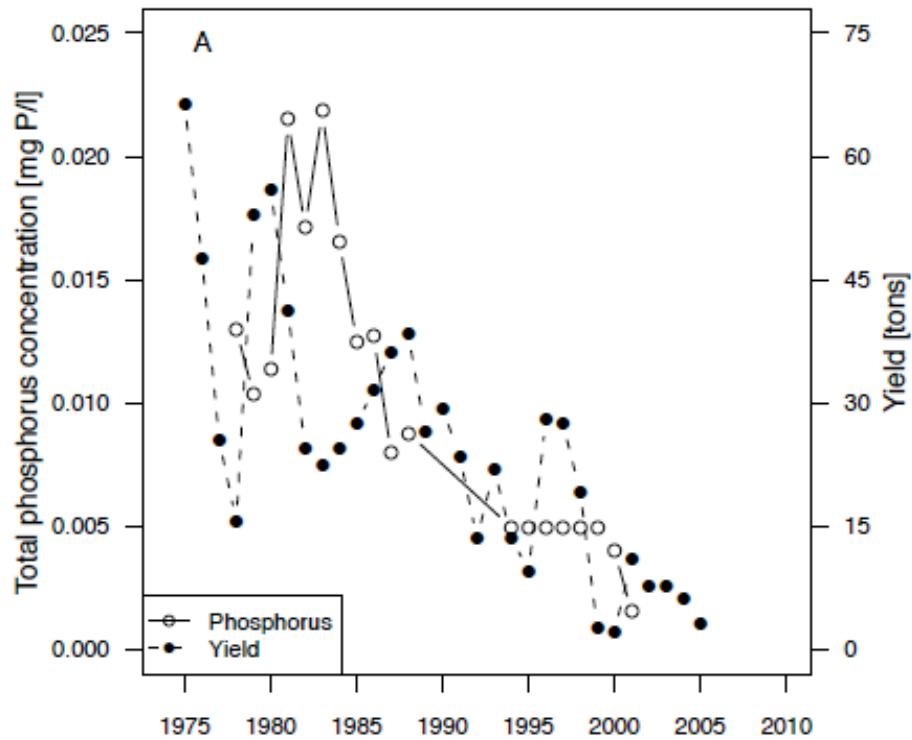
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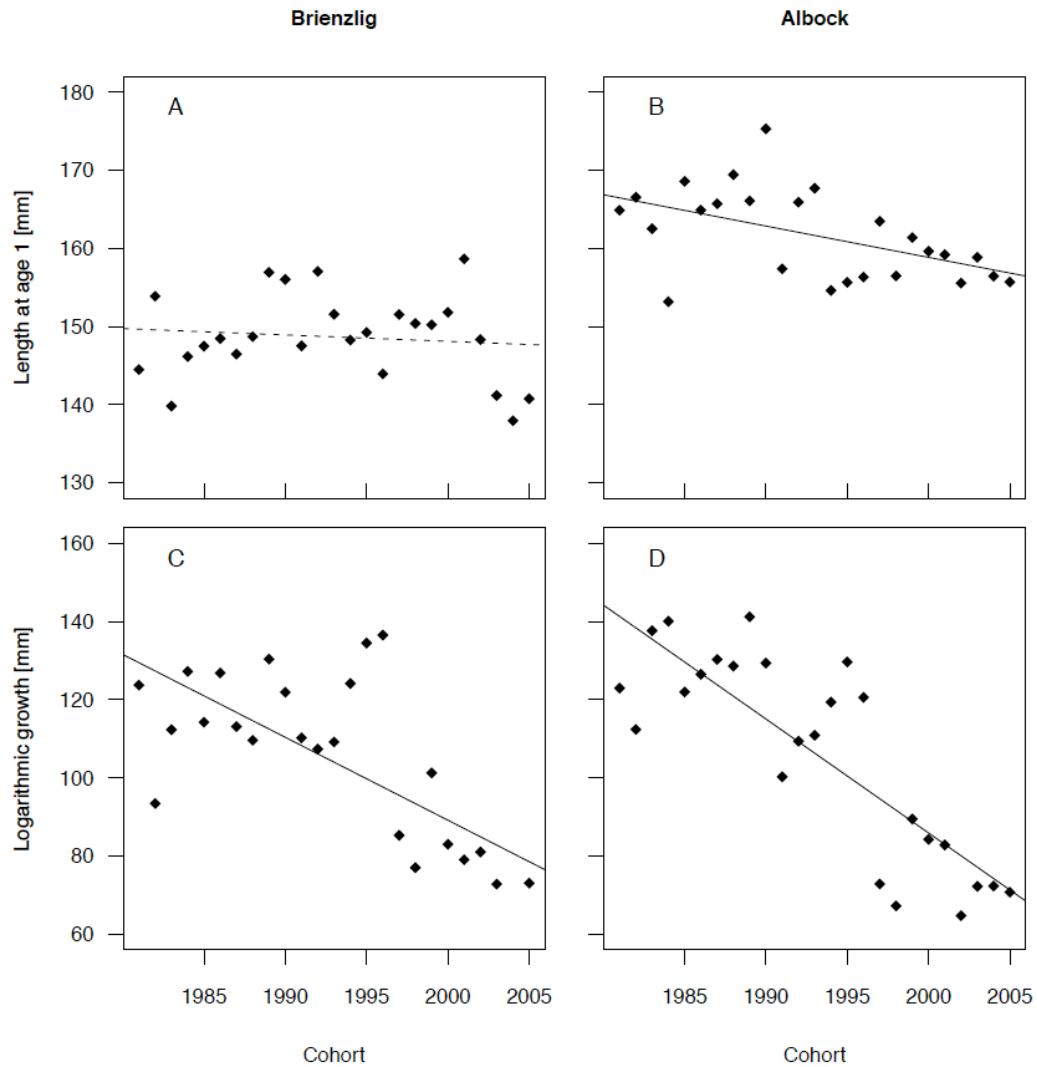
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1 Figure 1: (A) Total phosphorus (mg/L) (empty circles) in Lake Brienz during the last  
 2 decades, redrawn from (Hoyle 2004) and fishing yield in Lake Brienz in tons (full  
 3 circles). (B) Proportion of the total number of Brienzlig (black) and Albock (white)  
 4 caught each year.  
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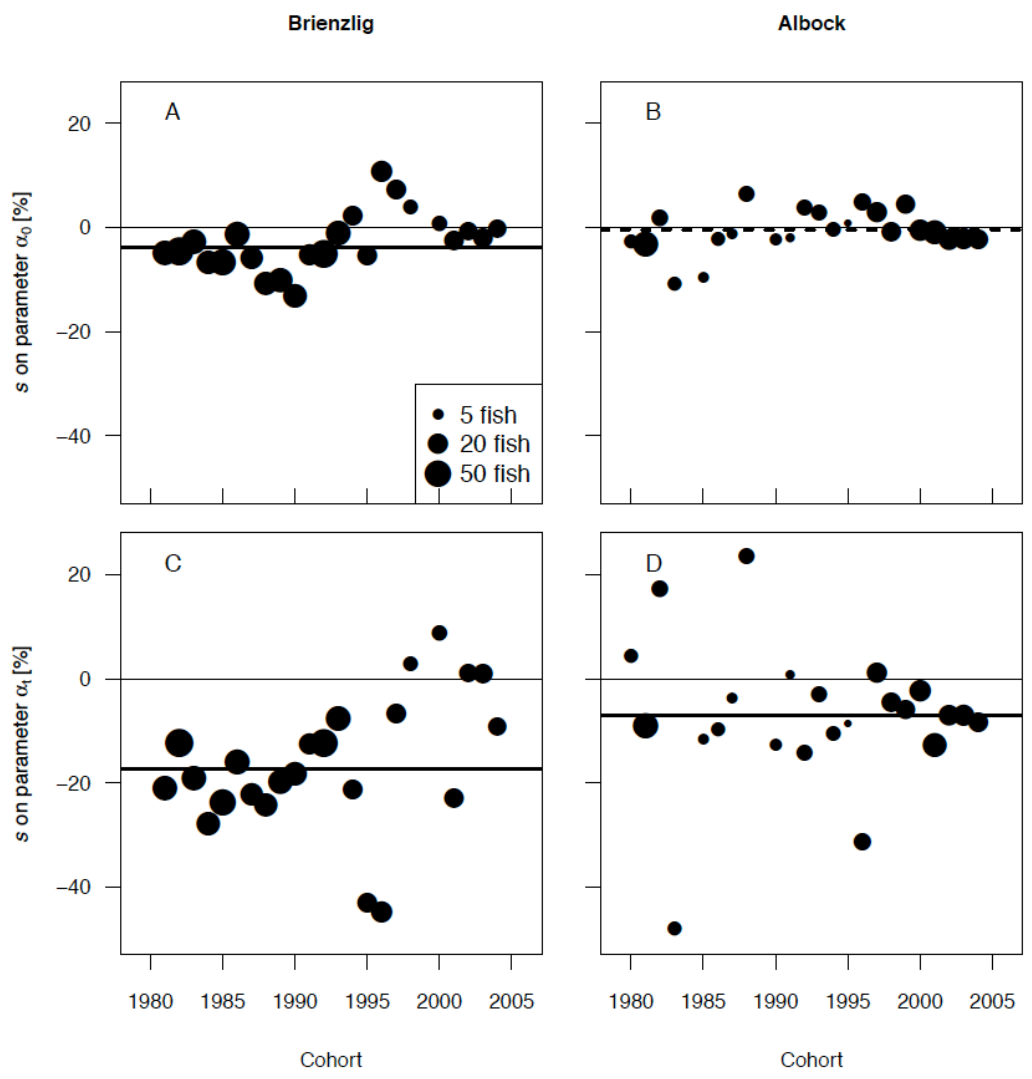
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- 1 Figure 2: Growth parameters per cohort: (A-B) average length at age 1 ( $\alpha_0$ ) and (C-D)
- 2 average logarithmic growth ( $\alpha_i$ ). The lines represent regression lines (solid =
- 3 significant linear relationship, dashed = non-significant).
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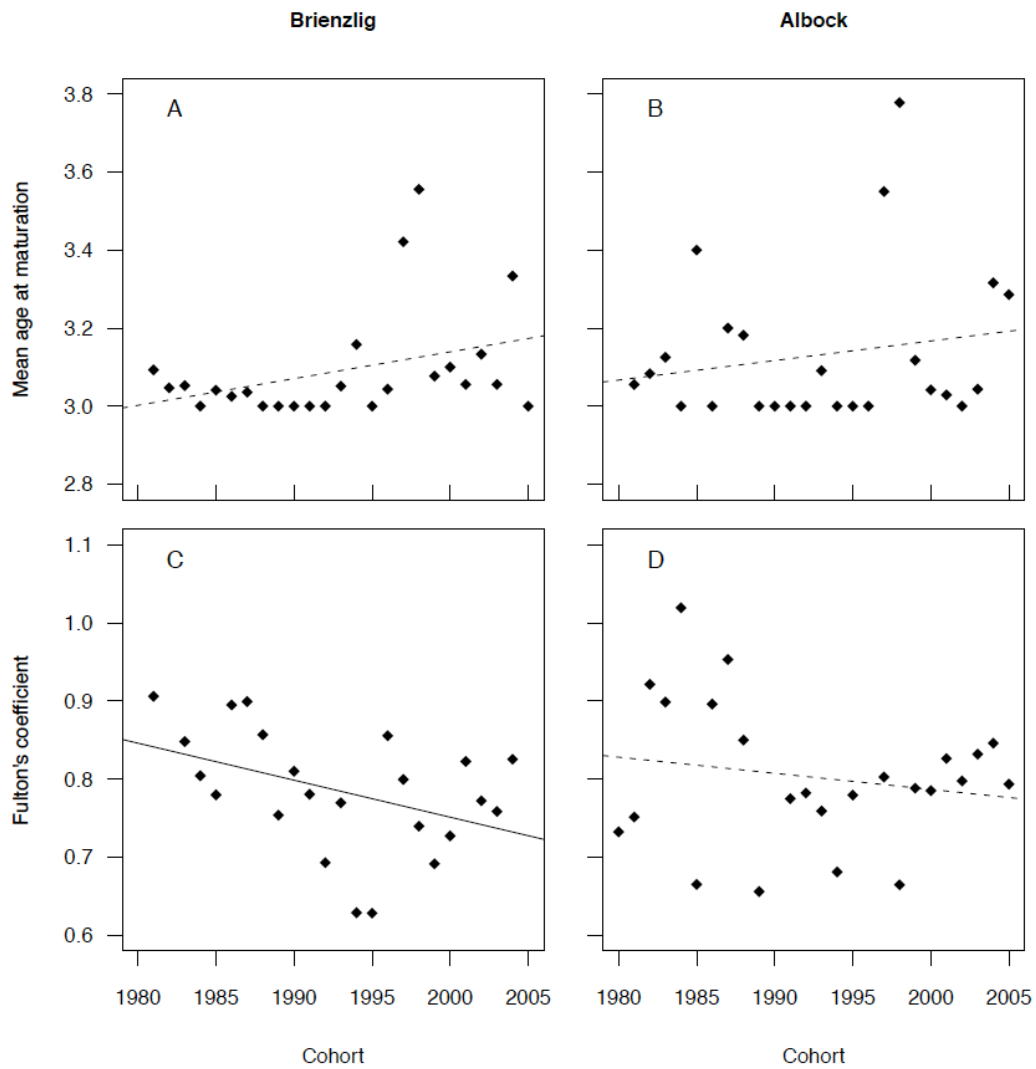
1 Figure 3: Selection differentials ( $s$ ) estimated for each cohort. (A-B)  $s$  for length at  
 2 age 1 ( $\alpha_0$ ), and (C-D)  $s$  for logarithmic growth ( $\alpha_t$ ). The width of the circle  
 3 corresponds to the number of fish within each cohort. The cohort is specified by the  
 4 year of hatching from egg. The lines represent the average selection differential (solid  
 5 = significantly different from zero, dashed = non-significant).  
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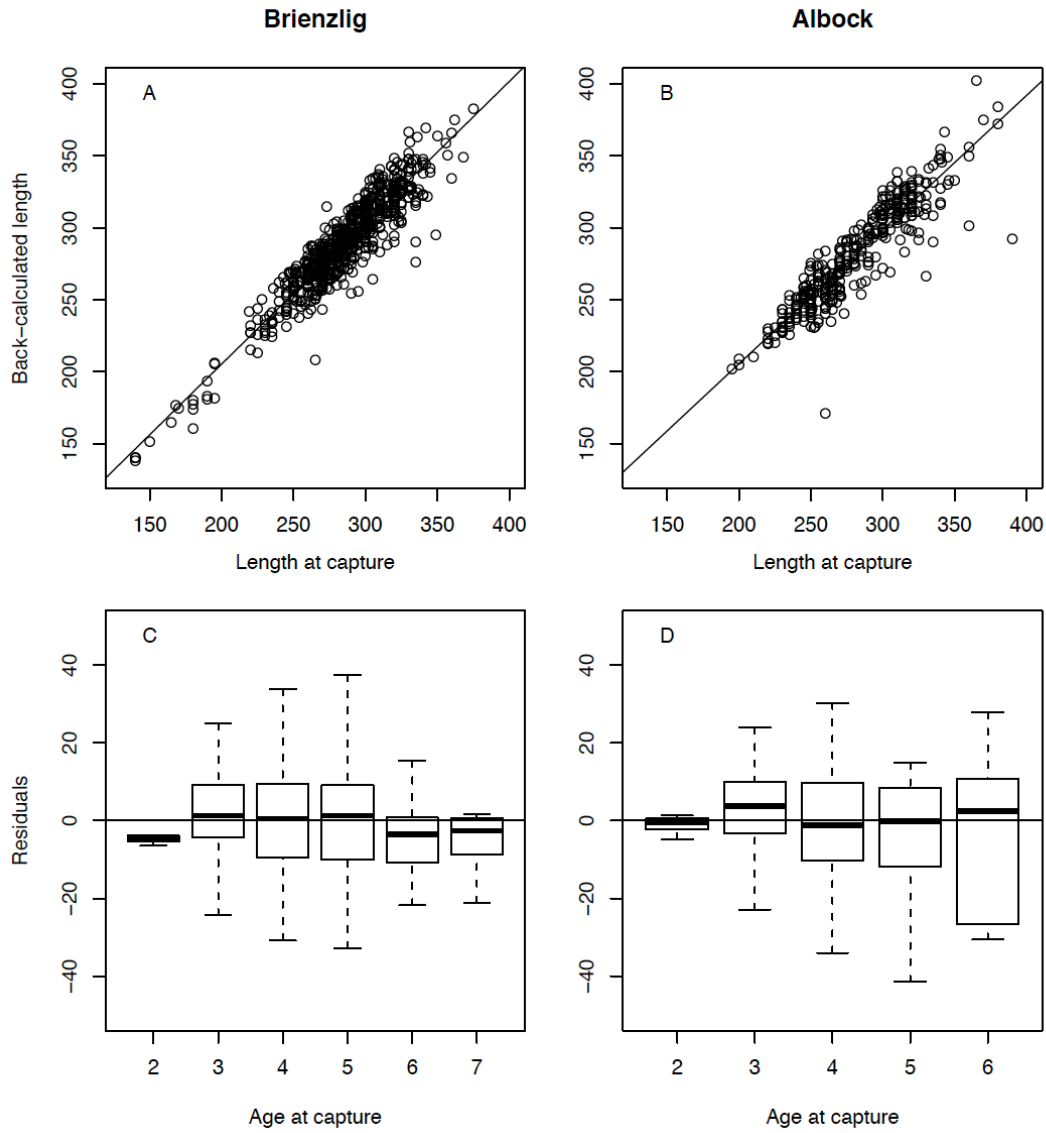


1 Figure 4: Indicators of resource allocation from growth to reproduction: (A) the mean  
2 age at maturation for each cohort and (B) the Fulton's coefficient of females during  
3 December and January. The lines represent the regression lines as in Fig. 2.  
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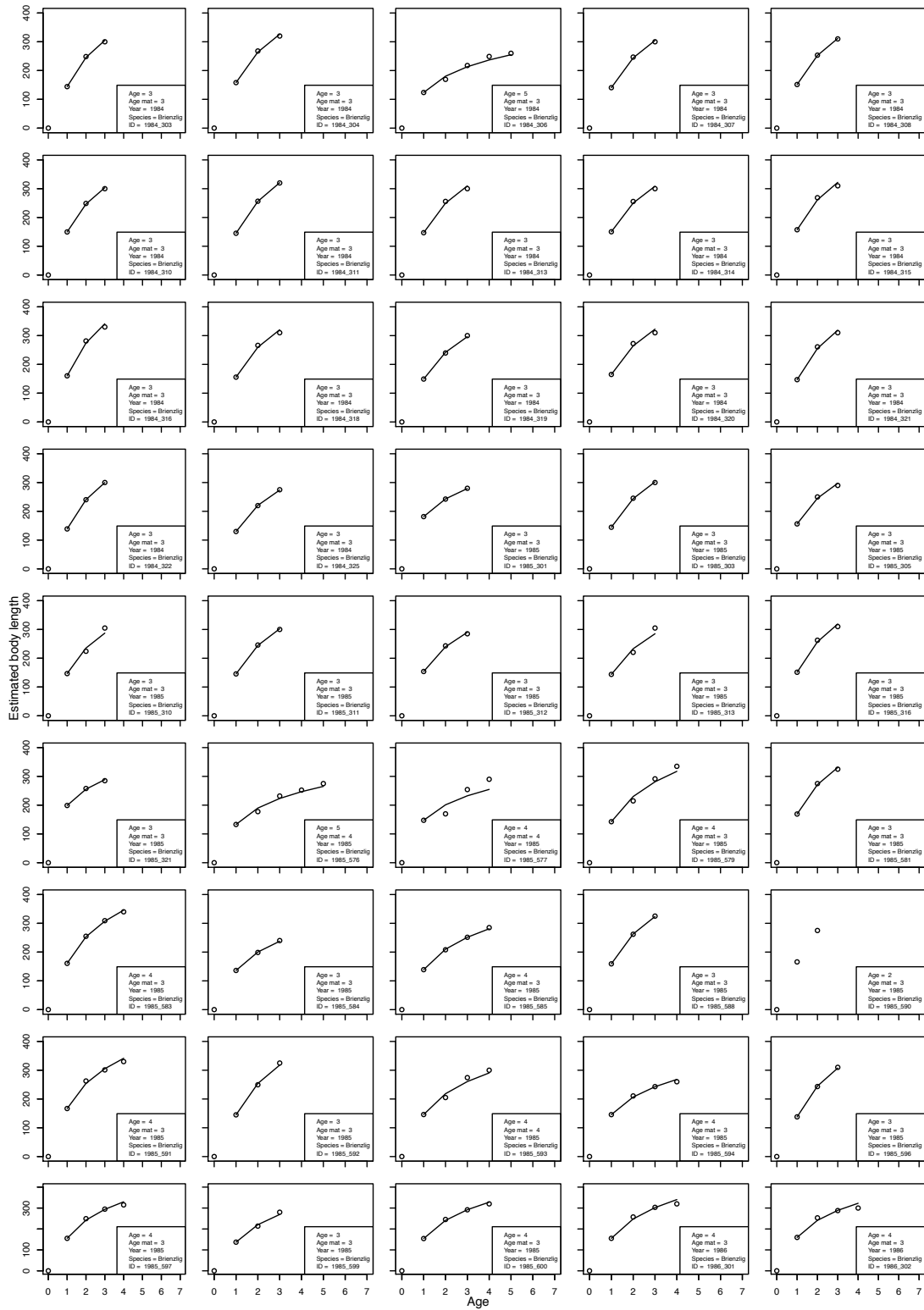
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1 Supplementary figure 1: Back-calculated length at capture versus observed length at  
2 capture (panels A and B; the lines represents the regressions), and residuals on these  
3 regressions (median, quartiles, and extremes) for each age at capture (panels C and D)  
4 for Brienzlig (A, C) and Albock (B, D).  
5



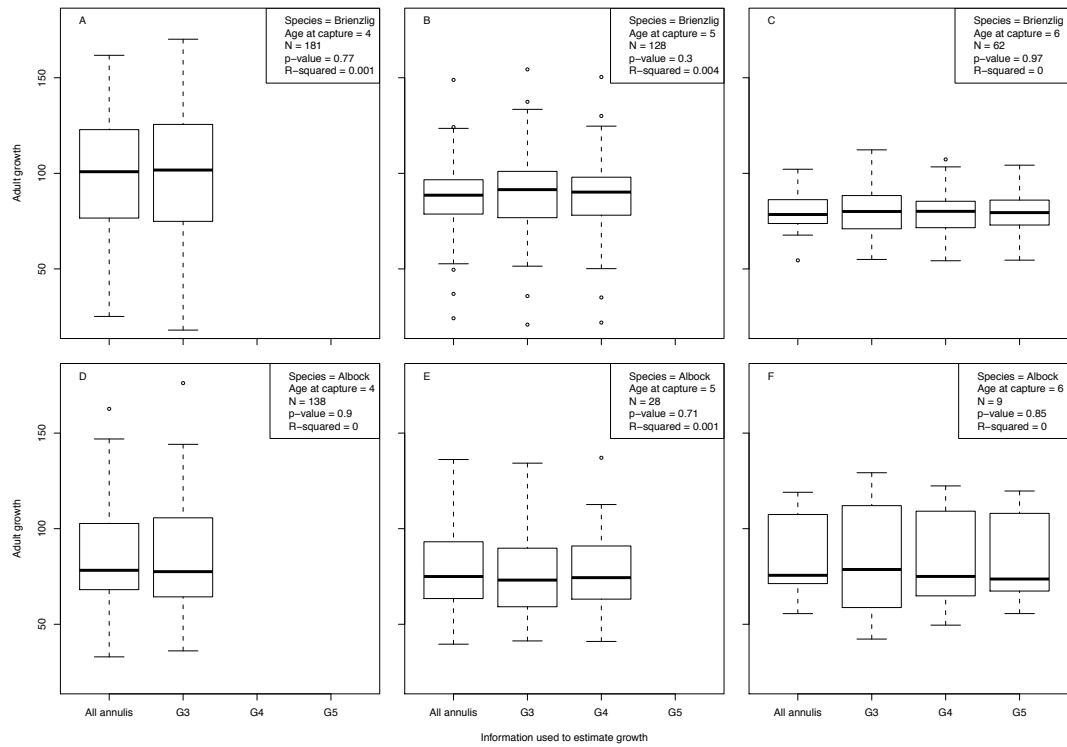
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1 Supplementary figure 2: Back-calculated body length (open circles) and modelled  
 2 length (with the two-parameter growth model) in mm (lines) for each individual fish  
 3 of the sample. Fish age, estimated age at maturation (“Age mat”), year of capture,  
 4 species and individual ID are indicated each.



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1 Supplementary figure 3: Medians (plus quartiles, extremes and values larger than 1.5  
 2 times the interquartile range) of the adult growth parameter  $\alpha_t$  of Brienzlig (panels A-  
 3 C) and Albock (D-F) caught at the age of 4 (A, C), 5 (B, E) or 6 (C, F), with growth  
 4 being estimated on all annuli, on the first three (“G3”), the first four (“G4), and the  
 5 first five annuli only (“G5”). The insert give the sample sizes, the p-values, and  $r^2$   
 6 from the respective one-way ANOVAs .  
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