

1 **Evidence for the linkage of survival of anadromous Arctic char and**
2 **brown trout during winter to marine growth during the previous**
3 **summer**

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13 Running head: Link between summer growth and winter survival

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18 **Abstract**

19 Data from a 25-year study of anadromous Arctic char (*Salvelinus alpinus*) and brown trout
20 (*Salmo trutta*) in the River Halselva provided evidence that survival during winter was linked
21 to marine growth during the previous summer. The study supported the “critical size and
22 critical period” hypothesis, which postulates that regulation of the abundance of adult
23 salmonids occurs in two major phases. The first phase is marine mortality that occurs shortly
24 after smolts enter salt water, and the second is during the following winter, when individuals
25 that have not attained a critical size are unable to meet minimum metabolic requirements and
26 die. In the present study, growth during summer appeared to be more important to winter
27 survival than body size. Size-selective mortality occurred both at sea during summer and in
28 fresh water during winter, and was more evident for first-time migrants than repeat migrants.

29 **Key words**

30 Growth, survival, size distribution, mark-recapture, salmonid

31 **Introduction**

32 It is generally accepted that animals need to gain weight and store enough energy
33 during periods of the year with rich food supplies to survive periods of the year with lower
34 food availability (Rogers and Smith 1993; Hutchings et al. 1999; Farley et al. 2007; Hurst
35 2007). For teleost fishes in temperate and alpine areas, winter is considered a survival
36 bottleneck (Johnson and Evans 1991; Cunjak et al. 1998; Cunjak and Therrien 1998), with
37 energy deficiency being the primary cause of mortality (Finstad et al. 2004; Hurst 2007).
38 Predation, thermal stress, parasites, and pathogens might also influence winter mortality
39 (Sogard 1997; Hurst 2007).

40 Reviewing size-selective mortality in the juvenile stage of teleost fishes, Sogard
41 (1997) found overwhelming evidence from field and laboratory studies that size-selective
42 mortality occurs during winter, and larger members of a cohort are better than smaller

43 members and conspecifics at tolerating physical extremes and enduring longer periods
44 without food. Further, size-selective mortality may depend on the predator field, but compared
45 to large fish, smaller fish are typically susceptible to a broader spectrum of predators and
46 experience higher mortality rates (Sogard 1997).

47 Effects of body size and growth rates on mortality of fish larvae and juveniles have
48 been summarized in the “growth-mortality” hypothesis, which suggests that larger and/or
49 faster growing compared to slower growing individuals in a cohort have a higher probability
50 of survival (Ware 1975; Anderson 1988). This hypothesis combines feeding success and
51 predation into an integrated framework: as feeding success increases, growth increases, and
52 the probability of mortality because of starvation and predation decreases (Hare and Cowen
53 1997). The functional mechanisms behind the “growth-mortality” hypothesis show three
54 concepts: “bigger is better”, “stage duration”, and “growth-selective predation”, which are
55 based on size, time, and actual growth rate, respectively (Takasuka et al. 2004; Islam et al.
56 2010; Takasuka et al. 2017). The first concept assumes mortality to be negatively size-
57 dependent, leading to a survival advantage for the largest individuals of a cohort (Miller et al.
58 1988). The “stage duration” hypothesis focuses on the relationship between growth rate and
59 stage duration. Individuals with higher growth rate shortens the vulnerable stage duration, and
60 hence selectively survive, since the probabilities of mortality events will be decreased
61 (Chambers and Leggett 1987; Houde 1987). The third concept, “growth-selective predation”,
62 which was proposed by Takasuka et al. (2003), links growth rates per se to survival directly.
63 A few attempts have been made to distinguish selection by body size from selection by
64 growth rate, and all have been growth analyses based on otolith studies on fish larvae (Hare
65 and Cowen 1997; Takasuka et al. 2003; Takasuka et al. 2004; Islam et al. 2010). These studies
66 concluded that growth rate per se may be as important as body size, and Takasuka et al.

67 (2004) observed that faster growing individuals survived even if they were smaller than their
68 slower-growing conspecifics.

69 Most studies on the “growth-mortality” hypothesis have been performed on larvae and
70 small juveniles of marine fishes, whereas few such studies on the marine life of anadromous
71 salmonids are available (Beamish and Mahnken 2001). The first 1–4 years of most
72 anadromous salmonids are spent in fresh water, until they smoltify and migrate to the sea,
73 usually when they are 10–25 cm in size (Quinn 2005; Thorstad et al. 2011). The transition
74 from fresh to salt water is a bottleneck in the life cycle of anadromous salmonids, with high
75 mortality, mainly caused by predation by marine fish species, birds, and mammals (Hvidsten
76 and Lund 1988; Hedger et al. 2011; Ward and Hvidsten 2011), and this mortality is partly
77 related to size (the “bigger is better” concept). Beamish and Mahnken (2001) studied Pacific
78 salmon (*Oncorhynchus* spp.) in general and coho salmon (*Oncorhynchus kisutch*) in
79 particular, and proposed that high mortality also occurs in autumn and winter during the first
80 year at sea. Their hypothesis stated that numbers of returning Pacific salmon are linked to
81 fluctuations in climate and oceanic environments during their growth. They introduced the
82 “critical size and critical period hypothesis” that regulation of the final abundance (total
83 returns) occurs in two major stages. The first stage in marine mortality is mostly predation-
84 based and occurs immediately after the smolts enter the sea. The second stage of major
85 mortality occurs in autumn and winter of the first year at sea, when juvenile salmon that have
86 not attained a critical size die, because they are unable to meet the minimum metabolic
87 requirements. According to this hypothesis, growth-based mortalities may occur throughout
88 the summer, but mortalities predominantly occur after summer of their first year at sea, i.e.,
89 survival during the winter is linked to growth during the previous summer.

90 Most anadromous salmonid species, including coho salmon, remain at sea for one or
91 more years before they return to their natal river to spawn, and hence, mortality rates during

92 the first summer at sea can hardly be separated from mortality rates during the following
93 winter. Only those individuals that survive both periods and return to the river are available
94 for further analysis. However, some salmonids such as anadromous Arctic char (*Salvelinus*
95 *alpinus*) and brown trout (*Salmo trutta*) in part of their distribution area, including northern
96 Norway, usually return to fresh water the summer following their migration to the sea as
97 smolts, and continue to migrate between fresh water and the sea twice each year for the rest of
98 their lives (Jørgensen and Johnsen 2014; Jensen et al. 2015; Thorstad et al. 2016). Hence, by
99 trapping and individually tagging the fish when they first leave fresh water and recording their
100 body size each time they pass the trap, growth and survival rates can be estimated each time
101 they leave or ascend fresh water. In this way, it is possible to distinguish quantitatively the
102 mortality rates during the two periods included in the “critical size and critical period
103 hypothesis” (i.e., the first summer and first winter after sea migration, respectively).

104 Such a study has been performed during a 25-year period for anadromous Arctic char
105 and brown trout in the River Halselva in the Arctic region of Norway. First time migrants
106 (smolts) of both species were captured in a permanent fish trap located 200 m above the outlet
107 to the sea, individually tagged, and thereafter recorded each time they passed the fish trap,
108 usually twice each summer, for the rest of their lives (up to the end of 2012, when the trap
109 was removed from the river). By examining these data, the “growth-mortality hypothesis” and
110 the “critical size and critical period hypothesis” were tested.

111 **Material and methods**

112 **Study area**

113 The Hals watercourse (70°2'N, 22°57'E) in the Arctic region of Norway has a catchment area
114 of 143 km² and drains into the Alta Fjord (Fig. 1). Approximately 20 km of the watercourse is
115 accessible to anadromous salmonids (Arctic char, brown trout, and Atlantic salmon [*Salmo*
116 *salar*]), including a 1.2-km² lake located 2.1 km inland and 30 m above sea level (Lake

117 Storvatn, Fig. 1). Both bodies of water are ice-covered from December to March or April, a
118 period characterized by low flow. A pronounced increase then occurs during the snow-melting
119 period (May–June), followed by a decrease during July–August, yielding a mean annual flow
120 of $4.3 \text{ m}^3 \cdot \text{s}^{-1}$. The outlet is the River Halselva, which empties directly into the sea without any
121 distinct estuary, resulting in limited freshwater areas for fish to overwinter downstream of the
122 fish traps (see below). Minimum temperature in the outlet—River Halselva—is approximately
123 0°C during the ice-covered period, then rises steadily until reaching a maximum temperature
124 of approximately 13°C in early August. Respectively, minimum and maximum sea
125 temperatures are approximately 2.5°C in late March and 11°C during late July–early August.

126 **Fish sampling**

127 During 1987–2012, fish were sampled via permanent fish traps placed 200 m upstream
128 from the sea: Wolf traps (Wolf 1951) (apertures 10 mm, inclination 1:10) for descending fish
129 and fixed box traps for ascending fish. All passing fish larger than 10 cm were trapped, and
130 Arctic char (sea char) and the brown trout (sea trout) were predominant in the watercourse,
131 but Atlantic salmon and European eels (*Anguilla anguilla*) were also present. The traps were
132 operated during the ice-free period (April through October) and were emptied twice per day
133 (at 8:00 and 20:00 h) to record morphological data before release. Natural tip length (L , in
134 mm) (i.e. total length of the fish with the tail fin in its natural position, Ricker 1979) and mass
135 (M , in g) were measured for all fish.

136 Smolts (i.e. first time migrants, see definition by Allan and Ritter 1977) of brown trout
137 and Arctic char were tagged with individually numbered Carlin tags (Carlin 1955). The size
138 range of these smolts were between 18–28 cm and all smolts that migrated to sea before 1
139 August 1988 to 2012 were included in the present study (in total, 11,900 Arctic char and
140 15,220 brown trout). Individuals migrating after 1 August (6.1% of brown trout and 1.7% of
141 Arctic char) were omitted because of an increasing proportion of parr among descending fish

142 during autumn. First time migrants smaller than 18 cm were also omitted. They were not
143 individually tagged, but fin clipped in a systematic manner to enable future identification of
144 year of descent (Jensen et al. 2012).

145 In general, smolts of Arctic char in the Hals watershed migrate before brown trout,
146 with pronounced peaks and median dates of descent of 25 June and 4 July, respectively,
147 although some smolts of both species leave the river throughout most of the ice-free period of
148 the year (Jensen et al. 2012). The annual descent of naturally produced Arctic char and brown
149 trout smolts were, respectively, 500–3600 (mean = 1350) and 300–1400 (mean = 950
150 individuals) (Jensen et al. 2012).

151 The standardized mass-specific growth rate (Ω , % d⁻¹) was used to eliminate the effect
152 of growth rate differences in initial body sizes, and was estimated as (Ostrovsky 1995):

$$\Omega = 100 \times \frac{M_1^b - M_0^b}{(t_1 - t_0) \times b}$$

153 where M_0 is the body mass of the fish at descent from the river and M_1 the body mass of the
154 same fish when returning to the river later the same year, t_0 is the date when the fish
155 descended, t_1 the date when the fish ascended again, $t_1 - t_0$ is the duration of the stay at sea,
156 and b is the allometric mass exponent for the relationship between specific growth rate and
157 body mass (0.31 for brown trout, Elliott et al. 1995). The same value of b was used for Arctic
158 char (Larsson et al. 2005). Ω effectively eliminated the effect of growth rate differences in
159 initial body sizes (Sigourney et al. 2008; Finstad et al. 2011a; Forseth et al. 2011).

160 Return rate to the fish trap was used as a proxy for survival rate in this study. Except
161 for the first summer at sea, the estimated return rates appeared to closely reflect survival rates
162 because only a few individuals of both species were absent from the river for one or more
163 years before they returned, and only a few others stayed more than one year in fresh water
164 before they returned to sea (Jensen et al. 2015). Further, as few as 3.9% and 2.4% of Arctic

165 char and brown trout, respectively, which were captured by anglers in the watercourse had
166 remained more than one year after their latest occurrence in the fish trap, and these may have
167 changed from a migratory to a stationary life. Return rates the first summer at sea, however,
168 underestimated sea survival, especially for brown trout (Jensen et al. 2015). Most of the
169 recovered Arctic char returned to the River Halselva to overwinter already the same summer
170 as they migrated to sea as smolts (97.8%), whereas more brown trout (39.6%) overwintered
171 one to four times in other watersheds before most of them eventually returned to the River
172 Halselva upon maturation (Jensen et al. 2015). The proportion of post-smolts re-occurring in
173 the fish trap the first summer, however, proved to be a significant early sign of overall
174 survival of each smolt cohort (Jensen et al. 2015).

175 **Statistical analyses**

176 SPSS (version 23) was used for statistical analyses. Comparisons of means were
177 conducted using a one-way analysis of variance (ANOVA), and duration of sea sojourns and
178 winter freshwater stays were tested using paired sample *t*-tests. Binary logistic regression was
179 used to distinguish the relative importance of increases in mass of Arctic char and brown trout
180 during sea sojourns on survival compared with their length at ascent after the sojourns on
181 survival during the subsequent winter in fresh water.

182 **Results**

183 During the 25-year study period, the mean duration of the first sea sojourn of
184 anadromous Arctic char and brown trout was 34.0 ± 1.2 (\pm SE) and 55.2 ± 0.9 days,
185 respectively. Moreover, their total growth during their first sojourn was 66.7 ± 5.2 and 148.0
186 ± 6.0 g, and the mean standardized mass-specific growth rate (Ω) was $7.24 \pm 0.40\%$ day⁻¹ and
187 $8.33 \pm 0.25\%$ day⁻¹, respectively. All these values were significantly higher for brown trout
188 than for Arctic char (pairwise *t*-tests, $P < 0.001$).

189 The return rate of Arctic char the same summer as they left the river as smolts was
190 32.7 ± 2.5% (± SE), and among the ascending individuals, 44.1 ± 3.0% returned to the sea the
191 subsequent spring. Correspondingly, 20.8 ± 1.9% of the brown trout that left the river as
192 smolts returned to the river later the same summer, and among the ascending individuals, 62.3
193 ± 2.9% descended the subsequent spring.

194 For both species, size selective mortalities were detected during both the first and
195 second sea sojourn, as well as for the third sea sojourn for Arctic char. Small individuals were
196 overrepresented among those that did not return (Fig. 2), and the mean length was
197 significantly smaller for those that died (Table 1).

198 For both species, significant relationships were established between survival during
199 the winter subsequent the first sea sojourn and standardized specific growth rate at sea during
200 the first sea sojourn (Fig. 3a, b). Furthermore, significant relationships between winter
201 survival and total marine growth increments in mass during the first sea sojourn (Fig. 3c, d),
202 as well as between winter survival and body length at ascent after the first sea sojourn were
203 detected (Fig. 3e, f). Growth increments in mass during the first sea sojourn proved to be
204 more important for subsequent winter survival than body length at ascent (Table 2). Similar
205 results were found after the second and third sea sojourn as well (Table 2).

206 For the first, second, and third sea sojourn for both species, the mean mass increment
207 during the sea sojourn was higher for individuals that returned from fresh water to the sea than
208 those that did not return, although this was not significant for Arctic char for their third sea
209 sojourn (Table 3). Frequency distributions of mass increments during the first three sea
210 sojourns for individuals that survived until the next winter, and those that did not return (Fig.
211 4), corroborate these results.

212 **Discussion**

213 The present study provides evidence that survival of anadromous Arctic char and
214 brown trout during winter is linked to growth during the previous summer at sea. High growth
215 rates at sea during summer resulted in increased survival in fresh water during the following
216 winter. Moreover, size-selective mortality occurred both at sea during summer and in fresh
217 water during winter, in accordance with the “growth-mortality” hypothesis. A clear
218 relationship between growth and survival during the first marine sojourn was previously
219 established for the same populations (Jensen et al. 2017), because fewer individuals return to
220 the river after the first sea sojourn in years with low growth rates compared with those with
221 higher growth rates at sea. Hence, individuals growing slowly while at sea face higher
222 mortality risks than faster growing individuals both when at sea in summer and during the
223 subsequent winter in fresh water. This is partly in line with the “critical size and critical
224 period” hypothesis by Beamish and Mahnken (2001). The main deviation from this
225 hypothesis is that marine growth per se during summer in the present study was more
226 important for winter survival than body size.

227 The findings that growth per se was more important for survival than body size is in
228 accordance with the “growth-selective predation” concept of the “growth-mortality”
229 hypothesis. This concept works when slower-growing individuals are more vulnerable to
230 predation mortality than faster-growing conspecifics of the same somatic size (Takasuka et al.
231 2017). Slower-growing individuals would be physiologically in a poor condition and thus
232 have a lower potential to initiate antipredator behaviours (Fuiman and Magurran 1994; Skajaa
233 et al. 2003; Takasuka et al. 2017).

234 The first period of high mortality after smoltification in anadromous salmonids occurs
235 shortly after the smolts enter sea water and is predation-based and size-dependent (Parker
236 1971; Klemetsen et al. 2003; Ward and Hvidsten 2011; Thorstad et al. 2016). The results of
237 the present study corroborate this, although survival rates were probably overestimated

238 because only first time migrants larger than 18 cm were included in the analyses. However,
239 mortality due to tagging effects might underestimate marine survival (Strand et al. 2002). In
240 addition, the present study demonstrated that in Arctic char, size-dependent mortality also
241 took place during the second and third sea sojourn, as well as during the second sea sojourn
242 for brown trout, corresponding to individual body lengths of up to approximately 350 mm
243 (400–450 g) for both species. Because Arctic char stay for a shorter period at sea than brown
244 trout (Jensen et al. 2017), they use longer time to reach this size.

245 The second period of high mortality, as proposed by Beamish and Mahnken (2001),
246 occurs during the autumn and winter following the first summer at sea. Although this second
247 period of high mortality may be difficult to prove for salmonid species that spend one year or
248 more at sea before they return to fresh water, it has been made probable for several species.
249 These include coho salmon (Beamish et al. 2004), pink salmon (*Oncorhynchus gorbuscha*)
250 (Moss et al. 2005; Cross et al. 2008), sockeye salmon (*Oncorhynchus nerka*) (Farley et al.
251 2007; Farley et al. 2011), chinook salmon (*Oncorhynchus tshawytscha*) (Tovey 1999; Duffy
252 and Beauchamp 2011) and Atlantic salmon (McCarthy et al. 2008). The results of the present
253 study demonstrated this second period of high mortality.

254 Are mortality rates during autumn and winter linked to the size of the fish at the end of
255 the previous summer or growth rates during that summer? The present study provided
256 evidence that high growth rates were more important than size for winter survival in both
257 Arctic char and brown trout. In most other salmonid studies, however, the methods used could
258 not distinguish between these two alternatives. Using data from coded wire tag release groups
259 of hatchery chinook salmon, Duffy and Beauchamp (2011) concluded that mortality after July
260 was strongly size dependent. Based on studies of spacing between circuli in scales of coho
261 salmon, Beamish et al. (2004) concluded that individuals that survived the winter had
262 significantly larger spacing between circuli on their scales, indicating that brood year strength

263 was related to growth during the first marine year. Similarly, Moss et al. (2005) found that
264 surviving pink salmon exhibited significantly wider circuli spacing on the region of the scale
265 formed during early marine residence than did juveniles collected at sea during their first
266 summer in the sea. At the same circuli, a significantly larger average scale radius for returning
267 adults than for juveniles suggested that faster-growing juveniles had higher survival rates and
268 that significant size-selective mortality occurred after the juveniles were sampled. Based on a
269 long-term study of circuli spacing in scales of a Norwegian Atlantic salmon population,
270 McCarthy et al. (2008) found a significant positive correlation between post-smolt growth and
271 pre-fishery abundance of Norwegian Atlantic salmon during the third, fourth, and fifth months
272 (July, August, and September) at sea. They suggested that a decrease in post-smolt growth
273 during that time might be driving the overall decrease in pre-fishery abundance in Norway.
274 Utilizing data from large-scale fisheries for Bristol Bay sockeye salmon, Farley et al. (2011)
275 provided evidence that marine mortality of juvenile fish after their first summer at sea could
276 be large and that the first winter at sea might be the critical period for survival. Furthermore,
277 they found differences in the seasonal energetic signatures for lipids and proteins, and
278 suggested that during winter, the fish did not starve, but instead the larger fish apparently used
279 energy stores to minimize predation.

280 All the above-mentioned studies were performed on species that remained more than
281 one year to sea before returning to their natal rivers, and were mainly based on analyses of
282 growth from scales. Here, we were able to address uncertainties that affected earlier work,
283 because Arctic char and brown trout return to fresh water the same summer as they migrate to
284 sea as smolts, and continue to move between the sea and fresh water twice each year for the
285 rest of their lives (Jensen et al. 2015). Hence, we were able to estimate growth directly via
286 measuring individual lengths and mass during both ascent and descent journeys, and had
287 precise data on migration and return dates. The main deviation from the previous studies was

288 that Arctic char and brown trout stayed in fresh water during winter, whereas the other species
289 remained in salt water.

290 Some human activities may affect marine growth of the two species, and hence affect
291 survival rates both at sea and in fresh water. One example is the future climate change, which
292 is expected to affect the timing of seaward migration and return migration, as well as marine
293 growth (Reist et al. 2006; Jonsson and Jonsson 2009; Jørgensen and Johnsen 2014). In the
294 Hals watercourse, the timing of the seaward migration was negatively correlated with mean
295 river temperature at descent (Jensen et al. 2012). Furthermore, a negative relationship was
296 detected between the mean duration of first sea sojourn and average sea temperatures during
297 late summer (Jensen et al. 2017). However, neither species exhibited a significant relationship
298 in their standardized mass-specific growth rate or total marine growth and sea temperatures,
299 possibly because of low inter-annual variation in sea temperatures during the study period
300 (Jensen et al. 2017).

301 Another example is the aquaculture industry for farmed salmonids, which might
302 experience stronger negative effects in the wild populations of these two species than earlier
303 expected. In areas with intensive farming, the abundance of salmon lice (*Lepeophtheirus*
304 *salmonis*) in the sea has increased, and negatively affects wild salmonid populations (Finstad
305 et al. 2011b; Vollset et al. 2014; Thorstad et al. 2015; Vollset et al. 2016). For anadromous
306 brown trout, premature return migration to fresh water because of high salmon lice
307 infestations has caused reduced sea growth and increased marine mortality (Birkeland 1996;
308 Wells et al. 2007; Fjørtoft et al. 2014; Gjelland et al. 2014; Skaala et al. 2014). Salmon lice
309 may induce osmoregulatory dysfunction, physiological stress, anemia, reduced feeding and
310 growth (Shephard et al. 2016), increased susceptibility to secondary infections, reduced
311 disease resistance, and ultimately mortality of individual fish (Thorstad et al. 2015). In
312 addition to these earlier known disadvantages, increased winter mortality might also occur

313 because of the premature return migration to fresh water and hence decreased marine growth
314 during the previous summer as stated above.

315 In conclusion, Arctic char and brown trout survival in freshwater during winter was
316 linked to marine growth during the previous summer. High growth rate at sea during summer
317 resulted in increased survival the following winter. Moreover, size-selective mortality
318 occurred both at sea during summer and in fresh water during winter, in accordance with the
319 “growth-mortality” hypothesis. Individuals growing slowly while at sea face higher mortality
320 risks than faster growing individuals both when at sea in summer and during the subsequent
321 winter in fresh water. This is partly in line with the “critical size and critical period”
322 hypothesis. The main deviation from this hypothesis is that marine growth per se during
323 summer in the present study was more important for winter survival than body size.

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528

529 Table 1. Mean length (mm, \pm 95% CI) of Arctic char and brown trout at migration to the sea
 530 in the first, second, and third summer after smoltification, separated between individuals that
 531 returned to the River Halselva (Returned) and those that did not return (Disappeared). Results
 532 of ANOVA tests to distinguish between the two groups. Pooled data for the period 1988–
 533 2012.

	Returned		Disappeared		ANOVA	
	Length	n*	Length	n	F†	P‡
Arctic char						
1. summer	218.14 \pm 0.76	3892	210.52 \pm 0.52	8008	266.5	< 0.001
2. summer	281.47 \pm 1.94	905	270.04 \pm 2.80	509	45.3	< 0.001
3. summer	338.24 \pm 2.73	547	326.17 \pm 6.38	157	15.01	< 0.001
Brown trout						
1. summer	213.08 \pm 0.69	4227	207.72 \pm 0.40	10972	182.2	< 0.001
2. summer	304.56 \pm 1.93	1003	301.58 \pm 2.14	943	4.14	0.042
3. summer	394.31 \pm 2.71	606	391.61 \pm 3.75	333	1.33	0.249

534 *n = number of individuals, †F = F-value of the ANOVA test, ‡P = significance level.

535 Table 2. Results of tests (binary logistic regression) to distinguish the relative importance of
 536 increase in mass (g) of Arctic char and brown trout during the first, second, and third sea
 537 sojourn from length at ascent (mm) after the same sojourns on survival during the subsequent
 538 winter in fresh water. Pooled data for the period 1988–2012.

	Increase in mass		Length at ascent		Alive	Dead	†Nagelkerke R ²
	Wald	P*	Wald	P	n ₁ †	n ₂ §	
Arctic char							
1. sojourn	143.6	<0.001	13.0	<0.001	1373	2244	0.187
2. sojourn	15.8	<0.001	1.72	0.19	598	303	0.032
3. sojourn	4.64	0.031	4.49	0.034	347	194	0.014
Brown trout							
1. sojourn	51.9	<0.001	0.18	0.668	1852	979	0.126
2. sojourn	13.7	<0.001	3.19	0.074	694	286	0.026
3. sojourn	5.9	0.015	0.03	0.854	393	193	0.035

539 *P = significance level estimated by Wald statistics; †Nagelkerke R² = Nagelkerke squared
 540 multiple correlation coefficient; †n₁ = number of individuals that descended to the trap after the
 541 winter; §n₂ = number of individuals that did not descend to the trap after the winter

542 Table 3. Mean mass (g, \pm 95% CI) of Arctic char and brown trout when they ascended the fish
 543 trap in the River Halselva after one, two, and three summers at sea, sorted by individuals that
 544 returned to the fish trap after the following winter (Returned) and individuals that did not
 545 descend (Disappeared). Pooled data for the period 1988–2012.

	Returned		Disappeared		ANOVA	
	Mass	n*	Mass	n	F†	P‡
Arctic char						
1. summer	84.0 \pm 2.16	1373	49.8 \pm 1.73	2244	579.5	< 0.001
2. summer	159.1 \pm 4.64	598	138.5 \pm 7.28	301	23.7	< 0.001
3. summer	216.6 \pm 11.4	347	209.1 \pm 11.2	194	1.08	> 0.05
Brown trout						
1. summer	170.3 \pm 2.69	1853	128.5 \pm 4.43	980	280.0	< 0.001
2. summer	322.8 \pm 6.88	694	298.7 \pm 10.0	286	14.3	< 0.001
3. summer	470.7 \pm 14.4	393	422.9 \pm 18.9	193	14.9	< 0.001

546 *n = number of individuals, †F = F-value of the ANOVA test, ‡P = significance level.

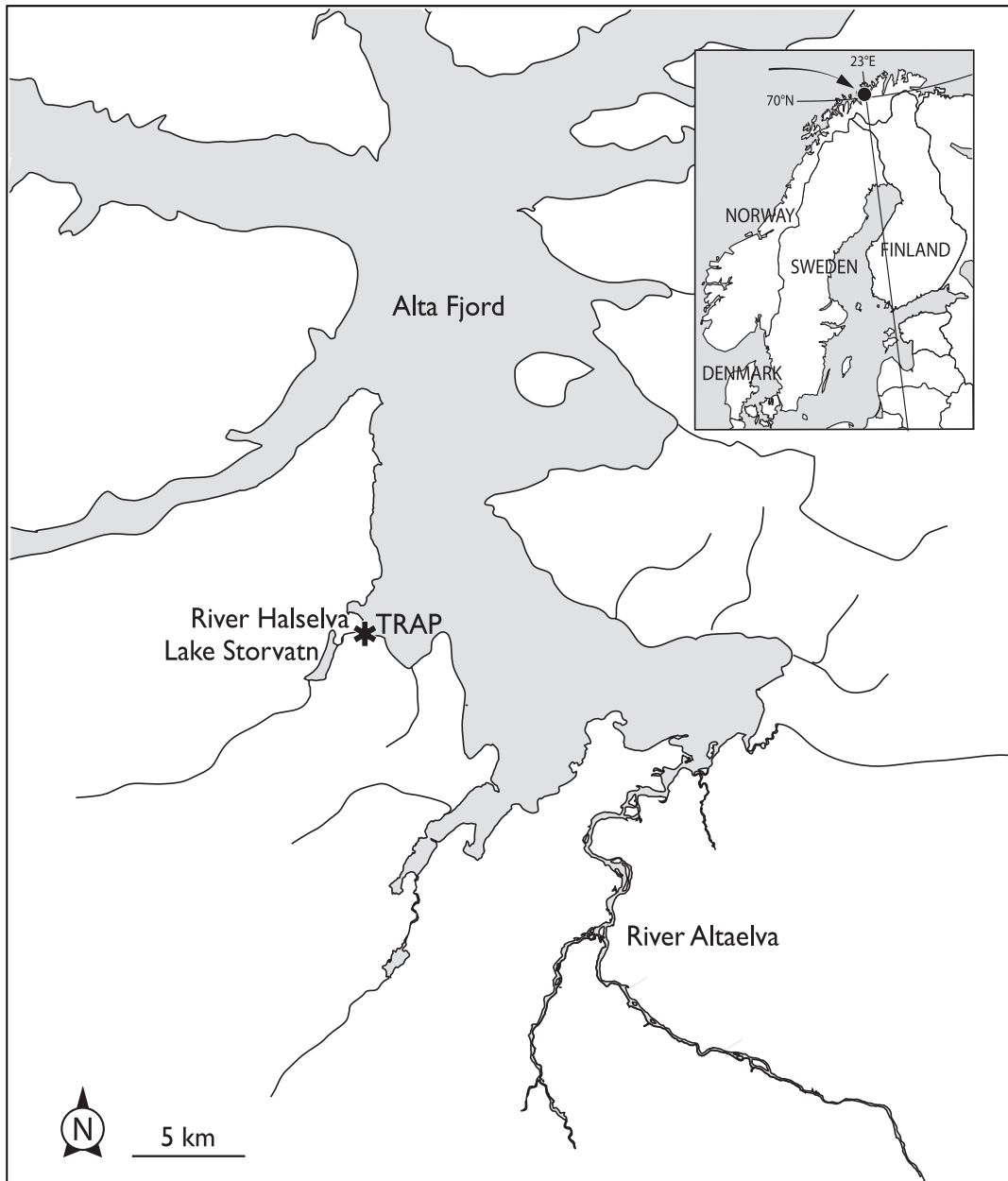
547 **Figure captions**

548 **Fig. 1.** Map of the study area, with the location of the fish traps in the River Halselva for
549 trapping of all ascending and descending fish.

550 **Fig. 2.** Length distribution of Arctic char and brown trout at their entrance to the sea,
551 separated between those that died during the subsequent sea sojourn (●), and those that were
552 still alive (i.e. had subsequently returned to the fish trap) after the sea sojourn (○). Arctic char
553 at their a) first, b) second, and c) third summer at sea, and brown trout at their d) first, e)
554 second, and f) third summer at sea. Pooled data for the period 1988–2012.

555 **Fig. 3.** Relationship between mean standardized specific growth rate (Ω , % d⁻¹) during the first
556 sea sojourn and fresh water survival (%) during the following winter for a) Arctic char ($y =$
557 $5.00 x + 7.44$, $r^2 = 0.469$, $F_{1,22} = 19.47$, $P < 0.001$) and b) brown trout ($y = 6.67 x + 6.47$, $r^2 =$
558 0.360 , $F_{1,22} = 12.37$, $P = 0.002$); relationship between mean total growth increment (g) during
559 the first sea sojourn and fresh water survival (%) during the following winter for c) Arctic
560 char ($y = 0.49 x + 11.0$, $r^2 = 0.784$, $F_{1,22} = 79.69$, $P < 0.001$) and d) brown trout ($y = 0.32 x +$
561 14.2 , $r^2 = 0.482$, $F_{1,22} = 20.48$, $P < 0.001$); and relationship between mean length (mm) at
562 ascent to the river after the first sea sojourn and fresh water survival (%) during the following
563 winter for e) Arctic char ($y = 1.03 x - 214$, $r^2 = 0.763$, $F_{1,22} = 70.70$, $P < 0.001$) and f) brown
564 trout ($y = 0.987 x - 213$, $r^2 = 0.445$, $F_{1,22} = 17.66$, $P < 0.001$).

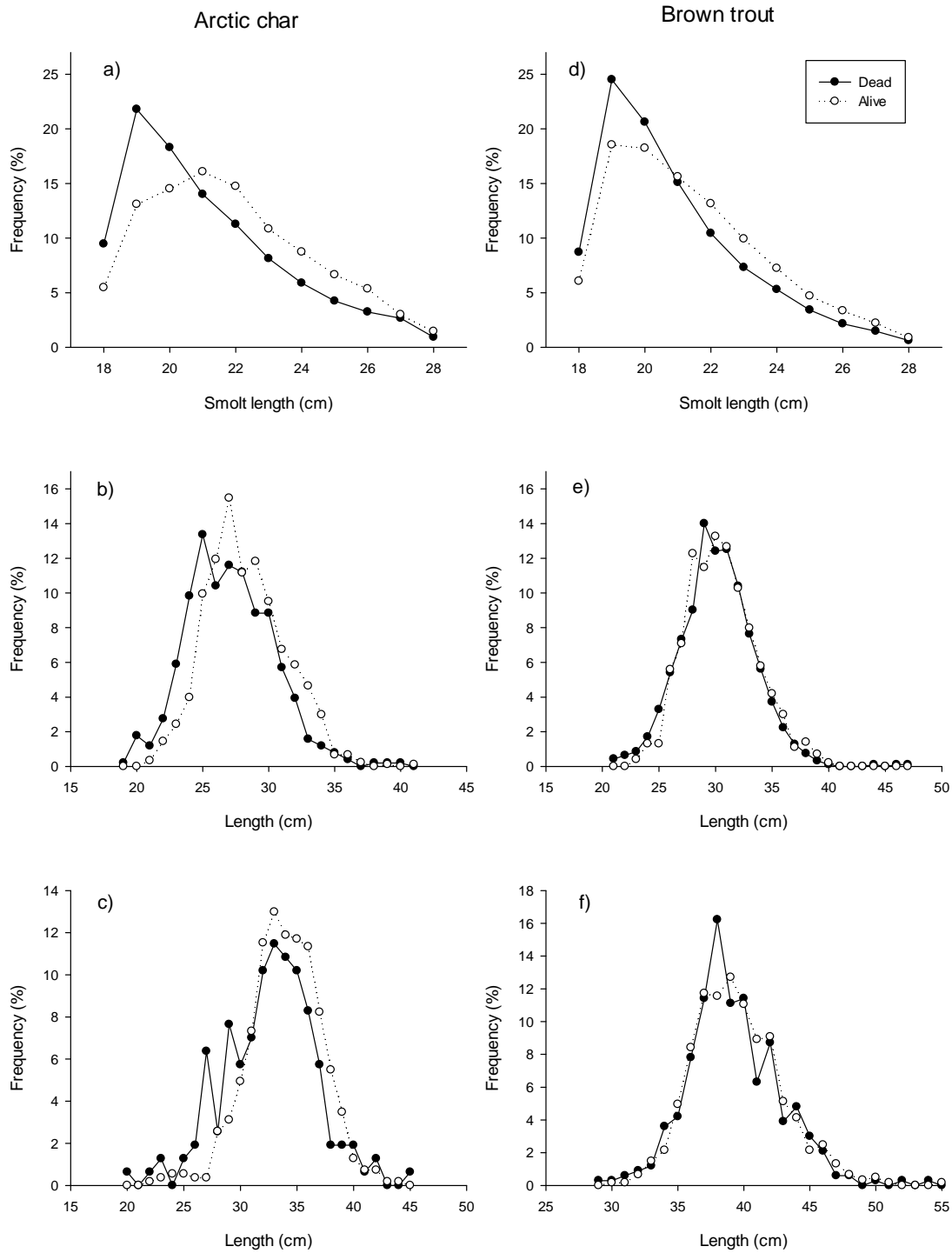
565 **Fig. 4.** Frequency distribution of mass increment (g) during the summer sea sojourn of
566 individuals that survived the following winter (○) and those that died during the winter (●) for
567 Arctic char during their a) first, b) second, and c) third sea sojourn, and brown trout during
568 their d) first, e) second, and f) third sea sojourn. Pooled data for the period 1988–2012.



570

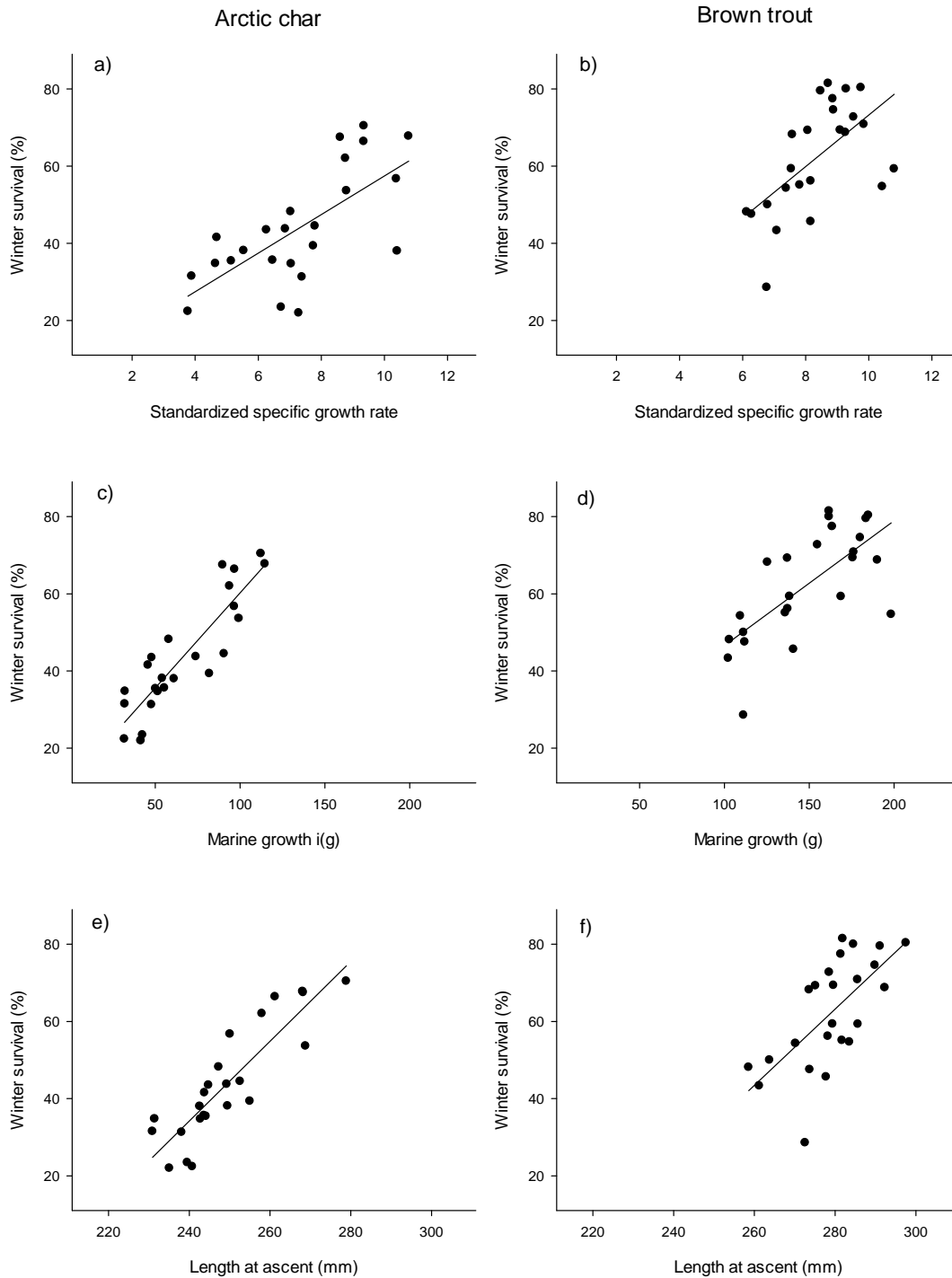
571 **Fig. 1.** Map of the study area, with the location of the fish traps in the River Halselva for

572 trapping of all ascending and descending fish.



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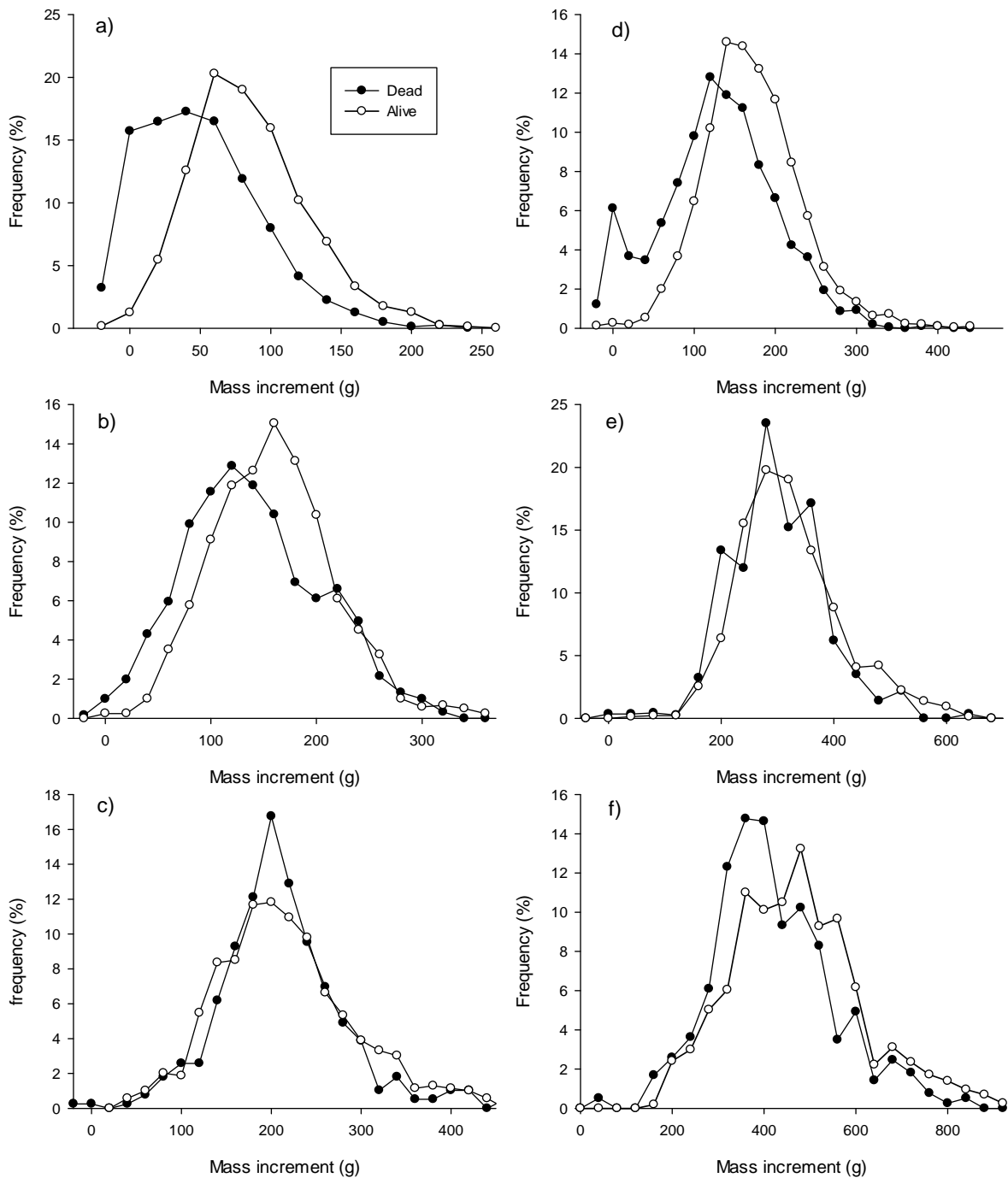
574 **Fig. 2.** Length distribution of Arctic char and brown trout at their entrance to the sea,
 575 separated between those that died during the subsequent sea sojourn (●), and those that were
 576 still alive after the sea sojourn (○). Arctic char at their a) first, b) second, and c) third summer
 577 at sea, and brown trout at their d) first, e) second, and f) third summer at sea. Pooled data for
 578 the period 1988–2012.



579

580 **Fig. 3.** Relationship between mean standardized specific growth rate (Ω , % d^{-1}) during the first
 581 sea sojourn and fresh water survival (%) during the following winter for a) Arctic char ($y =$
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 583 0.360 , $F_{1,22} = 12.37$, $P = 0.002$); relationship between mean total growth increment (g) during
 584 the first sea sojourn and fresh water survival (%) during the following winter for c) Arctic

585 char ($y = 0.49x + 11.0$, $r^2 = 0.784$, $F_{1,22} = 79.69$, $P < 0.001$) and d) brown trout ($y = 0.32x +$
586 14.2 , $r^2 = 0.482$, $F_{1,22} = 20.48$, $P < 0.001$); and relationship between mean length (mm) at
587 ascent to the river after the first sea sojourn and fresh water survival (%) during the following
588 winter for e) Arctic char ($y = 1.03x - 214$, $r^2 = 0.763$, $F_{1,22} = 70.70$, $P < 0.001$) and f) brown
589 trout ($y = 0.987x - 213$, $r^2 = 0.445$, $F_{1,22} = 17.66$, $P < 0.001$).



590

591 **Fig. 4.** Frequency distribution of mass increment (g) during the summer sea sojourn of
 592 individuals that survived the following winter (○) and those that died during the winter (●) for
 593 Arctic char during their a) first, b) second, and c) third sea sojourn, and brown trout during
 594 their d) first, e) second, and f) third sea sojourn. Pooled data for the period 1988–2012.