Abstract—We conducted laboratory starvation experiments on juvenile chum salmon (*Oncorhynchus keta*) captured in the neritic marine waters of northern Southeast Alaska in June and July 2003. Temporal changes in fish energy density (whole body energy content [WBEC], cal/g dry weight), percent moisture content, wet weight (g), length (mm), and size-related condition residuals were measured in the laboratory and were then compared to long-term field data. Laboratory water temperatures and salinities averaged 9°C and 32 psu in both months. Trends in response variables were similar for both experimental groups, although sampling intervals were limited in July because fewer fish were available (n=54) than in June (n=101). Overall, for June (45-d experimental period, 9 intervals), WBEC, wet weight, and condition residuals decreased and percent moisture content increased, whereas fork length did not change. For July (20-d experimental period, 5 intervals), WBEC and condition residuals decreased, percent moisture content and fork length increased, and wet weight did not change. WBEC, percent moisture content, and condition residuals fell outside the norm of long-term data ranges within 10–15 days of starvation, and may be more useful than fork length and wet weight for detecting fish condition responses to suboptimal environments.

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Effects of starvation on energy density of juvenile chum salmon (*Oncorhynchus keta*) captured in marine waters of Southeastern Alaska

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Energy density is an important measure of fish nutritional condition and is used to assess growth, construct energy budgets, and measure energy flow in ecosystems (Brett et al., 1969; Jobling, 1994; Ban et al., 1996; Edsall et al., 1999). Energy density is also a critical parameter for bioenergetic models (Orsi et al., 2004; Trudel et al., 2005; Wuenschel et al., 2006; Breck, 2008). Along with other measures of fish condition, such as body composition, growth, and length-weight condition indices, energy density integrates and reflects the history of fish feeding environments before the time of sampling (LeBrasseur, 1969; Edsall et al., 1999; Breck, 2008). During good feeding periods, fish condition will be high, whereas the reverse is expected during poor feeding periods as energy reserves are depleted to maintain standard metabolic needs (Jobling, 1994). However, an examination of how quickly energy density responds during periods of poor feeding that are usually associated with low growth has been limited to a few studies. In general, a balanced energy budget is expressed as the equation: *ingestion* = *metabolism* + *growth* + *excretion*, which outlines how an energy source is used by an organism and what proportion is allocated to each component of the equation (Jobling, 1994; Brett, 1995). These allocations depend on the initial amount of energy, as well as the environmental conditions that affect physiological rates, such as temperature and salinity (Brett et al., 1969; Hoar, 1988; Jobling, 1994). When fish are starved, growth typically ceases and energy density declines; when energy stores are used, the percentages of fat and protein in the fish decrease as the relative water content increases (Brett, 1995; Breck, 2008). Changes in fish energy density may be more detectable on small scales than other fish parameters, such as growth, during periods of poor feeding conditions in marginal habitats.

Juvenile Pacific salmon (*Oncorhynchus* spp.) use transitional habitats along their seaward migration from near shore to the open ocean and can experience rapid environmental changes that may affect growth and energy allocation (Orsi et al., 2000; Cross et al., 2008). Fish transit these demanding environments at the same time that they are experiencing increasing energy demands while undergoing ontogenetic changes in metabolic rate related to salinity and smoltification (Hoar, 1998). These transitional habitats are presumed to be critical feeding areas because prey fields also change dramatically, and juvenile salmon are often found in the presence of planktivorous forage fish species that potentially impact carrying capacity (Purcell and Sturdevant, 2001; Park et al., 2004; Orsi et al., 2004). Therefore, understanding how changes in juvenile salmon energy density reflect habitat quality may give insight into factors that affect their growth and survival, particularly if food resources may be limited during this critical time in their life history (Paul and Willette, 1997; Boldt and Haldorson, 2004; Cross et al., 2008).

We initiated a study to measure changes in condition of juvenile chum salmon (*O. keta*) captured at sea and later denied food resources in the laboratory. In previous studies on fish starvation, juvenile chum salmon were reared entirely in the laboratory (LeBrasseur, 1969; Akiyama and Nose, 1980; Murai et al., 1983; Ban et al., 1996); however, in our study they experienced variable environmental conditions at sea before being captured and transported back to the laboratory. Thus, these salmon from field collections represent natural variation of fish in marine waters better than fish reared in controlled laboratory environments. Our primary objective was to measure changes in energy density, moisture content, weight, length, and a size-related condition residual index for field-caught juvenile chum salmon in response to starvation in the laboratory over time. We also compared the condition of these experimentally starved fish to that determined from a long-term data series on field-caught fish 1) to assess the range of normally occurring condition values and 2) to identify the length of time before experimental values fell outside the observed range.

Methods

Juvenile chum salmon for the experiments were captured in the vicinity of Icy Strait (58°N latitude, 135°W longitude) about 50 km west of Juneau, Alaska, in June and July 2003. Fish were obtained during the Southeast Alaska Coastal Monitoring (SECM) Project long-term annual survey of juvenile salmon by the Auke Bay Laboratories (ABL) aboard the NOAA ship *John N. Cobb* (Orsi et al., 2004). Juvenile chum salmon were collected from the neritic waters of Icy Strait and Upper Chatham Strait, along the primary seaward migration corridor in the northern region of Southeast Alaska (Orsi et al., 2000, 2004). Preliminary observations along this corridor showed that juvenile chum salmon exhibit approximately a five-fold increase in body length, 100-fold increase in weight, 25% increase in energy density, and more than 6% decline in body moisture content between May and September. We used fish from this locality in June and July, the periods of highest abundance and greatest interaction with other juvenile salmon species. In June, fish were captured with a Kodiak pair-trawl fished at 1 m/sec for 10 min (Mortensen et al., 2000). In July, fish were captured with a Nordic 264 rope trawl fished at 1.5 m/sec for 20 min (Orsi et al., 2000). All fish caught were immediately transferred from the trawl codend to static live tanks containing sea water. Juvenile chum salmon were then identified and sorted into flow-through "live" tanks. The sea water for the tanks was pumped from a depth of 3 m and then filtered to prevent feeding on zooplankton prey. Before transfer to the laboratory, the juvenile chum salmon were held onboard for one day in June and four days in July while the surveys were completed. To establish a baseline for the start of the starvation experiments, on the day of capture a subsample of fish were measured (fork length, FL, mm) and frozen (–5°C) for later laboratory analysis. Daily temperature and salinity measurements were recorded and averaged 11.4°C and 26.1 psu in June and 12.7°C and 23.2 psu in July.

In the laboratory, the juvenile chum salmon were placed in two living-stream tanks (Frigid Units, Inc., Toledo, OH) (200×50×48 cm) with screened baffles separating the inflow and outflow pipes. One unit was allocated the salmon captured in June; the other unit—the salmon captured in July. Ambient sea water from a 25-m depth in Auke Bay was supplied to the tanks at a rate of 3 L/min. Daily temperature and salinity measurements were recorded in the laboratory tanks and averaged 8.6°C and 31.7 psu for June and 8.6°C and 32.1 psu for July. Sea water was filtered to prevent feeding on zooplankton prey. The fish were not subjected to any strong currents that would increase activity costs. To best mimic the photoperiod in the natural environment at the time of capture, light conditions in the laboratory were set at a standard eight hours of darkness, one hour of dusk, one hour of dawn, and 14 hours of daylight. Subsamples of 10–15 fish were removed from the tank at predetermined intervals and sacrificed with an overdose of tricaine methanesulfonate (MS-222), then frozen (–5°C) individually for later size and calorimetric analyses. Fish that had died between sacrifice intervals were not included in the experiments.

Frozen juvenile chum salmon were processed for data, including energy density in terms of whole body energy content (WBEC, cal/g wet weight [WW]), dry weight (DW, mg), percent moisture content (%MC), FL, and wet weight (mg). After excising each stomach and removing and weighing its contents, we dried the fish to obtain DW (full gut minus empty gut, nearest mg) so that undigested prey would not bias the final values. Stomachs examined from fish sacrificed after the first time interval were devoid of prey and therefore stomachs were not excised in subsequent time intervals. All viscera were replaced in the body cavity before the fish were dried to a stable weight (≤5 mg change), requiring a minimum of 48 hours at 55°C. The DW was recorded and %MC of each fish was calculated as $([1 - DW/WW] \times 100)$. Each fish was homogenized with a Waring pulverizer, then finely ground with a mortar and pestle to yield a uniform powder. Susamples of 15 mg were formed into pellets with a pellet press and stored in a desiccator to prevent rehydration. A 1425 Parr micro-bomb calorimeter was used to obtain cal/g DW for each fish; this measure was converted to WBEC by multiplying by DW/WW. Estimates of WBEC from replicate subsamples were consistent (<2% coefficient of variation). To account for potential effects of size variation on WBEC and %MC, size-related condition residuals (CR) were calculated by using the ln-transformed experimental FL and WW measures for each fish. We first derived a regression equation from all paired ln-weights and ln-lengths (n=8475; ~700 per year) of field-caught juvenile chum salmon collected during June–August for the SECM project from 1997 to 2008. We then used this regression equation to predict ln(WW) for each experimental ln(FL). Finally, we obtained the CRs by subtracting the predicted ln(WW) from the observed ln(WW) (Jakob et al., 1996; Brodeur et al., 2004).

To account for potential stock-related differences in condition of the experimental chum salmon (of unknown stocks), WBEC was determined for additional field-caught fish of known stocks. Historically, between 70% and 90% of fish caught in June originated from Macaulay Hatchery (MH), whereas mixed hatchery stocks were present during July (Orsi et al., 2004). Otoliths were not retained from the fish used in the experimental groups; however, stock of origin was determined from thermal marks present on the otoliths of juvenile chum salmon captured in the study area in July and these marks indicated that the fish were from unmarked stocks (UM, presumably wild) and MH and Hidden Falls Hatchery (HF) stocks. Both hatcheries mark 100% of chum salmon released. Energy densities were determined (as described above) for these three stock groups.

One-way analyses of variance (ANOVA) were used for initial statistical analyses to compare WBEC, %MC, FL, and WW of fish across sampling intervals for each experimental group and for July stock groups. If significant differences were detected, Tukey's paired comparison tests were performed to identify the interval in which they were found. We used graphical analyses to compare the WBEC and %MC for each experimental group to the norms (one standard deviation about the mean) derived from the entire SECM field data set (1997–2008) from June and July (n=1257; WBEC: 993.4 ±72.3 and %MC: 79.4 ±1.2). The temporal data from the experiments were compared to these norms to identify the duration of starvation before the experimental measures fell outside the long-term range of field values.

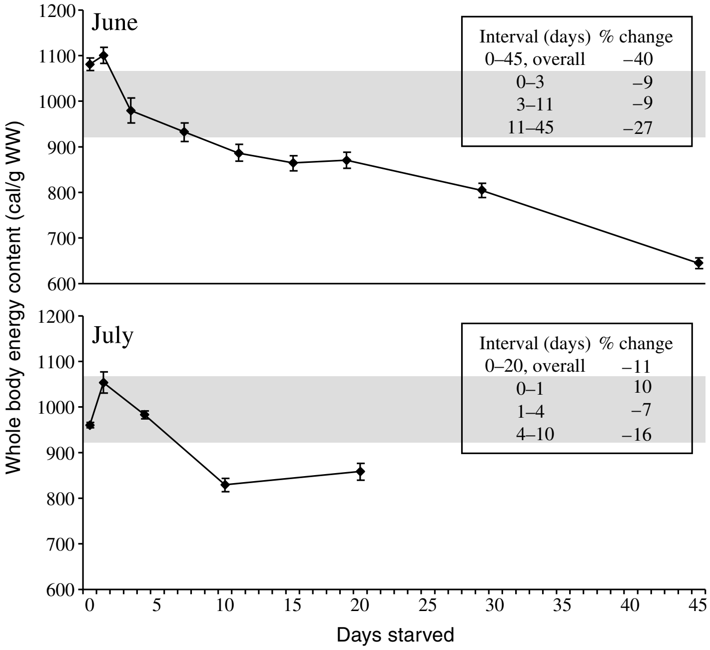

Figure 1

Average whole-body energy content (WBEC, cal/g wet weight) and one standard error about the mean for juvenile chum salmon (*Oncorhynchus keta*) starved over time in the laboratory after capture in the marine waters of Icy Strait and Upper Chatham Strait in the northern region of southeastern Alaska, June and July 2003. The grey band indicates one standard deviation about the mean for all field-caught juvenile chum salmon examined for WBEC during the Southeast Coastal Monitoring project, June–July (n=1257), 1997–2008. Significant differences (Tukey's paired comparisons; $P<0.05$) and percent change between sample intervals are shown in inset boxes.

Results

The numbers of juvenile chum salmon obtained for the two starvation trials included 101 fish for June and 54 fish for July. The higher number of juvenile chum salmon available in June allowed nine experimental time intervals to be tested, spanning 45 days (mean of five days per interval, range of 1–16 days between intervals). The smaller number of juvenile chum salmon available in July allowed only five experimental time intervals to be tested, spanning 20 days (mean of five days per interval, range of 1–10 days between intervals). Both experimental groups had common intervals at about 10 and 20 days. Mortality between sampling intervals was minimal in both groups: 13 fish died in June (70% during the first 10 days of the experiment) and two died in July (both during the first 2 days).

The energy content of juvenile chum salmon declined over time in both experimental groups (Fig. 1). Initial WBEC was significantly higher in June than in July (1081.2 cal/g WW compared to 960.5 cal/g WW; $P<0.001$). For the June sample group, WBEC decreased significantly ($P<0.001$) by 19% between days zero and 19 and by 40% between days zero and 45; see table insets in figures for significant differences (Tukey's paired comparisons) between intervals. For the July sample group, WBEC decreased significantly ($P<0.001$) by 11% between days zero and 20. Overall, the relative loss of energy content was almost twice as great in June as in July at day 20.

In contrast to WBEC, %MC of juvenile chum salmon increased over time in both

Table 1

Average fork length (FL, mm), wet weight (WW, g), percent moisture content (%MC, [(1–*dry weight*/*WW*) × 100]), and whole body energy content (WBEC, cal/g WW), for unmarked (presumably wild) and hatchery stock groups of juvenile chum salmon (*Oncorhynchus keta*) captured in the marine waters of Icy Strait and Upper Chatham Strait in the northern region of southeastern Alaska, July 2003. Standard errors are given in parentheses.

Stock group	*n*	FL	WW	%MC	WBEC
Unmarked	13	120 (1.7)	17.5 (0.8)	80.4 (0.1)	954.0 (5.7)
Macaulay Hatchery	10	137 (3.0)	29.0 (1.5)	80.3 (0.2)	957.5 (14.3)
Hidden Falls Hatchery	10	127 (2.9)	22.1 (1.6)	80.4 (0.1)	959.5 (9.6)

experimental groups (Fig. 2). Initial %MC was significantly lower ($P<0.001$) in June than in July (77.8% compared to 80.1%). For the June sample group, %MC increased significantly ($P<0.001$) by 4% between days zero and 19 and by 9% between days zero and 45. For the July sample group, %MC increased significantly ($P<0.001$) by 1% between days zero and 20. Overall, the increase in %MC was four times as great in June as in July at day 20.

Changes in the WW and FL of juvenile chum salmon over time were not consistent between the experimental groups (Fig. 3). For WW, initial values did not differ ($P>0.05$) between June and July (14.2 compared to 13.6 g). For the June sample group, WW decreased significantly ($P<0.01$) by 39% between days zero and 45. For the July sample group, no significant ($P>0.05$) differences in WW were observed. Similarly, initial FL values did not differ ($P>0.05$) between June and July (112 compared to 110 mm). For the June sample group, FL did not change significantly ($P>0.05$) between days zero and 45. For the July sample group, FL increased significantly ($P<0.001$) by 19% between days zero and 20.

The CR of juvenile chum salmon became increasingly negative over time in both experimental groups (Fig. 4). Initial CRs were positive in both months, but June CRs were lower than those for July. For the June sample group, CR declined significantly ($P<0.001$) between days zero and 19 and between days zero and 45. For the July sample group, CR declined significantly ($P<0.001$) between days zero and 20. Mean CRs shifted from positive to negative after approximately 10 days of starvation in each sample group and continued to decline, indicating increasingly poor condition for a given size fish.

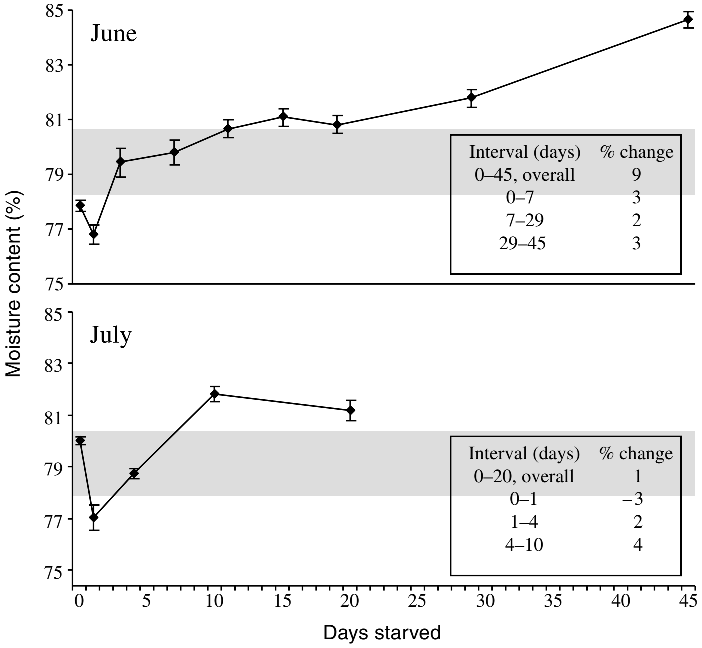

Figure 2

Average percent moisture content (%MC, [(1–*dry weight*/*wet weight*) × 100]) and one standard error about the mean for juvenile chum salmon (*Oncorhynchus keta*) starved over time in the laboratory after capture in the marine waters of Icy Strait and Upper Chatham Strait in the northern region of southeastern Alaska, June and July 2003. The grey band indicates one standard deviation about the mean for all field-caught juvenile chum salmon examined for %MC during the Southeast Coastal Monitoring project, June–July (n=1257), 1997–2008. Significant differences (Tukey's paired comparisons; $P<0.05$) and percent change between sample intervals are shown in inset boxes.

Hatchery stock group did not affect the WBEC or %MC of the July-caught juvenile chum salmon. A total of 33 fish were examined: UM (n=13), MH (n=10), and HF (n=10) (Table 1). Stock had no effect on WBEC or %MC ($P>0.05$). However, WW and FL did differ significantly ($P<0.001$) among stocks and were highest for the MH stock and lowest for the UM stock (Table 1).

Discussion

To our knowledge, this is the first published study of the change in energy density and %MC of field-captured

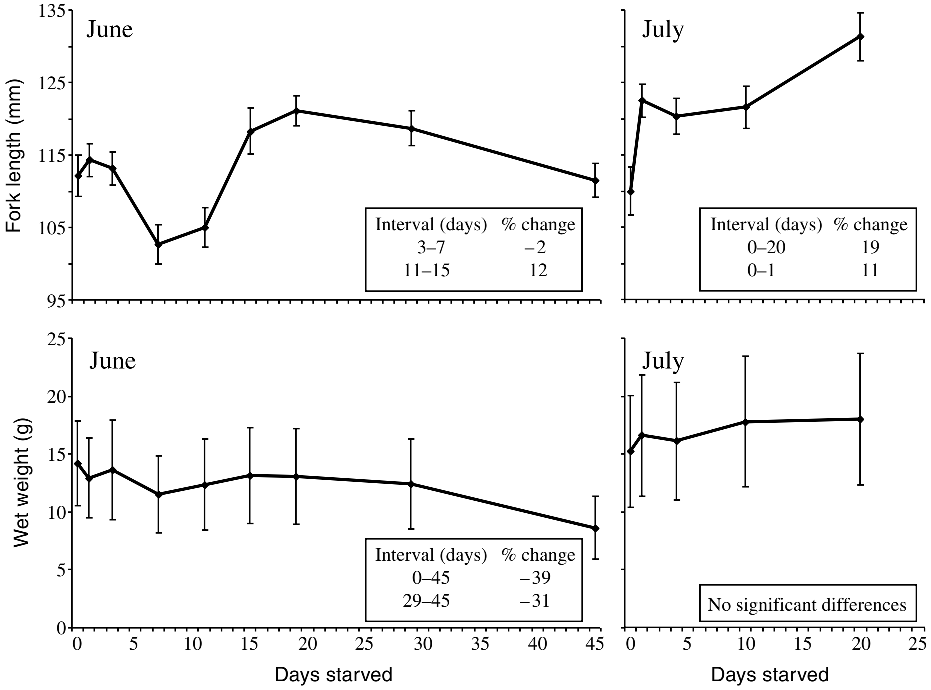

Figure 3

Average fork length (mm, top panels) and wet weight (g, bottom panels) for juvenile chum salmon (*Oncorhynchus keta*) starved over time in the laboratory after capture in the marine waters of Icy Strait and Upper Chatham Strait in the northern region of southeastern Alaska, during June (left panels) and July (right panels) 2003. Error bars are one standard error about the mean. Significant differences (Tukey's paired comparisons; $P<0.05$) and percent change between sample intervals are shown in inset boxes.

juvenile chum salmon during starvation. Limited information has been published on the changes in condition of laboratory-reared chum salmon due to starvation. Such studies typically show depletion of stored nutrients and declines in condition and size over time, despite differences in methods (LeBrasseur, 1969; Akiyama and Nose, 1980; Murai et al., 1983; Ban et al., 1996). For nutrient responses, lipid and serum protein levels of laboratory-reared juvenile chum salmon were lowest after 10 and 20 days of starvation, respectively (Ban et al., 1996); unfortunately, however, energy content was not determined. We did not directly measure lipid and protein, but the decline in WBEC that we observed between days zero and 10 and between days 20 and 45 in June could reflect similar declines in these nutrient measures. For condition responses, two studies showed that %MC of small starved juvenile chum salmon increased by 4.3% (41 mm and 0.45 g initial size; 42-d starvation; LeBrasseur, 1969) to 5.4% (0.26 g initial size; 28-d starvation; Murai et al., 1983) at ~15°C; another study showed that % MC of larger starved juvenile chum salmon increased by 12% (94.5 mm and 7.9 g initial size; 91-d starvation; Akiyama and Nose, 1980) at 17°C. Trends in %MC of our juvenile chum salmon were comparable despite the differences in fish size, duration of starvation, and water temperature. For size responses, weight decreased for five size-groups of juvenile chum salmon (0.46–7.95 g initial size; 5–13 wk starvation); however, the percentage weight loss decreased as fish size increased (Akiyama and Nose, 1980). These differences in weight loss among fish sizes indicate that physiological responses to starvation may vary with ontogeny.

Our results are also comparable to information available for other salmonid species and stages. For starved juvenile sockeye salmon (*O. nerka*), energy density declined more rapidly and %MC increased more rapidly with increasing temperatures (Brett et al., 1969). In our study, chum salmon in June exhibited a 40% decline in WBEC and a 9% increase in %MC after 45 days of starvation at an average temperature of ~9°C. By comparison, at similar temperatures (10°C), laboratory-reared juvenile sockeye salmon lost 37% of initial WBEC and gained 9% MC during 99 days of starvation (Table 3 in Brett et al., 1969). Such inverse relationships between fraction water and fraction lipid or energy content are often reported during starvation (Miglavs and Jobling, 1989; Simpkins et al., 2004; Breck, 2008). In a few studies, size changes similar to those that we observed have also been reported among other starved salmonids. Weight decreased for starved juvenile Arctic charr

(*Salvelinus alpinus*; Miglavs and Jobling, 1989), rainbow trout (*O. mykiss*; Simpkins et al., 2004), and Atlantic salmon (*Salmo salar*; Stefansson et al., 2009) for starvation periods of 4–6 weeks. Length and weight of small (30.1-mm and 0.14-g) sockeye salmon decreased significantly after 14–49 days of starvation in colder water (7.9°C; Bilton and Robins, 1973) than that used in our experiment. Like the salmonids in the above studies, weight of our juvenile chum salmon decreased for the June experimental group, but similar conclusions about the July fish could not be reported because of the shorter experimental period.

The chum salmon caught in June initially had approximately 11% higher WBEC and approximately 3% lower %MC than fish caught in July—differences that could be accounted for by both environmental and biological variables. In both the June and July experimental groups, a measurable increase in WBEC and decrease in %MC occurred between days zero and one. These changes may have been attributed to a physiological stress response that caused the fish to lose water and therefore increased the relative WBEC and decreased the %MC (Breck, 2008). Temperature and salinity both affect fish physiological rates and influence ingestion, metabolism, and growth (Brett et al., 1969; Mason, 1974; Sheridan et al., 1983; Jobling, 1994; Weatherley and Gill, 1995). In our study, field temperature was cooler and salinity was higher in June (11°C; 26 psu) than in July (13°C; 23 psu), but fish captured in both months were transferred into identical, colder (9°C) and more saline (32 psu) environments in the laboratory. Monthly differences in temperature and salinity were therefore eliminated as variables in the experiments. However, the fish captured in June had probably smolted more recently (Zaporozhec and Zaporozhec, 1993; Hoar, 1998) and spent less time in the marine environment, and probably had lower growth rates (Orsi et al., 2000) and energy requirements than fish captured in July, when it was warmer.

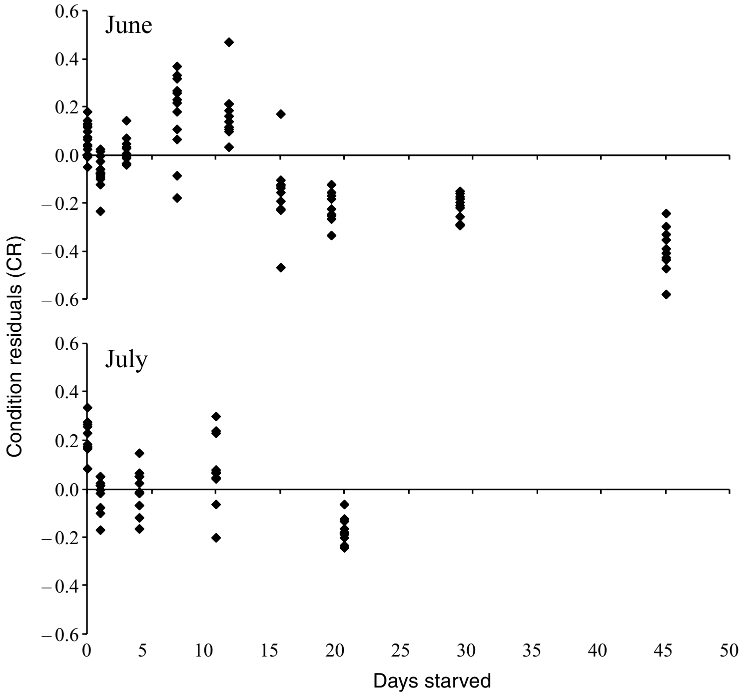

Figure 4

Condition residuals (CR) for individual juvenile chum salmon (*Oncorhynchus keta*) starved over time in the laboratory after capture in the marine waters of Icy Strait and Upper Chatham Strait in the northern region of southeastern Alaska, June and July 2003. The CRs were calculated by using the ln-transformed experimental fork length and wet weight measures for each fish in a regression equation derived from all paired ln-weights and ln-lengths of field-caught juvenile chum salmon collected during the Southeast Coastal Monitoring project, June–August (n=8476) from 1997 to 2008. The 0.0-line represents the expected CR of an average fish; therefore, positive values indicate above average condition and negative values indicate below average condition.

We accounted for potential size-related effects on WBEC and %MC by using length-weight regression analysis, which corrected for natural variation in fish size; however, the results may still be misleading because this regression did not account for differences in actual nutritional status or body composition, such as protein, lipid, and water content (Miglavs and Jobling, 1989; Edsall et al., 1999; Kotiaho, 1999; Trudel et al., 2005; Congleton and Wagner, 2006). Length-weight regression analysis is useful for initially identifying condition in relation to a long-term index and to anticipate trends in energy density, but to account for changes in nutritional status or body composition WBEC, %MC, or proximate composition, should be used to verify the CR results.

In our study, stocks of juvenile chum salmon sampled from the same habitat did not differ in WBEC or %MC, but size did differ significantly. By comparison, for juvenile pink salmon (*O. gorbuscha*) captured together in marine habitats of Prince William Sound, Alaska, differences in length and WBEC between stock groups have not been consistent (Paul and Willette, 1997; Boldt and Haldorson, 2004; Cross et al., 2008). For fish ~80 mm in length, the occurrence of length differences between juvenile pink salmon stocks depended on the size of hatchery fish at time of release (Cross et al., 2008). In a concurrent study, juvenile pink salmon length differed between stock groups, but WBEC did not (Boldt and Haldorson, 2004). Conversely, energy content (somatic) of smaller juvenile pink salmon (~35 mm) did differ between stock groups (Paul and Willette, 1997).

These studies, along with ours, support the idea that different stock groups of juvenile salmon may have similar WBEC in common habitats despite stock-specific size differences, and thus emphasize the importance of habitat quality on fish condition. These different results could also be related to ontogenetic changes in physiology (Hoar, 1998; Wuenschel et al., 2006).

Because so little mortality occurred within each experimental group, we conclude that juvenile salmon can survive for prolonged periods without food during the summer months, as has also been reported by Stefansson et al. (2009). Most of the mortalities occurred within the first eight days of the June experiment. As discussed previously, the June fish were younger and less robust (lower CR) and could have been more susceptible to environmental stresses because of scale loss (Bouck and Smith, 1979) from net abrasion during capture, for example. However, even though juvenile chum salmon were still alive after 45 days of starvation, many salmonids cannot recover physiologically after extended periods of starvation because of compromised seawater tolerance or impaired compensatory growth (Bilton and Robins, 1973; Ban et al., 1996; Stefansson et al., 2009); such recovery capabilities in juvenile chum salmon remain unclear.

The experimental WBEC, %MC, and CR differed from the long-term average of the SECM data sets during both months. After about 10 days of starvation, WBEC was below the normal range, %MC was above the normal range, and CR shifted from positive to negative, in both months. More specifically, by day 20, the June fish had lost twice their WBEC and CR, and had gained four times %MC as the July fish. The WBEC of the June fish required only 3–7 days of starvation before dropping to the lower initial level of the July fish.

Our study on the effects of starvation on field-caught juvenile chum salmon indicates that WBEC, %MC, and CR are more responsive measures than WW and FL to prolonged food deprivation in a controlled laboratory environment. Although starvation is an extreme case of limited food resources, clearly juvenile chum salmon can survive these conditions for extended periods, but may consequently be less tolerant of variable environmental conditions and more susceptible to other sources of mortality, such as predation. Future studies will focus on monitoring the seasonal response of juvenile salmon condition measures, such as WBEC, %MC, and CR, in different habitats at sea.

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