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[Article]

Buoyancy Regulation by Hatchery and Wild Coho Salmon during the Transition from Freshwater to Marine Environments

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Abstract.—One aspect of diadromy that has received little attention is buoyancy regulation in fish moving between freshwater and marine environments. Because of density differences between the two water types, fish must alter their whole-fish density (WFD) or they will become positively (float) or negatively (sink) buoyant as they change environments. This idea was first suggested over 80 year ago but has been largely overlooked by the scientific community. To explore how fish regulate buoyancy during this important transition, I measured WFD and lipid levels and estimated swim bladder volumes (SBVs) of juvenile coho salmon *Oncorhynchus kisutch* collected from freshwater and marine environments. These fish exhibited increased WFD with increasingly dense environments, suggesting active buoyancy regulation. Most of the WFD increase was attributable to decreases in SBV, although hatchery coho salmon also exhibited decreased lipid levels with increasing WFD. Hatchery coho salmon had significantly higher lipid levels than wild coho salmon in both freshwater and marine environments. These high lipid levels may impede the ability of hatchery fish to regulate buoyancy and may increase their vulnerability to surface predators. Furthermore, lipid levels that vary with both environmental water density and fish origin clearly complicate the interpretation of this variable during the important transition from freshwater to the ocean.

Buoyancy, defined as the density of an organism relative to its environment, is clearly important for fish, as indicated by their physical adaptations and behavior. Fish regulate their buoyancy by adjusting either swim bladder volume (SBV) or somatic lipid stores (in deposits throughout the body) because both substances are less dense than water (Pelster 1998; Phleger 1998). Many buoyancy-related adaptations have been documented in fishes (e.g., Jones and Marshall 1953; Love 1980; Pelster 1998). For example, fish inhabiting low-density freshwater typically have larger swim bladders than fish in dense marine environments. Bottom-dwelling fishes often lack swim bladders, while fish that making extensive vertical migrations frequently rely on lipid rather than gas for buoyancy regulation, because lipid is less compressible and because gas secretion–absorption in physoclistous fishes (those with no connection between the swim bladder and gut) is too slow to allow for rapid adjustments (Harden Jones and Scholes 1985; Parker et al. 2006). Seasonal or stage-specific changes in buoyancy have also been documented. For instance, juvenile Atlantic salmon *Salmo salar* become more buoyant as they transition from bottom-dwelling parr to actively migrating smolts (Saunders 1965; Pinder and Eales 1969), and the buoyancy of eggs and larvae of many marine fishes change with developmental stage (Sclafani et al. 1997; Kitajima et al. 1998; Ådlandsvik et al. 2001).

Fish also adjust their buoyancy at shorter time scales ranging from minutes to days. In response to perceived predation risk, surface-dwelling fish can rapidly become negatively buoyant by ejecting gas from the swim bladder (gas spitting) as a predator avoidance technique (Verheijen 1962). When stream velocity was experimentally increased, bottom-dwelling Atlantic salmon parr decreased their SBVs to become more negatively buoyant (Neave et al. 1966; Sosiak 1982). In response to implantation of negatively buoyant weights, Chinook salmon *Oncorhynchus tshawytscha* increased SBV to maintain preferred buoyancy (Perry et al. 2001). In a similar experiment, spiny dogfish *Squalus acanthias* fitted with weights compensated by increasing levels of buoyant liver lipids (Malins and Barone 1970).

Because of the density differences between freshwater and marine environments, diadromous fish are faced with a unique buoyancy challenge as they move between these environments. Fish that are neutrally buoyant in freshwater will be positively buoyant (float) in salt water because the latter is more dense; fish moving from salt water to freshwater will become negatively buoyant (sink). This buoyancy challenge was first recognized by Taylor (1921) for adult Atlantic salmon returning to freshwater, although he failed to provide observational data to indicate whether or how fish made buoyancy adjustments. Taylor's (1921) ideas have been largely forgotten by the scientific commu-

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nity as an obstacle to diadromy (Hoar 1976; Dadswell et al. 1987; McDowall 1988; Groot et al. 1995).

Lipid is also important for energy storage in fishes. High lipid stores may be seasonally important for survival, especially during winter, when food supplies are limited (Burrows 1969; Beamish et al. 2004; Biro et al. 2004; Finstad et al. 2004). However, several studies have used lipid levels to represent energy reserves available to anadromous fishes during their transition to marine environments under the assumption that higher energy reserves indicate healthier fish (Paul and Willette 1997; MacFarlane and Norton 2002; Stefansson et al. 2003; Meador et al. 2006). This assumption has not been tested. In addition, significant lipid loss has been observed during smoltification in most anadromous salmonids, including Atlantic salmon (Lovern 1934; Shearer et al. 1994) and all Pacific salmon *Oncorhynchus* spp. (e.g., Parker and Vanstone 1966; Burrows 1969; Fessler and Wagner 1969; Hoar 1976; Woo et al. 1978; Akiyama et al. 1983; Sheridan et al. 1985; Beckman et al. 2000). Whether this lipid loss is due to energetic demands of smoltification and downstream migration or merely results from the lipolytic nature of hormones that are active during smoltification (e.g., growth and thyroid hormones and cortisol; Folmar and Dickhoff 1980; Sheridan 1986) is unclear (Hoar 1976; McCormick and Saunders 1987). Fish exposed to salt water also undergo rapid lipid mobilization, resulting in decreased lipid levels (Daikoku et al. 1982; Sheridan 1988). Clearly, many factors affect lipid levels during the transition to marine habitats.

I studied juvenile coho salmon *O. kisutch* to address two questions concerning buoyancy regulation as fish move from freshwater to marine environments: (1) does whole-fish density (WFD; fish weight per volume) increase with increasing environmental water density, and (2) do fish achieve a WFD increase by decreasing SBV, lipid, or both? To answer these questions, the WFD, SBV, and lipid content of both hatchery and wild juvenile coho salmon collected in freshwater and marine environments were determined. Despite publication of Taylor's (1921) paper over 80 years ago, the results presented here are the first to document how diadromous fish regulate their buoyancy during this important transition. Buoyancy regulation may be a critical yet unappreciated hurdle during the transition between freshwater and marine environments.

Methods

I determined the WFD, SBV, and lipid content of 134 coho salmon collected from freshwater and marine habitats of the Columbia River and Puget Sound in 2003 and 2004. Freshwater collections were made at Columbia River and Puget Sound hatcheries in April, and wild coho salmon were caught in rotary smolt traps on the Snohomish and Skykomish rivers (tributaries to Puget Sound) in May. Wild and hatchery coho salmon in marine environments were collected during May and June with a surface tow net (fishing to 3-m depth) deployed in nearshore areas (mean bottom depth = 10.7 m) of Puget Sound (C. Rice, National Marine Fisheries Service [NMFS], Northwest Fisheries Science Center [NWFSC], unpublished data). Similar collections were not made in marine areas adjacent to the Columbia River. This collection scheme was intended for sampling fish at representative life history stages (immediately before and after ocean entry) rather than following a single population's transition from freshwater to marine environments.

Upon collection, all fish were immediately given a lethal dose of tricaine methanesulfonate (MS-222), measured (nearest 1 mm fork length [FL]), individually bagged, and frozen (−10°C to −20°C). In the laboratory, fish were thawed, length was measured again as before, and fish were weighed (nearest 0.001 g). To minimize lipid level variation caused by differences in degree of smoltification (Hoar 1976), all fish were examined for body and fin coloration and only individuals showing advanced stages of smoltification (i.e., silvery scales, clear fins with dark outer edges, and slender body shape) were used (smolt index $\geq$ 2; Gorbman et al. 1982). The origin (hatchery or wild) of coho salmon collected in marine waters was determined based on the presence of coded wire tags or adipose fin clips associated with mass marking of hatchery fish.

Whole-fish density was estimated using the water immersion technique described by Tester (1940) and Davenport (1999); this technique was further refined with the use of an electronic balance. Other techniques (e.g., volume displaced or neutral buoyancy in known water densities) were explored, but the immersion method provided the most consistent and accurate results. Using this method, WFD (ρ_f; g/mL) was determined from each fish's weight in air (W_a) and weight in water (W_w) during suspension from the electronic balance. Water measurements were made at a depth of 0.12 m in 10°C freshwater. Whole-fish density was calculated (Tester 1940) as:

$$\boldsymbol{\rho}_f = \frac{W_a}{(W_a - W_w)/\boldsymbol{\rho}_w},$$

where ρ_w is the density of the water in which fish were suspended (0.9997 g/mL). Whole-fish density was estimated first with the swim bladder intact and again after the abdominal cavity had been opened and the

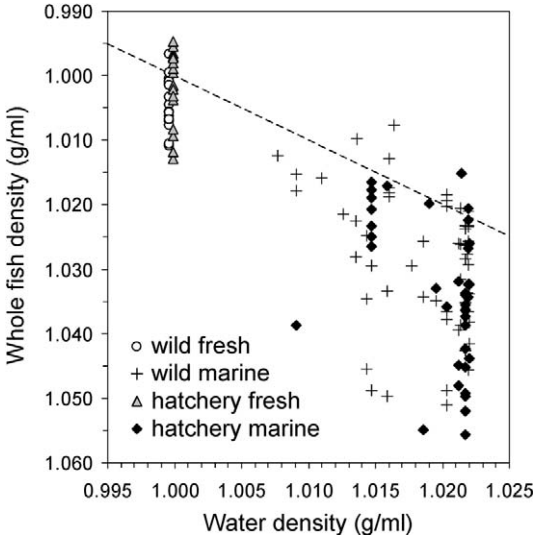

FIGURE 1.—Whole-fish density (WFD) of hatchery and wild coho salmon as a function of water density in freshwater (hatchery: Columbia River and Puget Sound hatcheries; wild: Snohomish and Skykomish rivers, Washington) and marine (Puget Sound) environments during 2003 and 2004 (WFDs in freshwater [water density = 0.9997 g/mL] are offset slightly for visual clarity). To facilitate interpretation of the data, the *y*-axis is reversed so that lower WFDs (less dense) are presented above higher WFDs (more dense). Dashed line indicates WFD equal to environmental water density; WFDs above this line indicate positive buoyancy (fish will float), and those below the line indicate negative buoyancy (fish will sink).

swim bladder had been completely deflated. The SBV (V_g, mL) was estimated from the difference between WFD measurements based on the full ($\rho_{f,\text{full}}$) and empty ($\rho_{f,\text{empty}}$) swim bladder as:

$$V_g = \frac{W_a}{\boldsymbol{\rho}_{f,\text{full}}} - \frac{W_a}{\boldsymbol{\rho}_{f,\text{empty}}}.$$

Swim bladder volume was scaled by fish weight in air (mL/g) to account for differences in fish size. Error due to surface tension or friction was assumed to be negligible; gas loss prior to or during WFD measurement with the full swim bladder was assumed to be negligible (see discussion).

After each fish was weighed in both air and water and with and without the swim bladder intact, fish were dried at 105°C for 48 h and mechanically homogenized. Whole-fish lipid levels (expressed as percent wet weight [ww]) were determined by Soxhlet extraction of dried homogenized tissue with methylene chloride (AOAC International 2002) using a 1-h reflux period.

Using a simple linear equation of state, environmental water density for fish collected in marine waters was calculated from temperature and salinity measurements made at 1-m depth immediately after each tow (Knauss 1997). Given the potentially large variation in salinity over the depth range sampled by the net (0–3 m) and the unknown depth distribution of fish within that range (C. Rice, personal communication), these environmental water densities must be viewed as approximations rather than true values of the water density experienced by the fish.

Differences in means between groups were evaluated using a one-tailed Mann–Whitney rank-sum test for differences in medians (test statistic, Z) because normality assumptions could not be met using standard transformations (Zar 1984). All regressions were ranged major axis regressions because of error in dependent and independent variables and differences in physical units between variables. Variables were ranged using $y_i' = y_i/y_{\max}$, where y_i and y_i' are the raw and transformed variables, respectively, and $y_{\max}$ is the maximum value of y_i (Legendre and Legendre 1998). Statistical significance of slopes and correlation coefficients were evaluated using 1,000 permutations (Legendre and Legendre 1998).

Results

Whole-fish densities of juvenile coho salmon increased with increasing environmental water density (Figure 1; slope = 1.915; $r^2 = 0.67$; $P < 0.01$) regardless of hatchery or wild origin. Eighty percent of the juvenile coho salmon measured had WFDs greater than the water density at the collection site (i.e., data points shown below the dashed line in Figure 1), indicating negative buoyancy. For coho salmon collected in freshwater, WFD was higher in wild fish (1.004 g/mL) than hatchery fish (1.001 g/mL; $Z = 2.1$, $P < 0.05$; Table 1). However, in marine environments, WFD was similar between hatchery (1.033 g/mL) and wild fish (1.029 g/mL; $Z = 1.5$, $P = 0.07$; Table 1). Hatchery coho salmon used in this study were significantly longer ($Z = 7.5$, $P < 0.01$) and significantly heavier ($Z = 7.1$, $P < 0.01$) than wild-origin fish, regardless of collection location (Table 1). However, WFD was not related to individual FL (slope < 0.001, $r^2 = 0.02$, $P = 0.07$) or weight (slope < 0.001, $r^2 = 0.02$, $P = 0.07$), strongly suggesting that observed differences in WFD were not due to ontogenetic changes but instead were environmentally driven.

Whether changes in WFD were due to changes in lipid levels, SBV, or some combination of the two was evaluated by considering lipid and SBV levels separately and then simultaneously with respect to fish origin and environment (freshwater or marine). Estimated SBV explained 96% of the variation in WFD (Figure 2; slope $= -1.103$, $r^2 = 0.96$, $P < 0.01$), and high explanatory power was observed for both hatchery (slope $= -1.081$,

TABLE 1.—Summary statistics (mean ± SE) for juvenile coho salmon collected from freshwater (FW; hatchery: Columbia River and Puget Sound; wild: Snohomish and Skykomish rivers, Washington) and marine (Puget Sound) environments during 2003 and 2004 (FL = fork length; ww = wet weight; WFD = whole fish density). Swim bladder gas volume (SBV) is expressed as volume of gas (mL) per weight of fish. Mean density of FW was estimated as 0.9997 g/mL; water density for hatchery and wild fish in marine environments was 1.0196 and 1.0185 g/mL, respectively.

Fish origin	Environment	n	FL (mm)	Mass (g)	Lipid (% ww)	SBV (mL/g)	WFD (g/mL)
Wild	FW	17	93.6 ± 1.8	9.6 ± 0.5	0.9 ± 0.1	0.052 ± 0.001	1.004 ± 0.001
	Marine	57	112.7 ± 2.5	18.6 ± 1.5	0.8 ± 0.1	0.032 ± 0.001	1.029 ± 0.001
Hatchery	FW	20	138.0 ± 1.5	29.9 ± 0.8	8.0 ± 0.3	0.054 ± 0.001	1.001 ± 0.001
	Marine	40	135.6 ± 3.3	29.5 ± 2.4	2.7 ± 0.3	0.027 ± 0.002	1.033 ± 0.002

$r^2 = 0.97$, $P < 0.01$) and wild coho salmon (slope = −1.140, $r^2 = 0.95$, $P < 0.01$). Mean SBV did not vary by fish origin when all fish were considered ($Z = 0.07$, $P = 0.47$), but hatchery fish had a significantly lower SBV (0.027 mL/g) than wild fish (0.032 mL/g) when only fish collected in marine waters were compared ($Z = 1.8$, $P < 0.05$; Table 1). Like WFD, SBV was independent of fish FL (slope = 0.004, $r^2 = 0.02$, $P = 0.06$) and weight (slope = 0.004, $r^2 = 0.02$, $P = 0.06$).

Lipid levels varied with WFD, environment, and fish origin (Figure 2). The relationship between lipid level and WFD (slope = −0.002, $r^2 = 0.12$, $P < 0.01$) was considerably weaker than that between SBV and WFD (Figure 2) and was due to the relatively strong lipid–WFD relationship for hatchery fish (slope = −0.004, $r^2 = 0.34$, $P < 0.01$). Wild fish did not exhibit a similarly strong lipid–WFD relationship (slope = −0.002, $r^2 < 0.01$, $P = 0.50$). Hatchery fish also had significantly higher lipid levels overall (4.5% ww) than wild fish (0.8% ww; $Z = 7.7$, $P < 0.01$) regardless of whether fish were collected in freshwater ($Z = 5.2$, $P < 0.01$) or salt water ($Z = 5.7$, $P < 0.01$; Table 1). Lipid levels also explained a significant proportion of the variation in gas-free WFD (measured with the swim bladder deflated) for hatchery coho salmon (slope = −0.001, $r^2 = 0.59$, $P < 0.01$; data not shown). Fish FL and weight explained a small amount of the variation in lipid level when all juveniles were considered ($r^2 \geq 0.1$, $P < 0.01$). However, when hatchery and wild fish were evaluated separately, this relationship dissolved ($r^2 \leq 0.02$, $P > 0.10$) because hatchery fish were larger and had higher lipid levels than wild fish (Table 1).

Finally, because both gas and lipid contributed to observed values of WFD (Figure 2), the correlation between lipid level and SBV was evaluated. When fish were examined separately based on origin (regardless of collection environment), the correlation between lipid level and SBV was significantly positive for hatchery fish (Spearman's rank correlation coefficient $r_s = 0.45$, $P < 0.01$) but not for wild fish ($r_s = -0.05$, $P = 0.66$).

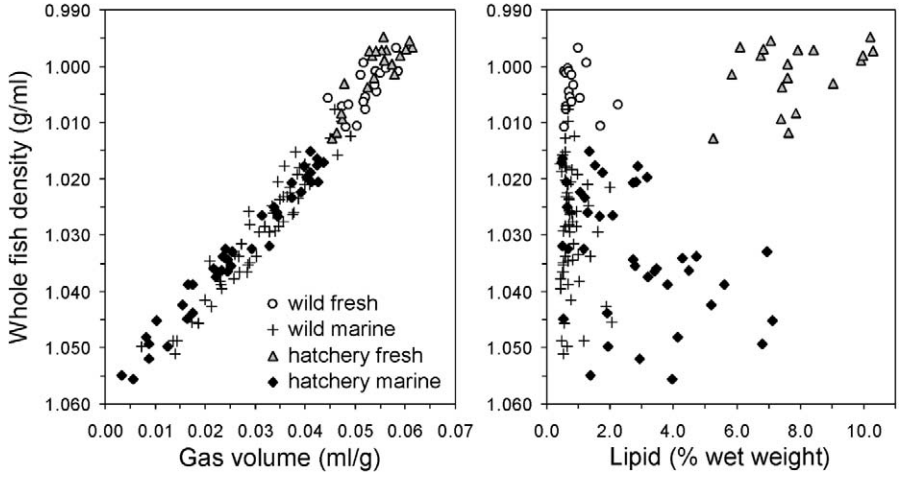

FIGURE 2.—Scatter plots of whole-fish density (WFD) in relation to swim bladder gas volume (left panel) and whole-fish lipid level (right panel) in hatchery and wild coho salmon collected from freshwater (hatchery: Columbia River and Puget Sound hatcheries; wild: Snohomish and Skykomish rivers, Washington) and marine (Puget Sound) environments during 2003 and 2004. The y-axis is reversed to facilitate interpretation (see Figure 1).

Discussion

As juvenile salmon move from freshwater to salt water, they will become positively buoyant as environmental water density increases unless they can actively increase their WFDs. The results presented here for juvenile coho salmon indicate that WFD did increase with increasing environmental water density (Figure 1) and that the fish were actively regulating their buoyancy. Both hatchery and wild coho salmon apparently achieved most of their WFD increases by decreasing SBV. This result is not surprising, given the much lower density of air (0.001 g/mL) than lipid (~0.9 g/mL), which allows small SBV changes to result in much larger WFD changes than could be achieved by similar volumetric changes in lipid. In addition, salmonids are physostomes (the swim bladder opens to the gut); therefore, changes in SBV should be nearly instantaneous relative to the period (days or weeks) required to metabolize lipid (Sheridan 1986), although salmon apparently do not make continual adjustments to SBV (Harvey 1963; Shrimpton et al. 1990a; Tanaka et al. 2001). However, some estimated SBVs were extremely low (<0.02 mL/g; Figure 2), suggesting that these fish had largely exhausted their ability to become more dense by further decreasing SBV. At this point, fish must rely solely on lipid depletion to increase WFD or on energetically expensive mechanical means (e.g., fin position and active swimming; Harvey 1963; Strand et al. 2005) to maintain preferred position in the water column.

Hatchery coho salmon had consistently higher lipid levels than wild fish; this difference was greatest in freshwater, where the mean lipid level of hatchery fish (8.0% ww) was nearly an order of magnitude higher than that of wild fish (0.9% ww; Table 1). These high lipid levels probably resulted from lipid-rich commercial feeds consumed in the hatchery during the first year of life. Dietary lipid levels directly influence fish lipid levels (Shearer et al. 1997; Molnar et al. 2006), and numerous prior studies have similarly reported that hatchery-reared fish had higher lipid levels than wild-reared conspecifics (e.g., McDonald et al. 1998; Rikardsen and Johansen 2003; Copeland and Carline 2004).

Hatchery coho salmon also exhibited marked decreases in both SBV and lipid level with increasing WFD (Figure 2). The overall decrease in lipids between freshwater and marine environments (66%) was greater than the estimated decrease in SBV between these environments (51%). By contrast, wild coho salmon exhibited a modest decline in SBV between freshwater and marine environments (39%) but a much smaller decline in lipid level (11%), largely because wild fish had very low lipid levels in freshwater (0.9% ww). The extremely low lipid levels observed in wild coho salmon from freshwater are lower than those reported previously (1.5–3.0% ww; Vanstone and Markert 1968; Higgs et al. 1995), suggesting a more advanced state of smoltification than was reflected in the previous studies or in hatchery fish sampled during the present study (Hoar 1976). However, substituting these reported lipid values for the ones measured here still leads to the conclusion that in freshwater, hatchery fish have much higher lipid levels than wild fish.

High lipid levels observed in hatchery coho salmon may interfere with their ability to survive the critical transition from freshwater to marine environments via buoyancy-dependent or buoyancy-independent processes (e.g., physiology, development, and general health; Beckman et al. 2000). Mommsen (2001) noted that lipids are both slow to metabolize and require more oxygen for metabolism than do other energy storage substances (protein, glycogen); this is a disadvantage given the low solubility of oxygen in water. Fish compensating for positive buoyancy by moving to greater depths and therefore attaining greater compression of gas in the swim bladder (Harvey 1963; Shrimpton et al. 1990a) will be hindered by the relative incompressibility of lipid. Furthermore, recent studies have found that Caspian terns *Sterna caspia*, which are avian surface predators, prey upon hatchery Chinook salmon, coho salmon, and steelhead *O. mykiss* in preference to wild fish in the Columbia River estuary (Collis et al. 2001; Ryan et al. 2003). Like the coho salmon in the present study, these hatchery fish undoubtedly had high lipid levels after spending a year consuming lipid-rich feeds, and such directed mortality may reflect buoyancy-related vulnerabilities.

The results presented here indicate that lipid levels of anadromous salmon during the transition between freshwater and marine environments are probably influenced by a multitude of factors, including fish origin and buoyancy regulation. Consequently, using lipids levels to indicate anadromous salmon "health" during the transition to marine environments is based on the potentially faulty assumption that fish health is synonymous with high lipid reserves. My results indicate that in areas with substantial hatchery production of salmon (i.e., West Coast of North America; NRC Committtee 1996; Teel et al. 2003), lipid levels early in ocean residence are most likely influenced by juvenile salmon origin rather than health.

Sampling was not conducted in marine waters adjacent to the Columbia River but would have provided an interesting contrast to Puget Sound collections, because the freshwater layer associated with the Columbia River plume is considerably deeper

(Hickey 1989). By remaining within the plume, juvenile salmon may delay exposure to salt water, thus delaying the need for buoyancy regulation. Current sampling programs for juvenile salmon in the Columbia River plume (e.g., Emmett et al. 2004; De Robertis et al. 2005) are insufficient for determining whether salmon use the plume as a buoyancy refuge or instead rapidly disperse to dense marine environments.

Because all fish were collected in the field, there are several limitations of the study design that probably affected measurements of environmental water density, WFD, and SBV. However, these limitations are not expected to alter the finding that juvenile coho salmon were regulating their buoyancy. For example, all juveniles were collected at or near the surface, although the actual depth of marine collections (between 0 and 3 m) was not known. Although I measured environmental water density at 1 m, juvenile coho salmon probably experienced water densities ranging from those of freshwater at the surface to full-strength salt water at 3 m; salinity changes greatly with Puget Sound depth in association with high spring freshwater runoff (Kozloff 1983). Better knowledge of true environmental water density affects measurement of buoyancy (i.e., whether a fish floats or sinks) but has little influence on WFD itself.

The depth of collection does, however, affect measurement of WFD and SBV due to expansion or contraction of gas in the swim bladder with changes in pressure (depth) and (to a lesser extent) temperature, following the ideal gas law. In the most extreme case, a juvenile coho salmon collected at 3-m depth (the bottom of the collection net) in pure salt water and immersed at a depth of 0.12 m in pure freshwater (for WFD measurement) at constant temperature would have had a greater SBV due to gas expansion than it did at the collection depth. Assuming that the swim bladder was sufficiently elastic to hold the extra volume (Shrimpton et al. 1990a), this gas expansion would have resulted in a 22% overestimate of SBV as measured. If this is the case, differences in WFD between fish inhabiting freshwater and marine environments should be even greater than those reported here (Table 1).

Another limitation is the assumption that (1) gas did not escape from the swim bladder prior to measurement of WFD or (2) any escape of gas was equally likely for all fish and therefore was not responsible for the differences in SBV and WFD between fish collected from freshwater and marine environments (Figures 1, 2). As discussed above, juvenile coho salmon collected in marine environments probably experienced gas expansion as they were brought to the surface. However, accounting for this expansion (assuming that *all* marine fish were at 3-m depth when collected) results in a mean SBV that is still lower (0.037 mL/g) than that measured for freshwater collections (0.053 mL/g). In addition, swim bladder pressure required for gas release is inversely proportional to pneumatic duct diameter and, thus, to fish size; considerably more pressure is required before gas escapes from small fish (like those used here) than from large fish (Shrimpton et al. 1990b). These patterns suggest that while the escape of gas from the swim bladder may have added noise to the measurements of WFD and SBV, it probably was not responsible for the observed differences between fish collected from freshwater and marine environments. Clearly, laboratory experiments would clarify the influence of these factors.

In summary, juvenile coho salmon appear to actively regulate their buoyancy as they move from freshwater to marine environments. Although most of this buoyancy regulation is attributable to decreased SBV, hatchery coho salmon also exhibited proportionally large lipid reductions with increasing WFD and had much higher lipid levels than wild fish regardless of the type of environment they inhabited. Inability to lose this lipid may interfere with the ability of hatchery fish to successfully transition to marine environments. These findings suggest that further investigation of buoyancy regulation in diadromous fishes is warranted.

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