

# Interacting effects of behavior and oceanography on growth in salmonids with examples for coho salmon (*Oncorhynchus kisutch*)

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**Abstract:** Positive and negative relationships between pre- and post-smolt growth rates in salmonids have been observed, but the mechanisms underlying these relationships are not understood. We hypothesize that growth at sea is controlled by interactions between behavior and ocean conditions and that no one relationship is correct. We present a growth model with habitat-specific rates of anabolism that allow resource acquisition to vary in response to the behavior–environment interaction. Our model predicts positive relationships between pre- and post-smolt growth rates when ocean resources have clumped, defensible distributions under which conditions that aggressive behaviors facilitate increased access to those resources. Negative relationships are predicted when resources are dispersed and aggressive behaviors are ineffective. We present data relating pre- and post-smolt growth rates for more than 15 stocks of coho salmon (*Oncorhynchus kisutch*). These data indicate that shortly after out-migrating, aggressive behaviors are not effective for securing resources in the ocean (i.e., there are negative or no relationships between pre- and post-smolt growth rates). As coho spend more time at sea, however, variability in environmental conditions can elicit a variety of growth responses.

**Résumé :** Il est possible d'observer des relations positives et des relations négatives entre la croissance des présaumoneaux et celle des postsaumoneaux, mais les mécanismes sous-jacents à ces relations ne sont pas connus. Nous posons en hypothèse que la croissance en mer est contrôlée par les interactions entre le comportement et les conditions océaniques et qu'aucune relation particulière n'est la bonne. Nous présentons un modèle de croissance avec des taux d'anabolisme spécifiques aux habitats qui permet à l'acquisition de ressources de varier en fonction de l'interaction comportement–environnement. Notre modèle prédit des relations positives entre les taux de croissance des présaumoneaux et des postsaumoneaux lorsque les ressources océaniques ont des répartitions contagieuses et défendables et que les comportements d'agressivité facilitent un accès accru à ces ressources. Il prédit des relations négatives lorsque les ressources sont dispersées et que les comportements agressifs sont inefficaces. Nous présentons des données qui mettent en relation les taux de croissance des présaumoneaux et des postsaumoneaux chez 15 stocks de saumons coho (*Oncorhynchus kisutch*). Ces données indiquent que, peu après l'émigration vers l'océan, les comportements agressifs ne sont pas efficaces pour procurer les ressources océaniques (c.-à-d., les relations entre les taux de croissance des présaumoneaux et des postsaumoneaux sont négatives ou nulles). À mesure que les saumons coho passent plus de temps en mer, la variabilité des conditions du milieu peut provoquer une variété de réponses de croissance.

[Traduit par la Rédaction]

## Introduction

The link between individual growth rates and age at maturity in salmonids is well established (e.g., Skilbrei 1989; Nieceza and Braña 1993), but conflict exists regarding the relationship between freshwater and salt-water growth performance. When smolt age is controlled for, positive rela-

tionships between smolt length and subsequent growth in salt water have been found for Atlantic salmon (*Salmo salar*; Skilbrei 1989; Friedland and Haas 1996), Chinook salmon (*Oncorhynchus tshawytscha*; Heath et al. 1996), and steelhead trout (*Oncorhynchus mykiss*; Johnsson et al. 1997). Negative relationships have been found for Atlantic salmon (Nieceza and Braña 1993) and coho salmon (*Oncorhynchus*

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*kisutch*; Johnsson et al. 1997). Even the absence of such a relationship has been found for Atlantic salmon (Nicieza and Braña 1993). The strengths and signs of these correlations are important at the population level because fast-growing fish typically mature at younger ages and smaller sizes. To our knowledge, this conflict has yet to be resolved.

In fresh water, links have been found between behavior and growth rates. Studies of Atlantic salmon have shown that fry with high standard metabolic rates rank high in dominance status and have higher growth rates (Huntingford et al. 1990; Metcalfe et al. 1995). Wild coho salmon parr with high dominance status defend territories, acquire more resources, and grow faster than less dominant individuals (Puckett and Dill 1985; Nielsen 1992; Martel 1996). Ultimately, dominant individuals have the potential to be the longest smolts (Martel 1996).

In salt water, the relationship between behavior and growth rate is less obvious. Aggressive behaviors in coho salmon may remain after the smolt transformation and possibly result in dispersed distributions at sea (Paszowski and Olla 1985; Jaenicke and Celewycz 1994), but other species of Pacific salmon are more aggregated during their ocean residence (e.g., Jaenicke and Celewycz 1994; McKinnell et al. 1997). Ultimately, growth rates at sea will depend on behavior and its interaction with resource distribution (e.g., Paszowski and Olla 1985; Martin-Smith and Armstrong 2002; Vøllestad and Quinn 2003).

Here, we illustrate how the conflicting relationships between freshwater and salt-water growth rates of salmonids can be explained by a growth model that parameterizes the behavior–environment interaction. We show how the effectiveness of aggressive behaviors for food acquisition and growth can vary both with environmental conditions in the ocean and with fish length. When environmental conditions cause resources to be relatively well mixed, energy expended through aggressive behaviors will lead to decreased growth rates; the reverse is predicted when environmental conditions cause resources to be clumped. We illustrate these interactions by constructing a growth model for coho salmon. We present data that provide information on the relationships between freshwater and salt-water growth performance of coho from British Columbia, Washington, Oregon, and California. We compare predictions from our model to these data and make inferences about how aggressive behaviors and resource distribution interact to influence growth at sea.

## Materials and methods

### The von Bertalanffy growth function (VBGF)

The metabolic growth model refined by von Bertalanffy (1938) describes changes in body mass ( $dW/dt$ ) from the difference between anabolism (energy gain) and catabolism (energy loss):

$$(1) \quad \frac{dW}{dt} = HW^m - cW^n$$

where  $W$  is body mass;  $t$  is time;  $H$  is the coefficient of anabolism; and  $c$  is the coefficient of catabolism. The exponents  $m$  and  $n$  respectively describe the allometric scaling of energy gain and loss.

We reformulated eq. 1 in terms of length ( $L$ ) by assuming that the length–mass relationship is described by  $W = L^3$ ;  $m = 2/3$ ; and  $n = 1$ :

$$(2) \quad \frac{dL}{dt} = E - kL$$

where  $E$  is a rescaled coefficient of anabolism, and  $E = H/3$ . Similarly,  $k$  is a rescaled coefficient of catabolism, and  $k = c/3$ . The assumption that  $m = 2/3$  is based on the idea that anabolism scales with surface area. Essington et al. (2001) estimated  $m$  for a variety of marine and freshwater fishes, and almost half of the estimates fell between 0.65 and 0.85. Essington et al. (2001) estimated a mean  $m$  of 0.77. Qualitative predictions from eq. 1 are robust to changes in  $m$  over the range (0.65, 0.85), and for mathematical convenience, we used the convention  $m = 2/3$ . The assumption that  $n = 1$  is based on the idea that catabolism scales with volume; Essington et al. (2001) found that this convention is reasonable.

Integrating eq. 2 identifies the more common, mathematical interpretation of  $k$  as a growth coefficient describing the rate at which a fish approaches its asymptotic size. The solution of eq. 2 is

$$(3) \quad L_t = L_\infty - (L_\infty - L_0)e^{-kt}$$

where  $L_t$  is length at time  $t$ , and  $L_0$  is the initial length.  $L_\infty$  is the asymptotic size at which the growth rate is zero. From eq. 2,  $L_\infty$  can be described as

$$(4) \quad L_\infty = \frac{E}{k}$$

Although the dual interpretations of  $k$  seem confusing (i.e., a rate of catabolism in eq. 2 and a growth coefficient in eq. 3), a biological argument can be constructed to suggest that an individual's rate of energy loss may be functionally related to its rate of energy gain.  $E$  is related directly to the amount of resources available to an individual and will vary with environmental conditions and individual behavior. Higher levels of  $k$  equate to higher metabolic rates (von Bertalanffy 1938; Beverton and Holt 1959), and standard metabolic rates can be positively correlated with dominance behavior (e.g., Metcalfe et al. 1995). The effectiveness of aggressive behaviors associated with dominance status in securing more resources will depend on how environmental conditions distribute those resources in time and space (Martin-Smith and Armstrong 2002). When environmental conditions facilitate the defense of feeding territories by dominant individuals, those individuals may be able to sequester more resources and achieve increased levels of  $E$ . Under these conditions,  $E$  may be positively related to  $k$ . When conditions do not facilitate increased food acquisition by dominant individuals,  $E$  may be the same for all individuals. Under these conditions,  $E$  may be independent of  $k$ , and from eq. 2, individuals with a higher  $k$  will grow slower because they acquire the same amount of resources but have higher metabolic demands. Considering the two scenarios described here, it seems logical to describe energy gain as a function of energy loss. We explicitly accounted for such behavioral and environmental effects on growth by parameterizing  $E$  as a function of  $k$ :

$$(5) \quad E = \gamma k^\psi$$

where  $\gamma$  and  $\psi$  respectively determine the degrees to which  $E$  depends on environmental and behavioral factors, and  $0 \leq \psi \leq 1$ .

When  $\psi$  is close to 1, dominant behaviors associated with  $k$  are effective for sequestering resources from the environment. When  $\psi$  is close to 0, an individual's ability to sequester resources from the environment is controlled mostly by the environment itself. Limnologic and oceanographic processes can influence the value of  $\psi$  by making resources more or less clumped; the distribution of resources ultimately influences both their accessibility and defensibility by fishes. Similarly, growth itself can influence the value of  $\psi$ ; larger fish may have increased access to resources. Extreme parameterizations of  $E$  can be made by setting  $\psi = 1$  (i.e.,  $E$  is only determined by behavioral factors related to  $k$ ) or  $\psi = 0$  (i.e.,  $E$  is only determined by environmental conditions). Salmonids will have at least two  $E$ s, one for fresh water and one for salt water, although there may be multiple  $E$ s for the different salt-water growth stanzas.

**Application of the VBGF to coho salmon**

We described the growth of coho salmon during three stanzas (one stanza in fresh water and two stanzas in salt water) that approximate Sandercock's (1991) description of the dominant life cycle of these fish. After emergence from the gravel, growth in fresh water occurs for 12 months. We assumed that the smolt transformation occurs in month 12, and growth in salt water occurs while coho are 13–30 months old. Fish that mature early spend 6 months at sea; they experience zero sea winters and one growing season. Fish that mature late experience one sea winter and two growing seasons while spending 18 months at sea. The three growth stanzas are temporally separated by the smolt transformation and the sea winter between early and late maturation; the three stanzas are also differentiated by shifts in  $E$ .

For growth in fresh water, we considered only an extreme parameterization of anabolism. We assumed that an individual's  $k$  is determined prior to its emergence from the gravel and that  $k$  is constant throughout its life. Thus, the length of an individual at some time after its emergence from the gravel is conditioned on  $k$ , which again is directly related to metabolic rate (von Bertalanffy 1938; Beverton and Holt

1959) and indirectly related to dominance behavior (Metcalfe et al. 1995). Since the freshwater environment is heterogeneous and dominant coho parr (large individuals with higher values of  $k$ ) are more able to secure food resources (Puckett and Dill 1985; Nielsen 1992; Martel 1996), we applied eq. 5 by assuming that  $\psi = 1$  and  $\gamma_{FW} > 0$ .

$$(6) \quad E_{FW} = \gamma_{FW} k$$

The subscript FW indicates fresh water, and considering eq. 4,  $\gamma_{FW}$  is equal to the maximum length at smolt transformation. Growth through the freshwater stanza is described by substitution from eqs. 4 and 6 into eq. 3.

$$(7) \quad L_{FW}(t|k) = \gamma_{FW} - (\gamma_{FW} - L_f) e^{-kt}$$

$L_f$  is the length of a postemergent fry, and  $t$  is time (months) since emergence from the gravel. This parameterization of  $E_{FW}$  predicts a positive relationship between smolt length and  $k$  (e.g., Fig. 1).

For anabolism at sea, we used the general approach described by eq. 5.

$$(8) \quad E_{SW} = \gamma_{SW} k^\psi$$

The subscript SW identifies salt water;  $\gamma_{SW} \geq 0$ ; and  $0 \leq \psi \leq 1$ . We explored 5 alternatives: (i) aggressive behaviors associated with  $k$  are heldover from fresh water and increase access to resources in salt water, regardless of environmental conditions ( $\gamma_{SW} > 0$  and  $\psi = 1$ ), (ii) anabolism in salt water is entirely determined by environmental conditions ( $\gamma_{SW} > 0$  and  $\psi = 0$ ), and (iii–v)  $\psi = 0.75, 0.5, \text{ or } 0.25$ , and  $\gamma_{SW} > 0$ . We constrained all five alternatives by assuming that the expected value of  $E_{SW}$  is greater than the expected value of  $E_{FW}$  and that  $E_{SW} \geq kL$ . The first constraint acknowledges that a primary mechanism for the evolution of anadromy in salmonids is increased food availability at sea. Such an increase presumably allows for increased adult size and fecundity (Gross et al. 1988). The second constraint ensures non-negative growth rates. Regardless of how we characterized  $E_{SW}$ , we assumed that an individual's length after the smolt transformation remains conditioned on  $k$ .

$$(9) \quad L_{SW}(t|k) = \begin{cases} \frac{E_{sw,1}}{k} - \left( \frac{E_{sw,1}}{k} - L_{FW}(12|k) \right) e^{-k(t-12)} & \text{for } 13 \leq t \leq 23 \\ \frac{E_{sw,2}}{k} - \left( \frac{E_{sw,2}}{k} - L_{SW}(23|k) \right) e^{-k(t-23)} & \text{for } 24 \leq t \leq 30 \end{cases}$$

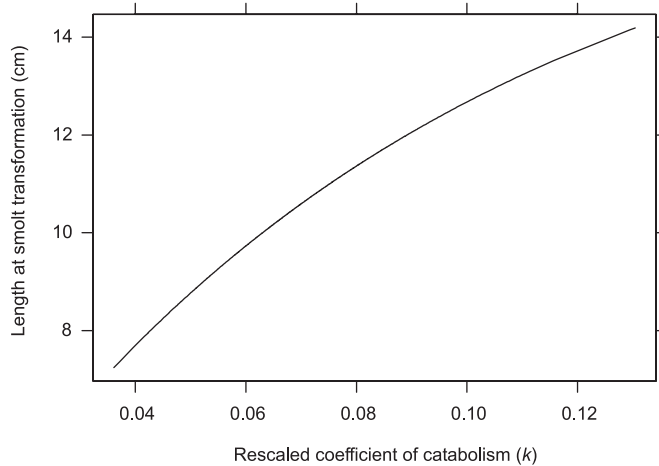
Initial length for growth during the first salt-water stanza,  $L_{FW}(12|k)$ , is the length at the smolt transformation. Initial length for growth during the second salt-water stanza,  $L_{SW}(23|k)$ , is the length at the start of the second growing season.  $E_{SW}$  is further subscripted by 1 and 2 to indicate the number of growing seasons that an individual experiences at sea.

**Net salt-water growth of coho**

We used information from Shapovalov and Taft (1954) to

obtain reasonable values for the parameters in eqs. 6–9 and simulate representative growth trajectories for coho. Note that we did not fit our growth model to the data provided by Shapovalov and Taft (1954); our intention was to describe growth patterns in general rather than to predict size at age. We fixed  $L_f$  (2 cm) and  $\gamma_{FW}$  (18 cm) and treated  $k$  as a random variable describing individual and intercohort variation in dominance status and freshwater growth performance. We found that drawing  $k$  from a gamma distribution with a mean

**Fig. 1.** The relationship between  $k$  and smolt length described by eq. 5, where smolt length is measured 12 months after emergence from the gravel.



of 0.07 and coefficient of variation (CV) equal to 0.30 predicted a distribution of smolt lengths (individuals within a cohort) that was consistent with those observed by Shapovalov and Taft (1954). Thus, we simulated intercohort variation in freshwater growth by randomly drawing mean levels of  $k$  from a normal distribution with mean of 0.07 and standard deviation (SD) of 0.01. Within cohorts, we then drew individual values of  $k$  from gamma distributions around the cohort-specific mean values of  $k$  with a fixed CV (0.30).

Each individual's  $k$  was carried over to the salt-water growth stanzas. To describe growth during the two salt-water stanzas and simulate intercohort variation in anabolism at sea, we drew  $E_{SW,1}$  and  $E_{SW,2}$  from random normal distributions with means of 6.4 and SDs of 0.5. We considered the five previously described formulations of  $E_{SW}$  to predict lengths at 13–30 months after smolt transformation. For each cohort and each parameterization of  $E_{SW}$ , we drew  $E_{SW,1}$  and  $E_{SW,2}$ , set  $k = 0.07$ , and set  $\psi = 1, 0.75, 0.5, 0.25$ , or 0. We then solved for  $\gamma_{SW}$  in eq. 8 (one solution each for  $E_{SW,1}$  and  $E_{SW,2}$ ). The net growth of each individual was estimated as  $L(18|k) - L(12|k)$  for fish that mature early and spend zero winters at sea or  $L(30|k) - L(12|k)$  for fish that mature late and spend one winter at sea. We simulated the growth of 100 individuals from each of 50 cohorts using the five parameterizations of  $E_{SW}$ .

We computed cohort-specific estimates of mean net growth and plotted these against cohort-specific estimates of mean smolt length. We used cohort-level summary statistics because the empirical data we have to compare with our model output is primarily in the form of annual averages for smolt length and for adult return lengths.

#### Data on coho salmon

We compared predictions from our model of coho growth to observations on the relationship between smolt length (an index of growth performance in fresh water) and net growth after one growing season (i.e., zero sea winters) and after two growing seasons (i.e., one sea winter). We made comparisons with observational data from the Coded Wire Tag (CWT) database (<http://www.rmis.org>), literature sources, and the University of Washington Hatchery (data provided

by A. Vøllestad and T. Quinn, Aquatic and Fisheries Sciences, University of Washington, Seattle, WA 98195, USA; Quinn et al. 2004 and Vøllestad et al. 2004 presented these same data in a different manner). We ensured that all the observational data from each source represented fish that smolted at one age (i.e., observations on age 0+ and age 1+ smolts were not mixed); this allowed us to use smolt length as a proxy for freshwater growth performance (e.g., Fig. 1).

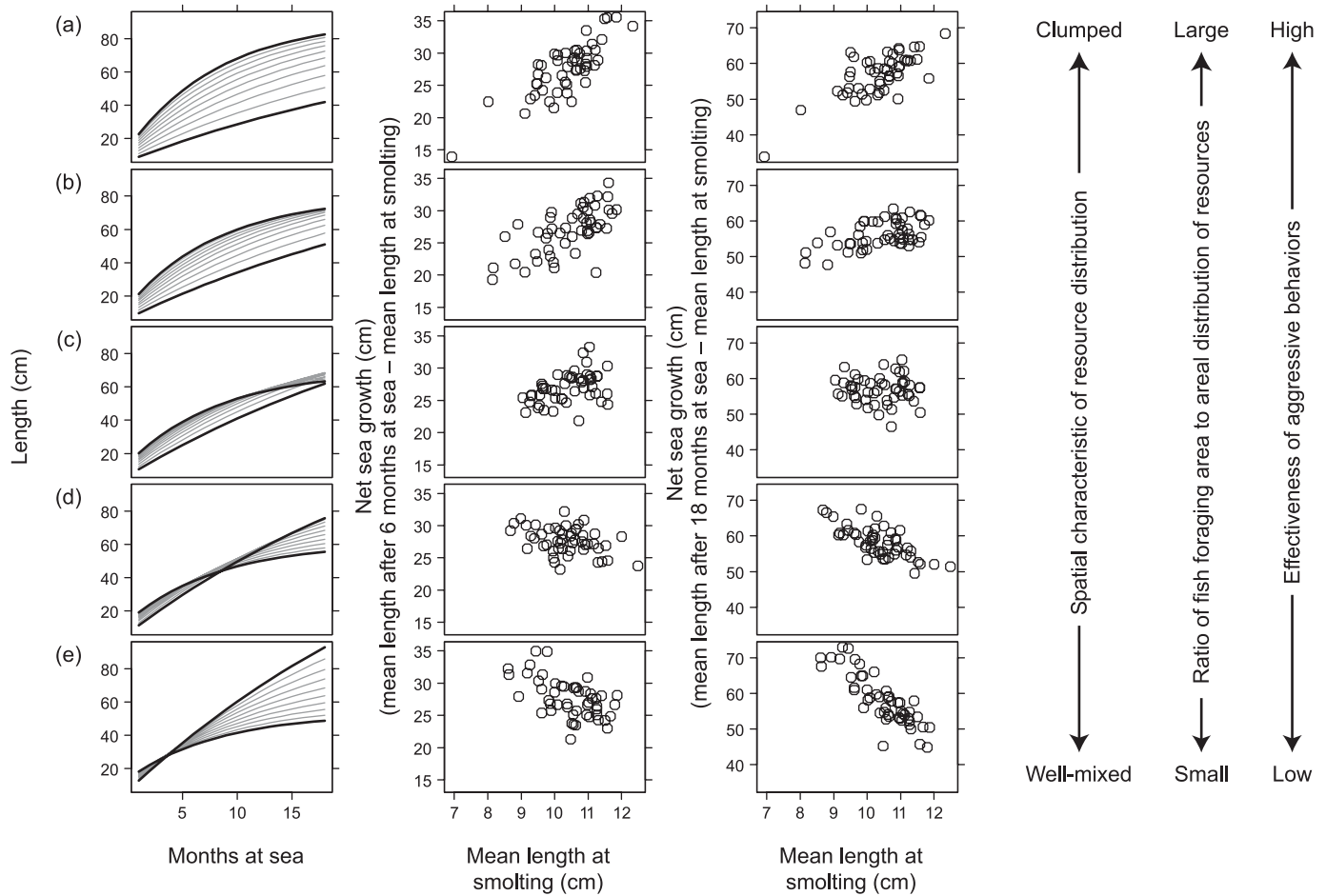
The CWT data required extensive preprocessing. We used information on coho that could reasonably be assumed to have outmigrated shortly after release by the hatcheries. We considered only those tag codes representing releases of age 1+ smolts and in which the month of release was reported to be within the range March–June for stocks from California and Oregon or April–July for stocks from Washington and British Columbia. We classified release groups as comprising age 1+ smolts when differences between reported release and brood years were equal to two. We also limited our consideration to tag codes for which the average mass of individuals within a release group was within the range 5–50 g. We converted group-specific estimates of average mass at release ( $w$ ) to estimates of average smolt length ( $l$ ) with  $l = [w/(4.36 \times 10^{-6})]^{0.31}$ . The parameters of this equation were estimated by fitting a robust regression model to data on log-release masses and log-release lengths. To fit this model, we combined data from all stocks for which we had such information. We computed return lengths and ages only for fish that were reported to have been captured in terminal fisheries or returned to hatcheries. The numbers of winters that fish spent at sea were computed as differences between reported recovery and release years, but we subtracted a year if fish were recovered during January–March. We computed age- and tag-code-specific estimates of mean length at return. These means were weighted by the estimated number of fish that each length observation (CWT recovery) represented in the total catch.

Many stocks are represented by the CWT data, but we used a three-step protocol to limit the stocks used in our analyses. First, we limited the data to 3 release months as described above. Second, so that release timing within those 3 months would not substantially impact smolt length, we used stock-specific analyses of variance (ANOVAs) to select stocks for which release month explained less than 5.0% of the variation in mean smolt length. Third, of the remaining stocks, we chose the five for which there was the most data. Although we controlled for smolt age and release timing, the CWT data presented here still contains variation arising from cohorts, hatchery influences such as feeding practices, and fish health. We therefore expected the data that successfully passed through our selection protocol to display an overall mean relationship between smolt length and growth performance at sea.

It is likely that individual cohorts will experience different ocean conditions. We addressed this by attempting to control for brood year and observe interannual variability in the relationship between smolt length and growth performance at sea. After applying our data-selection protocol, there were few stocks remaining with enough data to demonstrate such variability. Nevertheless, we selected four stocks from the Columbia River system that retained sufficient data to demonstrate the relationship between smolt



**Fig. 2.** Predicted growth trajectories from eq. 9. Rows *a–e* identify alternative parameterizations of  $E_{SW}$ : (a)  $\psi = 1$ ; (b)  $\psi = 0.75$ ; (c)  $\psi = 0.5$ ; (d)  $\psi = 0.25$ ; and (e)  $\psi = 0$ . The first column of graphs illustrates simulated, at-sea growth trajectories for 10 individuals with different rescaled coefficient of catabolism ( $k$ ) values; the bold trajectories identify those individuals that were the largest and smallest smolts. The second column illustrates predicted relationships between smolt length and net growth after 6 months at sea. The third column illustrates predicted relationships between smolt length and net growth after 18 months at sea. In both of these latter columns, each data point represents the mean from a cohort of 100 individuals, and 50 cohorts are illustrated in each panel. On the right side of the figure, schematic scale bars indicate the behavioral and oceanographic interpretations of the parameterizations of  $E_{SW}$ .



length and growth performance at sea for 3 separate years within each stock.

It is worth noting that the empirical data presented here represent both hatchery and wild fish and were developed from a variety of methodologies. The CWT data represent 14 hatchery stocks and 1 wild stock and were estimated from mean weights reported in the CWT database. The literature data were from individual measurements of hatchery (Mathews and Ishida 1989; Hager and Noble 1976) and wild (Shapovalov and Taft 1954; Holtby and Healey 1986) coho. Data from two of the literature sources (Holtby and Healey 1986; Mathews and Ishida 1989) were developed by back-calculating lengths from annulus spacing on the scales of individual fish.

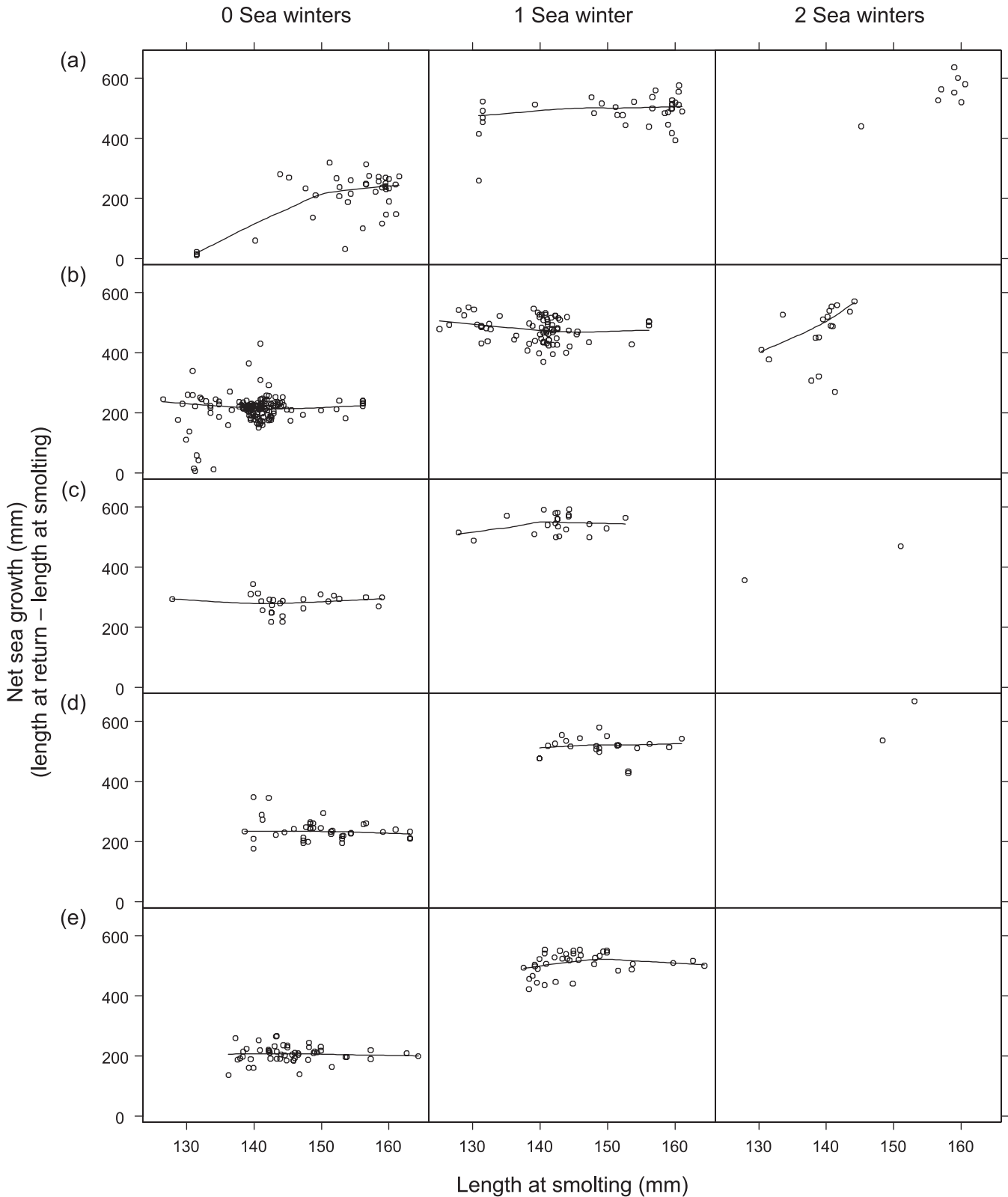
**Results**

Since growth potential at sea is  $L_{\infty} - L(12|k) \sim \gamma_{SW} k^{\psi-1}$ , our formulation of  $E_{SW}$  had a strong impact on how smolts of varying lengths were predicted to grow in salt water (Fig. 2). Individual growth trajectories converged when  $\psi \neq 1$ . When  $\psi \leq 0.5$ , a crossover occurred, and the largest

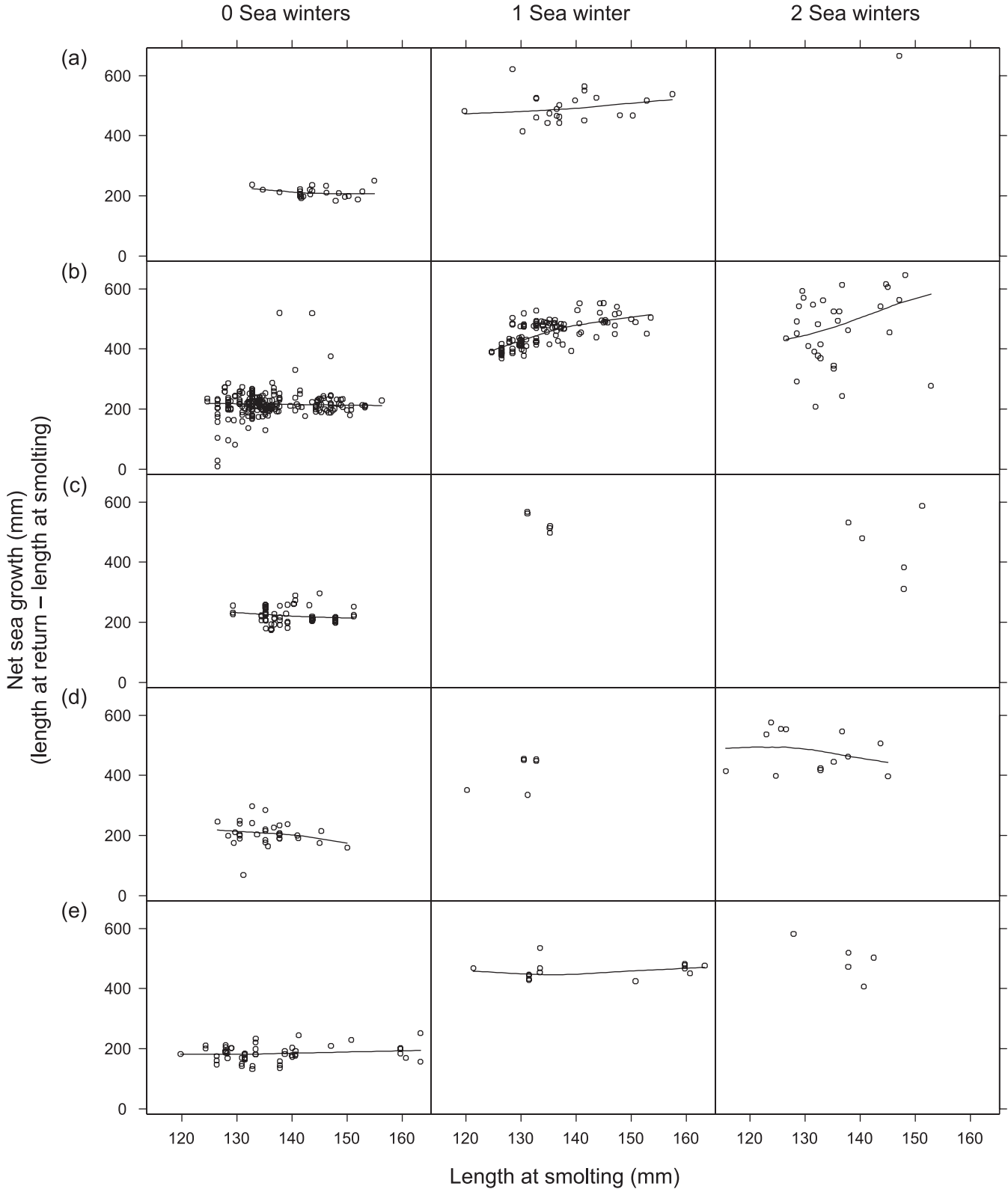
smolts eventually became the smallest individuals. As  $\psi$  decreased from 1 to 0, the largest smolts had declining growth potentials at sea, and the reverse was true of the smallest smolts. The age at which individual growth trajectories crossed each other decreased as  $\psi$  decreased. When  $\psi = 0$ , the smallest smolts had substantially greater salt-water growth potential than did the largest smolts, and the crossover occurred soon after the smolt transformation. When  $\psi = 1$ , the model predicted positive relationships between mean smolt length and mean net growth after both 6 and 18 months at sea. Conversely, when  $E_{SW}$  was independent of  $k$  (i.e., or  $\psi = 0$ ), the model predicted negative relationships between smolt length and net growth after 6 and 18 months at sea. The transition from a positive to a negative relationship between smolt length and net growth at sea with decreasing  $\psi$  was predicted both across individuals (data not shown) and across cohorts (Fig. 2, second and third columns. Note that we illustrate cohort-level predictions in the second and third columns of Fig. 2 for direct comparison to the observational data presented in later figures).

The CWT data demonstrated a range of average relation-

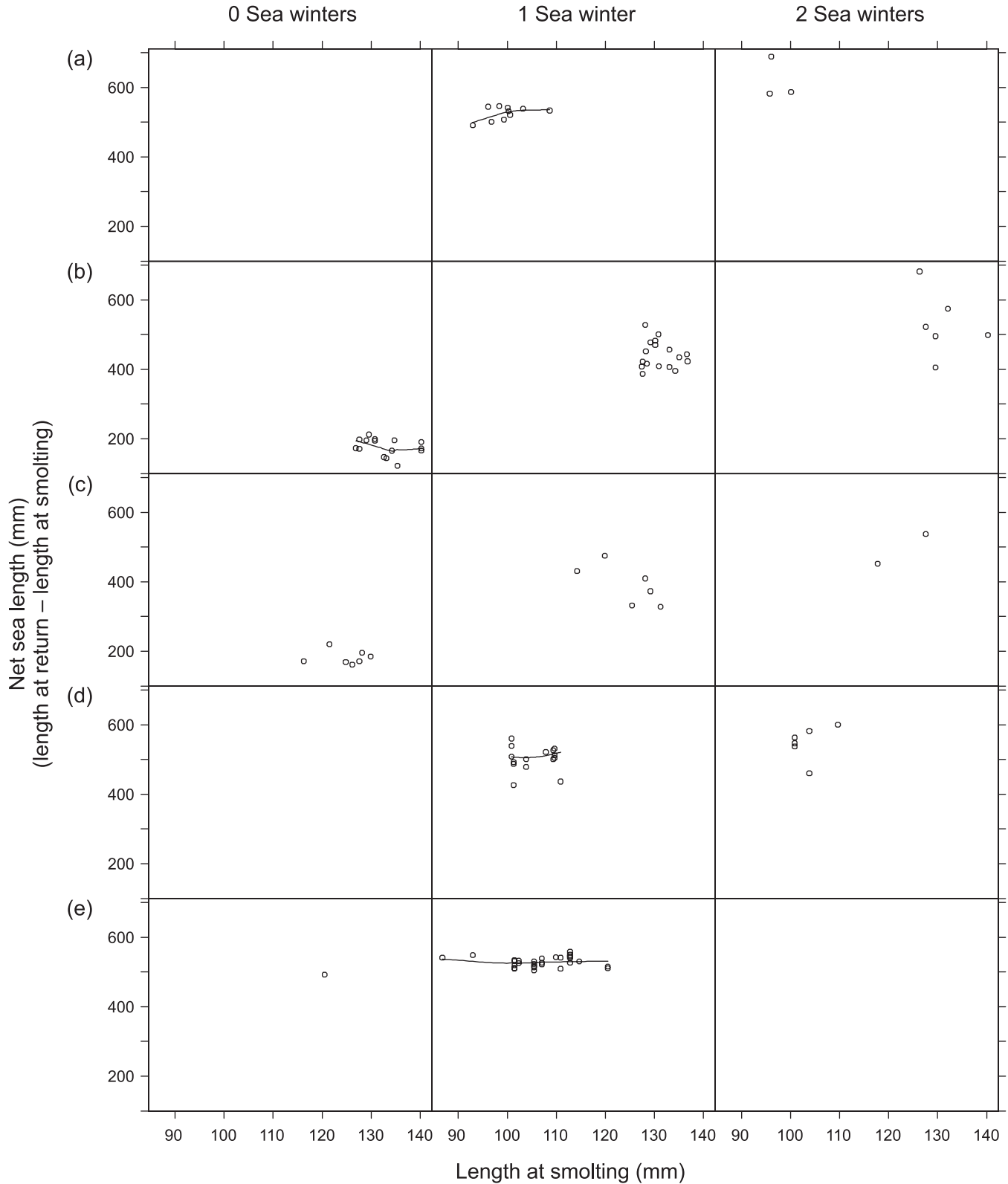
**Fig. 3.** Average net growth of coho salmon (*Oncorhynchus kisutch*) released as age 1+ smolts from five hatchery stocks in Oregon. Rows are identified by stock location names recorded in the Coded Wire Tag database: (a) Umpqua River (Rock Creek Hatchery), (b) Sandy River (Sandy Hatchery), (c) Nehalem River North Fork and tributaries, (d) Klaskanine River, and (e) Clackamas River Early. Circles identify mean length at release and mean growth increments for multiple groups of fish marked with unique tag codes and from different cohorts. Trend lines are loess smooths. Smooth curves were fitted only when there were at least 10 data points in a panel and the range of smolt lengths was at least 10 mm.



**Fig. 4.** Average net growth of coho salmon (*Oncorhynchus kisutch*) released as age 1+ smolts from five hatchery stocks in Washington. Rows are identified by stock location names recorded in the Coded Wire Tag database: (a) Lewis River 27.0168, (b) Cowlitz River 26.002, (c) Cook Creek 21.0429, (d) Big Soos Creek 09.0072, and (e) Big Quilcene 17.0012. Circles identify mean length at release and mean growth increments for multiple groups of fish marked with unique tag codes and from different cohorts. Trend lines are loess smooths. Smooth curves were fitted only when there were at least 10 data points in a panel and the range of smolt lengths was at least 10 mm.

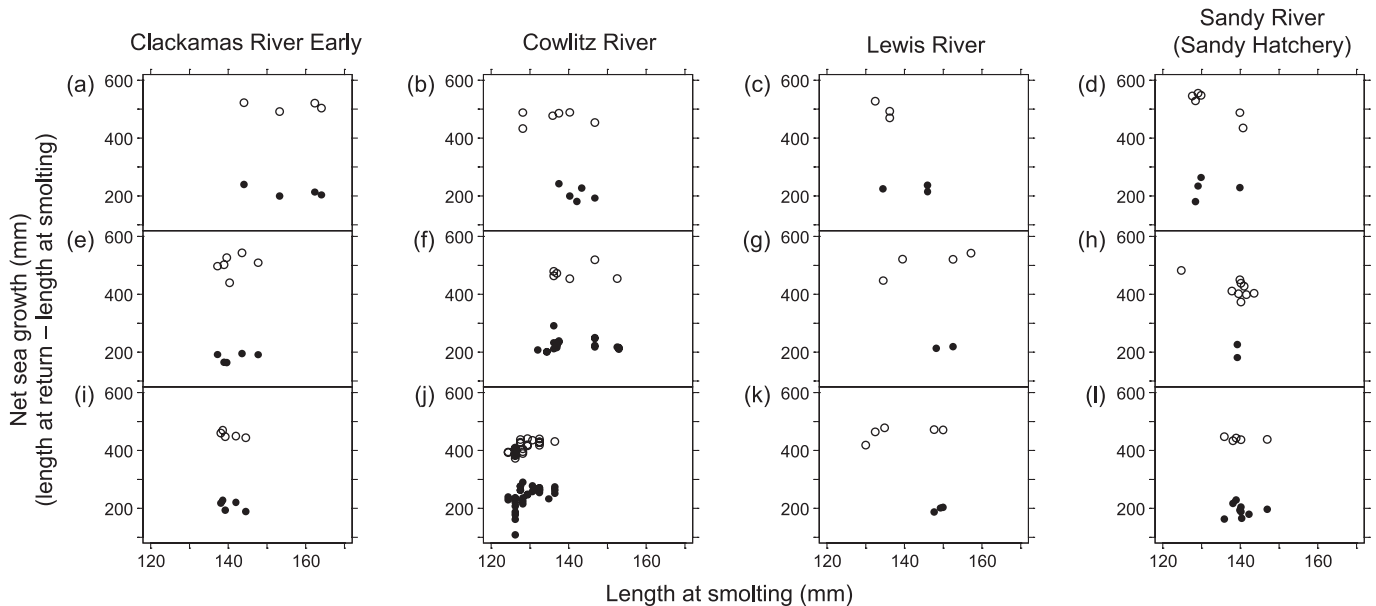


**Fig. 5.** Average net growth of coho salmon (*Oncorhynchus kisutch*) released as age 1+ smolts from five stocks in British Columbia. Rows are identified by stock location names recorded in the Coded Wire Tag database: (a) S-Zolzap Creek, (b) S-Quinsam River, (c) S-Puntledge River, (d) S-Bulkley River Up, and (e) S-Babine River. Data from Zolzap Creek (row a) are for wild fish; all other data are for hatchery stocks. Circles identify mean length at release and mean growth increments for multiple groups of fish marked with unique tag codes and from different cohorts. Trend lines are loess smooths. Smooth curves were fitted only when there were at least 10 data points in a panel and the range of smolt lengths was at least 10 mm.





**Fig. 6.** Cohort-specific net growth of coho salmon (*Oncorhynchus kisutch*) released as age 1+ smolts from four hatchery stocks in the Columbia River Basin. The data are a subset of those presented in Figs. 3 and 4. Columns are identified by stock location names recorded in the Coded Wire Tag (CWT) database. Panels are identified by the year in which smolts were released: (a) 1996, (b) 1992, (c) 2000, (d) 1994, (e) 1993, (f) 1986, (g) 1998, (h) 1992, (i) 1991, (j) 1982, (k) 1996, and (l) 1991. These years were arbitrarily selected to represent the range of responses seen in the CWT data. Solid circles are estimated growth increments for fish that spent zero winters at sea, and open circles are estimated growth increments for fish that spent one winter at sea. Each circle identifies the mean size at smolting and mean growth increment for a group of fish that shared a common tag code recorded in the CWT database (note, however, that all tag codes within a panel identify fish from a single cohort).



ships between pre- and post-smolt growth performance of coho salmon. Relationships between smolt length and net growth at sea were mostly absent for 0- and 1-sea-winter coho from stocks in Oregon (Fig. 3). For the five coho stocks from Washington, the relationships for 0-sea-winter fish were slightly negative or absent (Fig. 4), and the relationships for 1-sea-winter fish were mainly absent or positive (Fig. 4). The data from British Columbia were sparse and difficult to interpret, but relationships between smolt length and net growth at sea were predominately absent for both 0-sea-winter and 1-sea-winter coho (Fig. 5). Data for 2-sea-winter coho from all 15 stocks represented by the CWT data were sparse, and trends ranged from negative to positive (Figs. 3–5).

When we controlled for annual variability in oceanographic conditions, additional variation in the relationship between smolt length and growth performance at sea was revealed (Fig. 6). For example, 1-sea-winter coho from the Lewis River showed the possibility of a negative relationship in 1 year and positive relationships in 2 subsequent years (Figs. 6c, 6g, and 6k). Similarly, for fish from the Sandy River, a negative relationship was suggested for two of the years, and no trend was suggested in a third year (Figs. 6d, 6h, 6l). Overall, the cohort-specific average relationships between smolt length and growth performance at sea varied from negative to positive, as with the CWT data that were combined across cohorts and years.

Relationships between pre- and post-smolt growth performance recorded in the literature were not as varied as those from the CWT data. Negative relationships between smolt

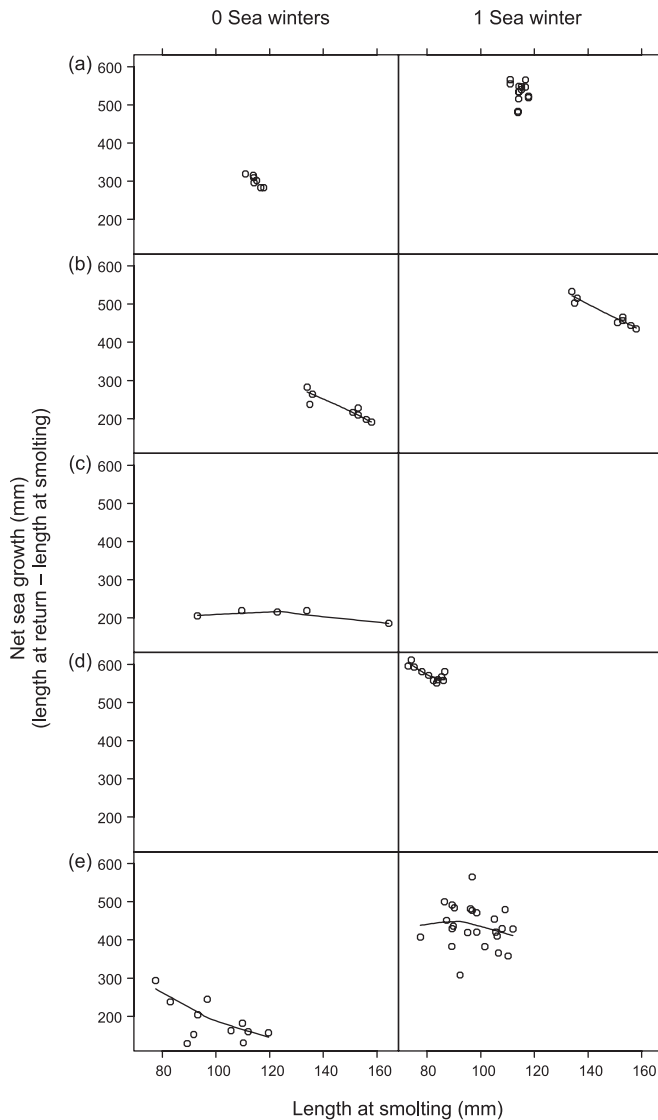
length and net growth at sea were primary for 0-sea-winter coho (Fig. 7). For 1-sea-winter and 2-sea-winter fish from hatchery and wild stocks, relationships were absent or negative (Fig. 7).

We compared patterns observed in the CWT and literature data with predictions from our growth model. In our model, negative relationships between freshwater and salt-water growth performance corresponded to cases where  $0 \leq \psi \leq 0.25$ , while relationships were absent when  $0.25 \leq \psi \leq 0.5$ . These ranges of  $\psi$  appeared to be the most descriptive for 0-sea-winter coho (Figs. 2–5), suggesting that resources were well to moderately mixed at sea and were not defensible by dominant or aggressive coho smolts. For 1-sea-winter and 2-sea-winter coho, the relationships ranged from positive to negative, but the majority showed no clear relationship (Figs. 3–5). In comparing these observations with our predictions, a parameterization of  $0.25 \leq \psi \leq 0.75$  appeared most appropriate. This suggested that as the coho grew and spent more time at sea, they gained increased access to food resources as dominant or aggressive behaviors became more effective.

## Discussion

We offer a theory that unifies the conflicting relationships (see the references that were cited in the Introduction) observed between freshwater and salt-water growth performance by salmonids. This unification is achieved by considering growth in terms of the behavior–environment interaction. Effective dominance behaviors combined with re-

**Fig. 7.** Average net growth of coho salmon (*Oncorhynchus kisutch*) reported in the literature. Rows are identified by author: (a) Shapovalov and Taft (1954), (b) Mathews and Ishida (1989) (note that the data for 0 sea winters are back-calculations of length at the first ocean annulus on scales), (c) Hager and Noble (1976), (d) Holtby and Healey (1986), and (e) University of Washington Hatchery. Fish represented by data in row (e) were released as age 0+ smolts; all other fish were released as age 1+ smolts. Circles are estimated growth increments, and trend lines are loess smooths. Smooth curves were fitted only when there were at least five data points in a panel and the range of smolt lengths was at least 10 mm.



source distributions that are clumped at appropriate scales lead to positive relationships between freshwater and salt-water growth. On the other hand, ineffective dominance behaviors combined with relatively well-mixed resources lead to negative relationships between freshwater and salt-water growth. Infinitely many behavior–environment interactions are possible, and the signs and strengths of relationships between freshwater and salt-water growth performance will vary in response to these interactions.

We used coho salmon as a case study, and laboratory observations of this species seem to confirm the influence of the behavior–environment interaction. Paszkowski and Olla (1985) found both that postsmolt coho remained territorial and aggressive for months after the smolt transformation and that the most aggressive fish acquired the most food. Importantly, however, Paszkowski and Olla (1985) presented food to captive fishes at a single source, thus providing a consistent and defensible resource that might not be found in the ocean. In another laboratory experiment on coho parr, Ryder and Olla (1996) presented food in both localized and dispersed manners. Aggressive behaviors did not differ between the two feeding regimes, but all individuals had equal access to food resources when food was dispersed over the tank while only the most aggressive fish acquired food under the localized treatment. Together, these two studies (and many of the studies mentioned in the Introduction) reiterate the necessity for caution in making inferences from the growth of captive fishes. Variation in the method of feeding may influence the relationship between pre- and post-smolt growth performance. More importantly, these studies suggest that while coho may remain aggressive after the smolt transformation, aggressive individuals will not necessarily acquire more resources — resource acquisition also depends on environmental conditions.

Ineffective aggression (i.e., defending territories that do not offer competitive advantages) may have detrimental consequences for growth at sea. The largest coho smolts are probably the most territorial in fresh water (Martel 1996), and Vøllestad and Quinn (2003) found that the growth rates of territorial coho parr actually decreased when food was presented in a dispersed manner and made equally available to all individuals. Aggressive, territorial individuals have higher metabolic demands than their nonterritorial counterparts (Puckett and Dill 1985; Vøllestad and Quinn 2003), and if aggression does not increase resource acquisition, high metabolic demand may ultimately slow growth at sea (Vøllestad and Quinn 2003). The CWT and literature data presented here suggest that when coho spend only one growing season at sea, the same territorial behaviors that increase growth rates in fresh water have either no effect on or a potentially detrimental effect on growth rates in salt water.

For coho that spend more than one growing season at sea, the relationship between freshwater and salt-water growth performance is less clear. In most instances, we did not find convincing average relationships between smolt length and net growth of 1-sea-winter and 2-sea-winter fish. This suggests that dominance behaviors can be ineffective for acquiring resources in the second and third growing seasons, opposite of what appears to be likely in the first growing season. We did, however, find some positive relationships for coho that mature late, suggesting that the effectiveness of aggression and dominance can increase as coho spend more time at sea. Our model does not currently allow an individual's foraging range to increase as that individual grows. One can envision that as the ratio of an individual's foraging area to the area over which resources are distributed increases, resources may be more readily acquired and aggressive behaviors may be more effective. It may be more realistic to parameterize  $E_{SW}$  so that  $\psi$  is a function of length

or age that reflects possible ontogenetic shifts in the effectiveness of aggressive behavior.

Clues about alternative parameterizations of  $\psi$  might be obtained from scales and otoliths of spawners. For example, length- or age-specific estimates of  $\psi$  might be developed from back-calculated lengths at smolting, at the end of the first growing season, and at the end of the second growing season. Additionally, scales obtained from individuals in the same stock but different cohorts could provide information on the degrees to which environmental conditions affect  $\psi$ . Ultimately, it may be possible to relate growth performance to indices of oceanographic condition and predict how growth performance changes in response to environmental forcing. Such studies were, in fact, motivations for us to develop the growth model described here.

We have noted age-specific differences in the relationships between growth in fresh water and growth in salt water, but it is also striking that we observed substantial variation in these relationships across stocks and geographic regions. The CWT data presented here suggest that the different migratory paths and ocean conditions experienced by different stocks can affect the relationships between pre- and post-smolt growth performance. This suggestion must, however, be tempered by acknowledging that the stock-specific differences in growth performance noted here may be related to differential effects of hatchery practice. Nevertheless, over the geographic range of coho salmon, we do not expect a single relationship between freshwater and salt-water growth performance.

Negative relationships between freshwater and salt-water growth performance by salmonids have interesting implications for reproductive strategy. Theoretical studies of alternative reproductive tactics within a single sex suggest that for some measures of individual condition, there is a switch point at which an individual in condition greater than the switch point should choose an alternative reproductive strategy (Charnov 1993; Gross 1996). For coho salmon, the proposed measure of condition is juvenile body size (Charnov 1993) or smolt length. At a body size greater than the switch point, individuals are predicted to mature early. However, previously published studies do not provide the proximate mechanisms linking large smolt size and early maturation. In coho salmon, and possibly salmonids in general, that mechanism appears to be the habitat differences associated with anadromy. Migrating from fresh water to salt water can have profound effects on growth performance because the behavior-environment interaction is abruptly altered. We intend to use our growth model as a foundation for developing fitness functions that predict ages at maturity conditioned on smolt size.

It is important to identify some of the caveats related to our work. In modeling freshwater growth, we set  $\psi = 1$ , making the assumption that the more dominant individuals will always be larger smolts. Some studies of Atlantic salmon indicate, however, that individuals with higher dominance status do not always display higher growth rates (Martin-Smith and Armstrong 2002; Harwood et al. 2003). Martin-Smith and Armstrong (2002) found no relationship between growth, measured as specific growth rate and aggressive behavior in Atlantic salmon. They studied fish in a

seminatural stream system supplied with natural food sources, and their results suggest that it is possible that  $\psi < 1$  in some freshwater environments. We did not consider  $\psi < 1$  in our model, as the overwhelming evidence for both hatchery and wild coho indicates that  $\psi = 1$  (Puckett and Dill 1985; Nielsen 1992; Martel 1996). Nevertheless, future applications of our model, particularly to other salmonids, may need to consider other values of  $\psi$  in fresh water.

We also assumed that  $k$  remains the same in both habitats, and this assumption may need further evaluation. As noted in the Methods section,  $k$  is closely related to metabolic rate and activity (Beverton and Holt 1959). Morgan and Iwama (1998) found no difference between the oxygen consumption rates of coho salmon in fresh water and salt water, but temperature was held constant in all treatments. There is a positive relationship between environmental temperature and  $k$  (Beverton and Holt 1959), and it is possible that  $k$  declines upon out-migration to cooler temperatures in the ocean. We considered a formulation in which  $k$  was habitat-specific:

$$k_{SW} = k_{FW} - \kappa$$

where  $\kappa$  is the average decline in  $k$  from fresh water to salt water. The qualitative predictions of this formulation did not change from those described previously. It is also possible that rankings of  $k$  may switch upon the out-migration (i.e., the smolts with the largest  $k$  switch to having the smallest  $k$ ), as, from a physiological standpoint, what works well in fresh water may not work well in salt water (Thorpe 1987; Einum et al. 2002). This seems unlikely from the data presented here and from the studies cited in the Introduction, as one would expect negative relationships between freshwater and salt-water growth rates to be predominant.

We have presented a growth model that describes growth stanzas typical of salmonid life histories. This growth model can accommodate the life history of any salmonid (and possibly any diadromous fish) and is flexible enough to allow for all possible relationships between freshwater and salt-water growth performance. Appropriate parameterizations of anabolism can be determined both by considering how behavior and environmental conditions interact to affect resource acquisition and by making appropriate observations (e.g., analyses of mark-recapture data, otoliths, and scales). We presented a case study for coho salmon and suggest that during the first salt-water growing season, aggressive behaviors interact with environmental conditions in a way that does not facilitate increased resource acquisition by large smolts. During subsequent growing seasons, aggressive behaviors may or may not interact with environmental conditions to increase resource acquisition. Ultimately, the relationship between freshwater and salt-water growth performance will vary by stock and geographic region.

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