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Ecophysiology of juvenile California halibut *Paralichthys californicus* in relation to body size, water temperature and salinity

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ABSTRACT: Food consumption, metabolism, growth, conversion efficiencies (food assimilation, gross and net growth) and whole-body water content of small (118 to 172 mm TL) and large (237 to 310 mm TL) juvenile California halibut *Paralichthys californicus* exposed to various combinations of water temperatures (14, 20, 25 and 28°C) and salinities (8, 17 and 34 ppt) were quantified in laboratory experiments. Small juvenile halibut were able to grow and maintain water balance over almost the entire ranges of water temperatures and salinities tested, except at 14°C and 8 ppt, where they lost weight but gained about 2% body water. Large juvenile halibut were far less tolerant of variations in water temperature and salinity. Regardless of salinity, large juvenile halibut exposed to 14 and 25°C lost weight due to greatly reduced energy intake, and experienced >90% mortality at 28°C; in diluted seawater at 14 and 25°C they also experienced water balance problems. Only at 20°C did surplus energy and lack of water balance problems allow large juvenile halibut to grow across all salinities. Differences in energetic and water balance responses of small and large juvenile halibut correspond to the habitat preferences of each size group. Small juvenile halibut are estuarine, and their ability to tolerate wide variations in water temperatures and salinities allows them to exploit estuaries and coastal lagoons with abundant small prey (gobies), warm temperatures, and few predators. However, in winter, with the increased probability of estuarine or lagoon mouth closures, water temperatures and salinity can rapidly drop to levels unfavorable for growth of small juvenile halibut. Large juvenile halibut, with their reduced tolerance for varying temperatures and salinities, must migrate from lagoons and estuaries into open-coast environments, where they also benefit from abundant large prey. Closure of river mouths likely pose the greatest risk to large juvenile halibut, should they become trapped in cold, hyposaline coastal wetlands.

KEY WORDS: Mouth closures · Flatfish · Bays · Energetics · Physiological ecology

INTRODUCTION

Many marine fish utilize coastal wetlands as nursery habitats for foraging and refuge (Miller et al. 1986, Kneib 1997, Kwak & Zedler 1997). In the US alone, an estimated 75% of commercially important fish harvested annually rely upon lagoons, bays, and estuaries during some part of their life cycle (Chambers 1992). Marine fish that utilize coastal wetlands typically spawn offshore; as larvae and juveniles they move into coastal wetlands, where they remain a season to several years, after which they emigrate to the open coast as sub-adults or adults (Miller et al. 1986, Boehlert & Mundy 1988, Kramer 1991). Fish that migrate between relatively stable marine environments and coastal wetlands with variable water temperature, salinity, and dissolved oxygen levels must be adapted to the environmental conditions of their transitory habitats.

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The California halibut *Paralichthys californicus* is a commercially and recreationally valuable flatfish in southern California coastal waters (Haaker 1975, Plummer et al. 1983, Allen 1988). It requires coastal wetland habitats as nursery grounds (Plummer et al. 1983, Kramer 1990). Peak spawning of *P. californicus* occurs in winter and spring within 6 km off shore (Gruber et al. 1982, Barnett et al. 1984, Lavenberg et al. 1986, Walker et al. 1987, Moser & Watson 1990). Metamorphosing larvae probably utilize surface slicks associated with internal waves to move inshore (Kramer 1991). Once nearshore, metamorphosing larvae or newly settled juveniles search for entrances to coastal wetlands, where they live for at least the first year of their life (Boehlert & Mundy 1988, Kramer 1991). It appears that coastal wetlands are critical for the survival of the smallest juvenile *P. californicus* (18 to 72 mm total length [TL]) and to the growth of larger juveniles (72 to 150 mm TL) due to their high production of easily obtainable food items (primarily gobies), warm temperatures, and relatively lower abundance of predators compared to coastal waters (Allen & Horn 1975, Allen 1982, Drawbridge 1990, Kramer 1990). Once juvenile halibut reach a size of 200 to 250 mm TL, they migrate to coastal waters (Drawbridge 1990, Kramer 1990).

The migration of juvenile halibut from coastal wetlands to offshore habitats may have a physiological basis. The coastal ecosystems occupied by small juvenile halibut have more variable water temperatures and salinities compared to offshore benthic habitats (Kramer 1990, Nordby & Zedler 1991). In addition, anthropogenic influences (e.g. partial closure of river mouths) on coastal habitats can lead to extreme water temperatures, salinities and dissolved oxygen conditions in habitats of juvenile halibut. These differences in habitat characteristics probably lead to different levels of physiological stress imposed on different size-groups of juvenile halibut, and potentially different physiological responses to these environmental conditions. Alternatively, a decline in the ability of halibut to cope with variations in water temperature and salinity in coastal wetland habitats may force them to move to open coast waters with a more stable environment.

The abiotic requirements of juvenile halibut and their changes through ontogeny were evaluated by comparing several physiological parameters (food consumption, metabolism, growth, conversion efficiencies, and whole body water content) in 2 size-groups of juvenile halibut exposed to combinations of water temperature and salinity typical of halibut nursery areas. The small size-group (118 to 172 mm TL) represents halibut using coastal wetlands as nursery areas, and the large size-group (237 to 310 mm TL) represents halibut known to emigrate from coastal wetlands to open coast environments.

MATERIALS AND METHODS

General procedures and acclimation. Experimental fish were obtained from the Leon Raymond Hubbard Jr. Marine Fish Hatchery in Carlsbad, CA, transported in aerated water coolers to the Pacific Estuarine Research Laboratory (total transport time = 0.8 h), and acclimated to experimental conditions. Groups of 15 fish were individually distributed to 50 l aquaria filled with filtered Pacific Ocean water obtained from the pier at Scripps Institution of Oceanography in La Jolla, CA, USA, and stored in a 1895 l tank outside the laboratory. Water was periodically tested for salinity, pH and dissolved oxygen content and pumped from the storage tank to individual aquaria as required.

All experimental aquaria were placed in either of 2 adjacent 670 l insulated water baths (2.4 × 0.9 × 0.3 m) which were fitted in-line with a water pump ($^1/_3$ hp, flow capacity = 4353 l h^{-1}), a heavy-duty chiller ($^3/_4$ hp, 1725 W, flow capacity range = 3785 to 7570 l h^{-1}), and a heater (1000 W, flow capacity range = 757 to 5687 l h^{-1}). Solid-state electronic temperature controllers (±0.3°C sensitivity) on the heater and chiller allowed precise temperature control of bath and aquaria water (±0.5°C).

The acclimation period lasted approximately 3 wk. During the first 4 d, the water temperature of the bath was raised or lowered as necessary by 1 to 2°C each day until the experimental temperature was reached in all aquaria; the halibut were then acclimated to this temperature for 2.5 wk. During the acclimation period, all halibut were held at 34 ppt and fed their principal natural diet of live gobies, mainly *Clevelandia ios*, some *Quietula y-cauda* and *Ilypnus gilberti* (Haaker 1975, Allen 1988, Drawbridge 1990). Feces and dead gobies were siphoned daily out of each aquarium, and about 15 to 20 l of seawater was replaced during the process. Partial replacement of water was conducted daily even when feces or dead gobies were absent. Excess algal growth on the aquarium walls was prevented by occasional scrubbing with a sponge. Only fish that were judged to be healthy and behaving normally (i.e. no visible skin lesions, no abnormal breathing, and actively feeding and orienting like other experimental fish held under similar conditions) were used in the experiment. To serve as replacements if required, 2 to 3 spare fish were maintained under similar conditions.

Experimental regime. Eight experiments were conducted between August 31, 1999, and April 13, 2001, using small and large juvenile halibut (Table 1). Experiments were conducted in random order over 11 d periods at 1 of 4 water temperatures (14, 20, 25, or 28°C). Each experiment had 3 salinity treatments (8, 17, 34 ppt) made by diluting seawater with deionized water 1 d

Table 1. *Paralichthys californicus.* Means (±SE) and ranges of size and wet body mass, and mean dry:wet mass ratios for each experimental period

Date of expt	Temperature (°C)	Size range (mm TL)	Mean size (mm TL)	Body mass range (g)	Mean body mass (g)	Dry:wet mass
Small halibut						
6–17 Mar 2000	14	149–172	158.4 (2.0)	30.0–46.9	38.1 (1.3)	0.255
31 Aug–11 Sep 1999	20	118–148	133.6 (2.5)	12.8–31.1	23.1 (1.4)	0.214
30 Nov–11 Dec 1999	25	125–147	139.6 (1.5)	15.0–26.1	22.6 (0.8)	0.220
1–12 Feb 2000	28	139–170	151.3 (2.4)	21.4–39.4	28.2 (1.3)	0.236
Large halibut						
5–16 Feb 2001	14	255–310	276.7 (4.5)	175.5–315.4	220.4 (11.0)	0.257
2–13 Apr 2001	20	237–289	264.3 (4.5)	113.3–248.8	189.3 (10.7)	0.238
27 Nov–8 Dec 2000	25	247–295	271.2 (3.4)	159.4–285.0	214.5 (7.1)	0.234
11–22 Sep 2000	28	243–310	264.9 (5.3)	129.9–227.9	181.0 (7.7)	–[a]

[a]Not estimated (>90% mortality)

(Day 0) prior to its commencement. For each salinity treatment 5 fish were randomly assigned to their individual aquaria (5 replicates per treatment). Feeding of the halibut was stopped on Day 0 and all remaining prey were removed from each aquarium. Salinities were monitored daily throughout the 11 d period and adjusted to within ±1 ppt. At 28°C, large juvenile halibut suffered >90% mortality within 4 wk (3 wk acclimation + 1 wk experiment), and this temperature was identified as the upper tolerance limit.

Vital rates. ***Food consumption:*** Food consumption was measured on Day 1–2, 4–7 and 8–9 in each experiment. Halibut were not fed for at least 24 h prior to each feeding trial to ensure that guts were empty. For the feeding trials, total initial wet wt of batches of live gobies were measured before being fed to the halibut. Each halibut was fed an excess of live gobies of the appropriate sizes, approximately 20 to 25 gobies for small halibut and 55 to 60 gobies for large halibut, amounts determined in preliminary feeding trials. After 24 h (Day 1–2 and 8–9) or 72 h (Day 4–7), all remaining gobies were retrieved from the aquaria and re-weighed. Food consumption (g g^{-1} d^{-1}, dry wt basis) was determined as the difference between initial and final goby weights, adjusted for halibut dry wt (see Eq. 3 below) and trial duration. I also estimated mean dry wt and dry wet wt ratios of gobies by sacrificing and drying 100 randomly selected gobies at 105°C for 24 h. Food consumption was expressed as caloric food intake (cal g^{-1} d^{-1}, dry wt basis) by using a caloric value of 4053 cal g^{-1} goby dry wt (Drawbridge 1990) and a goby dry:wet mass ratio of 0.22 (this study).

Metabolism: Routine metabolic rate measurements (oxygen consumption) were made on Day 0–1, 3–4, 10–11 using the modified Winkler chemical titration method for seawater (Grasshoff et al. 1983). Routine metabolism is defined here as the combined metabolic costs of maintenance and routine activity (swimming to change and adjust position on the bottom) under starved conditions. Fish were starved for a minimum of 24 h prior to each metabolic rate trial to ensure adequate time for gut clearance and to standardize measurements. On the first day of each trial (Day 0, 3, 10), the fish were transferred to metabolic chambers for acclimation. The chambers were filled with water of the appropriate salinity, covered with a 4 mm mesh sieve and immersed completely in their respective experimental aquaria. The metabolic chambers ranged in volumes from 10.8 to 11.1 l (approximately 320 × 180 × 200 mm) for large halibut and 2.1 to 2.3 l (approximately 260 × 150 × 60 mm) for small halibut. Air diffusers in the experimental aquaria ensured thorough exchange of water between the aquaria and the sieved metabolic chambers as determined in preliminary dye trials. In this manner, halibut were allowed to adjust to their metabolic chambers overnight.

The next day, with the metabolic chambers still completely immersed in their respective aquaria, the sieves were slipped off, water-tight gasket-lined lids with access ports on top were clamped on and access ports sealed off with rubber stoppers. Because the whole procedure was conducted with metabolic chambers completely immersed in water, no air bubbles were trapped in the chambers. Preliminary dye tests showed that all chambers were water-tight and no water from the aquaria diffused into the metabolic chambers after they were sealed. Similarly, control chambers (without fish, 0.9 l capacity) were also placed in each aquarium to account for oxygen consumption or release by microorganisms (bacteria and algae). Immediately after the metabolic chambers were sealed, water samples from individual aquaria were siphoned with plastic tubes into 60 ml BOD bottles until at least twice the bottle volume was replaced, and initial dissolved oxygen levels determined in 50 ml samples. After 1 h (for large halibut) or 2 h (for small halibut), water was sampled via

the access port on the metabolic chambers and final dissolved oxygen levels were determined. At this time, water was also sampled from the control chambers and BOD determined. Metabolic rates (g O_2 g^{-1} d^{-1}, dry wt basis) were estimated as the difference between initial and final dissolved oxygen measurements and adjusted for BOD in controls, halibut dry wt, metabolic chamber volume and trial duration. I used Eq. (3) to estimate halibut dry wt on Day 1 and 4, but used final measured dry wt for Day 11. An oxycalorific value of 3240 cal $g^{-1}O_2$ (Elliot & Davidson 1975) was used to convert metabolic rates to their caloric equivalents (cal g^{-1} d^{-1}).

Growth: Halibut growth was estimated over an 11 d period in each experiment by measuring initial total lengths (TL, mm) and weights (g) of halibut on Day 0 and at the end of each experiment (Day 11). On Day 0, the fish were mildly anesthetized in a solution of MS-222 (0.2 g l^{-1}) for 0.5 to 3.0 min depending on size, and weighed to the nearest 0.1 g. The fish were then returned to a temporary container filled with 34 ppt seawater for recovery (approximately 15 to 20 min). On Day 11, after conclusion of the final metabolism trial, all halibut were immediately sacrificed with an overdose of MS-222 (1 g l^{-1} for 5 to 6 min), blotted, weighed, dried for 72 h at 105°C, and reweighed to obtain dry wt. Initial dry wt on Day 0 was estimated from measured initial wet wt using appropriate mean dry:wet wt ratios (Table 1) determined at 34 ppt. Growth (g d^{-1}, dry wt basis) was estimated as:

$$\frac{W_{11} - W_0}{t} \quad (1)$$

where W_0 is the dry weight of halibut on Day 0, W_{11} is the dry weight of halibut on Day 11 and t = 11 d. Growth rates were adjusted for initial dry wt of halibut to obtain weight-specific growth rates (g g^{-1} d^{-1}), which were then converted to their caloric equivalent (cal g^{-1} d^{-1}) using a caloric value of 4927 calories g^{-1} dry weight of halibut tissue (Thayer et al. 1973).

To predict the dry wt of halibut on any given day between the initial and final weight measurements (Day = 2 to 10), I first estimated the instantaneous growth coefficient (G):

$$G = \frac{\ln(W_{11}) - \ln(W_0)}{t} \quad (2)$$

I then estimated halibut dry wt on a given day (W_D) according to the Ricker growth method (in Yamashita & Bailey 1989):

$$W_D = W_0 * [1 + (e^G - 1)]^D \quad (3)$$

Conversion efficiencies. Food assimilation, gross growth, and net growth efficiencies were estimated from measured food consumption (C), metabolism (M) and growth (G) rates (cal g^{-1} d^{-1}).

(1) Food assimilation efficiency (AE), defined as the proportion of energy consumed that is used for growth and metabolism, was estimated as:

$$AE = \frac{G + M + (0.172 \times C)}{C} \quad (4)$$

assuming that 17.2% of the consumed energy is used in the specific dynamic action (SDA), the metabolic energy required for processing consumed food (Hanson et al. 1997).

(2) Gross growth efficiency (K_1), defined as the proportion of consumed food that is used for growth, was estimated as:

$$K_1 = \frac{G}{C} \quad (5)$$

(3) Net growth efficiency (K_2), defined as the proportion of assimilated food that is used for growth, was estimated as:

$$K_2 = \frac{G}{AE \times C} \quad (6)$$

Body water. Final dry wt (D_W) and final wet wt (W_W) of individual fish were used from each experiment to estimate percent body water (%BW):

$$\%BW = \frac{W_w - D_w}{W_w} \quad (7)$$

Standardization of rates: Food consumption, metabolism, growth, and percent body water data for individual fish were standardized to the mean dry wt of small (6.6 g) and large halibut (50.5 g) in the experiment, to allow comparisons across temperatures and salinities:

$$Y_S = \left(\frac{W_S}{W_M}\right)^b \times Y_M \quad (8)$$

where Y_S is the standardized rate (cal g^{-1} d^{-1}), W_S is the standard dry wt of the fish (6.6 or 50.5 g), W_M is the estimated dry wt of the fish (g), b is the allometric exponent (Table 2), and Y_M is the measured rate (cal g^{-1} d^{-1}). The allometric exponents were obtained for small and large halibut by regressing the mean

Table 2. *Paralichthys californicus.* Body mass-dependent exponents (b) used to standardize rates of food consumption, metabolism, growth, and body water content to standard dry body masses of 6.6 g (small halibut) and 50.4 g (large halibut)

	Small halibut	Large halibut
Food consumption	−1.392	−3.278
Metabolism	−0.750	−0.920
Growth	−1.766	−1.535
Body water content	−0.051	−0.023

weight-specific rates (cal g^{-1} d^{-1}) of fish on their dry wt across all temperature sets. In each case, negative exponential equations best fit the relationships. Conversion efficiencies were not standardized, because they showed no relationship with dry wt.

Statistical analyses. For each experiment, multiple measurements of response variables (food consumption, metabolic and growth rates, assimilation, gross growth and net growth efficiencies, and percent body water) were pooled after testing for differences between measurements, and finding none. For each size group (large and small halibut), I used a 2-way ANOVA to assess interactions of weight-standardized response variables with water temperature and salinity treatments, and to determine main effects of treatments on response variables. I also analyzed the effects on weight-standardized response variables of salinity treatments within each temperature treatment, and temperature treatments with each salinity treatment, using Tukey's HSD multiple comparisons of treatment effects generated with 1-way ANOVA. To correct for non-normality and non-homogenous variances, I used only log-transformed or arcsin-transformed data in my analyses. Because some fish did not consume any food, all food consumption data were $\log_{10}(x + 1)$-transformed. Metabolic rate data were $\log_{10}(x)$-transformed. Because fish exhibited growth rates as low as −50 cal g^{-1} d^{-1} in some experiments, all

Table 3. *Paralichthys californicus.* Effects of water temperature and salinity on vital rates ($\log_{10}$-transformed), conversion efficiencies (arcsin $x^{0.5}$-transformed) and body water content (arcsin $x^{0.5}$-transformed) in small juveniles (2-way ANOVA). ***Indicates significance level of $p < 0.05$

Source of variation	SS	df	MS	*F*	p
Vital rates					
Food consumption rate (cal g^{-1} d^{-1})					
Temperature	1.256	3	0.419	19.425	<0.001***
Salinity	0.002	2	0.001	0.036	0.964
Temperature × Salinity	0.170	6	0.028	1.315	0.269
Error	1.013	47	0.022		
Metabolic rate (cal g^{-1} d^{-1})					
Temperature	0.804	3	0.268	39.262	<0.001***
Salinity	0.040	2	0.020	3.001	0.052
Temperature × Salinity	0.026	6	0.004	0.638	0.699
Error	0.321	47	0.007		
Growth rate (cal g^{-1} d^{-1})					
Temperature	3.017	3	1.006	15.420	<0.001***
Salinity	0.748	2	0.374	5.733	0.006***
Temperature × Salinity	2.643	6	0.440	6.754	<0.001***
Error	3.065	47	0.065		
Conversion efficiencies					
Assimilation efficiency (%)					
Temperature	4.107	3	1.369	14.747	<0.001***
Salinity	0.424	2	0.212	2.283	0.113
Temperature × Salinity	1.717	6	0.286	3.082	0.013***
Error	4.363	47	0.093		
Gross growth efficiency (%)					
Temperature	3.834	3	1.278	13.303	<0.001***
Salinity	0.293	2	0.146	1.523	0.229
Temperature × Salinity	0.557	6	0.093	0.966	0.459
Error	4.515	47	0.096		
Net growth efficiency (%)					
Temperature	2.215	3	0.738	14.217	<0.001***
Salinity	0.039	2	0.019	0.373	0.691
Temperature × Salinity	0.581	6	0.097	1.865	0.107
Error	2.441	47	0.052		
Body water content (%)					
Temperature	0.0004	3	0.0001	2.584	0.064
Salinity	0.0007	2	0.0004	6.758	0.003***
Temperature × Salinity	0.0002	6	0.0004	0.747	0.615
Error	0.0025	47	0.0001		

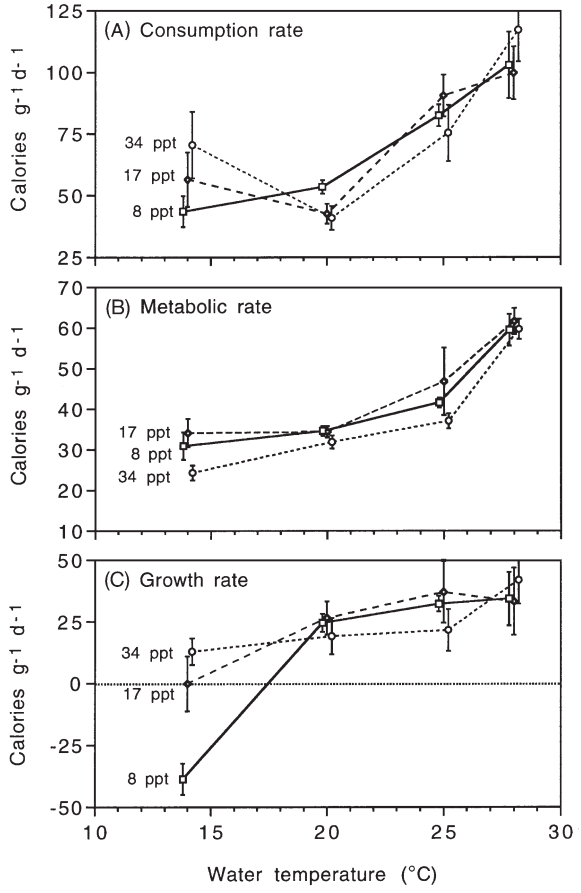

Fig. 1. *Paralichthys californicus*. (A) Food consumption, (B) metabolism, and (C) growth of small juveniles at various combinations of water temperature and salinity. Rates are standardized to the mean halibut size of 6.6 g dry wt. Symbols are staggered to show SE bars. In (C), dotted horizontal line indicates zero growth

growth rate data were $\log_{10}(x + 51)$. All proportional response variables such as conversion efficiencies and percent body water were arcsin $(x)^{0.5}$-transformed.

RESULTS

Vital rates

Food consumption

Food consumption rates of small halibut varied with water temperature, but not with salinity (Tables 3 & 4), and there were no significant interactions in food consumption rates between temperature and salinity treatments (Table 3, Fig. 1A). Small halibut generally increased their food consumption rates as water temperatures increased from 14 to 28°C across all salinities tested (Fig. 1A). Small halibut exposed to salinities of 8 and 17 ppt consumed significantly more food at water temperatures of 25 and 28°C than at 14 and 20°C, while fish exposed to 34 ppt consumed more food at 28°C than at 14 or 20°C (Table 5).

Food consumption by large halibut varied with both water temperature and salinity, with no significant interactions between the treatments (Table 6, Fig. 2A). Large halibut exposed to 20°C consumed more food at 34 ppt than fish at 8 or 17 ppt, but food consumption did not vary with salinity at 14 or 25°C (Table 7). At all 3 salinities tested, food consumption peaked and was significantly higher at 20°C than at 14 or 25°C (Table 8).

Table 4. *Paralichthys californicus*. Tukey's multiple comparisons of treatment means of salinity effects on vital rates, conversion eficiencies and body water content in small juveniles. Continuous lines joining salinity levels indicate no significant differences between treatments ($p > 0.05$)

Parameter Temperature (°C)	Salinity (ppt)
Vital rates	
Food consumption rate (cal g^{-1} d^{-1})	
14	8 17 34
20	8 17 34
25	8 17 34
28	8 17 34
Metabolic rate (cal g^{-1} d^{-1})	
14	8 17 34
20	8 17 34
25	8 17 34
28	8 17 34
Growth rate (cal g^{-1} d^{-1})	
14	8 17 34
20	8 17 34
25	8 17 34
28	8 17 34
Conversion efficiencies	
Assimilation efficiency (%)	
14	8 17 34
20	8 17 34
25	8 17 34
28	8 17 34
Gross growth efficiency (%)	
14	8 17 34
20	8 17 34
25	8 17 34
28	8 17 34
Net growth efficiency (%)	
14	8 17 34
20	8 17 34
25	8 17 34
28	8 17 34
Body water content (%)	
14	8 17 34
20	8 17 34
25	8 17 34
28	8 17 34

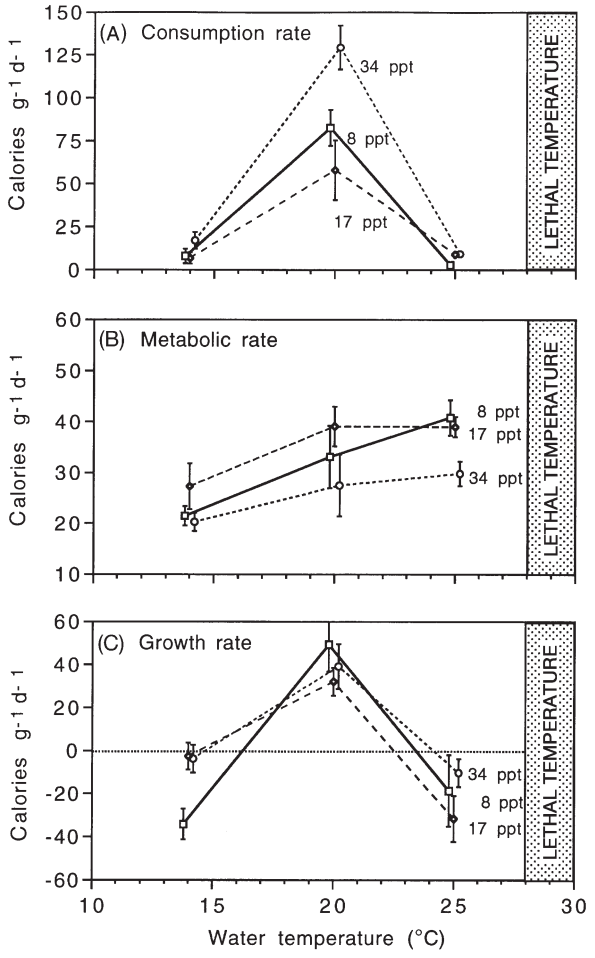

Fig. 2. *Paralichthys californicus*. (A) Food consumption, (B) metabolism, and (C) growth of large juveniles at various combinations of water temperature and salinity. Rates are standardized to the mean halibut size of 50.4 g dry wt. Symbols are staggered to show SE bars. In (C), dotted horizontal line indicates zero growth. The shaded bar indicates the lethal temperature for large juveniles

Metabolism

Routine metabolic rates of small halibut varied significantly with water temperature but not with salinity (Tables 3 & 4), and no significant interactions were detected between the 2 treatments (Table 3, Fig. 1B). Metabolic rates of small halibut generally increased as water temperature increased from 14 to 28°C at all salinities tested (Table 5, Fig. 1B), much in the same fashion as consumption rates (Fig. 1A).

Routine metabolic rates of large halibut varied significantly with both water temperature and salinity, but no significant interactions were detected between these treatments (Table 5, Fig. 2B). Although no significant salinity effects were detected on metabolism of large halibut at 14 and 20°C, metabolic rates at 25°C were significantly higher in fish exposed to 8 and 17 ppt than those at 34 ppt (Table 7, Fig. 2B). Routine metabolic rates of halibut exposed to 17 and 34 ppt did not vary significantly with water temperature; however, metabolic rates increased linearly with temperature in fish exposed to 8 ppt (Table 8, Fig. 2B).

Growth

Growth rates of small halibut were affected by both water temperature and salinity, with significant interactions between the 2 treatments (Table 3, Fig. 1C). At 14°C, small halibut lost considerable weight at 8 ppt, compared to fish at 17 and 34 ppt, but between 20 and 28°C, growth rates did not vary significantly with salinity and stayed in the positive range (Table 4, Fig. 1C).

Table 5. *Paralichthys californicus.* Tukey's multiple comparisons of treatment means of temperature effects on vital rates, conversion eficiencies and body water content in small juveniles. Continuous lines joining temperature levels indicate no significant differences between treatments ($p > 0.05$)

Parameter Salinity (ppt)	Temperature (°C)
Vital rates	
Food consumption rate (cal g^{-1} d^{-1})	
8	14 20 25 28
17	14 20 25 28
34	14 20 25 28
Metabolic rate (cal g^{-1} d^{-1})	
8	14 20 25 28
17	14 20 25 28
34	14 20 25 28
Growth rate (cal g^{-1} d^{-1})	
8	14 20 25 28
17	14 20 25 28
34	14 20 25 28
Conversion efficiencies	
Assimilation efficiency (%)	
8	14 20 25 28
17	14 20 25 28
34	14 25 28 20
Gross growth efficiency (%)	
8	14 20 25 28
17	14 25 28 20
34	14 25 28 20
Net growth efficiency (%)	
8	14 20 25 28
17	14 25 28 20
34	14 20 25 28
Body water content (%)	
8	14 20 25 28
17	14 20 25 28
34	14 20 25 28

Growth of small halibut exposed to 8 ppt was significantly lower at 14°C than at 20 to 28°C, but growth rates did not vary significantly with temperature at 17 or 34 ppt (Table 5, Fig. 1C).

Growth rates of large halibut were also influenced by both water temperature and salinity, with significant interactions between the 2 treatments (Table 6, Fig. 2C). Growth of large halibut did not vary significantly with salinity, except at 14°C, where halibut exposed to 8 ppt lost more weight than fish at 17 and 34 ppt (Table 7, Fig. 2C). Large halibut grew only at 20°C, but lost weight at 14 and 25°C, at all salinities tested (Fig. 2C). Growth rates of halibut exposed to 8 and 34 ppt were significantly higher at 20°C than at 14 and 25°C where growth rates were also similar (Table 8, Fig. 2C). Growth rates also peaked at 20°C in halibut exposed to 17 ppt, but were significantly different at all 3 temperatures (Table 8, Fig. 2C).

Conversion efficiencies

Food assimilation efficiency (AE)

Food assimilation efficiencies of small halibut varied with water temperature, and although the main effects of salinity were not significant, interactions of the 2 treatment variables were significant (Table 3,

Table 6. *Paralichthys californicus.* Effects of water temperature and salinity on vital rates (log_{10}-transformed), conversion efficiencies (arcsin $x^{0.5}$-transformed) and body water content (arcsin $x^{0.5}$-transformed) in large juveniles (2-way ANOVA), ***indicates significance level of $p < 0.05$

Source of variation	SS	df	MS	*F*	p
Vital rates					
Food consumption rate (cal g^{-1} d^{-1})					
Temperature	8.258	2	4.129	24.447	<0.001***
Salinity	1.298	2	0.649	3.843	0.032***
Temperature × Salinity	0.467	4	0.177	0.691	0.604
Error	5.236	31	0.169		
Metabolic rate (cal g^{-1} d^{-1})					
Temperature	0.328	2	0.164	8.986	0.001***
Salinity	0.143	2	0.071	3.912	0.029***
Temperature × Salinity	0.023	4	0.006	0.314	0.866
Error	0.638	35	0.018		
Growth rate (cal g^{-1} d^{-1})					
Temperature	2.837	2	1.419	17.457	<0.001***
Salinity	0.575	2	0.287	3.535	0.041***
Temperature × Salinity	1.081	4	0.270	3.324	0.022***
Error	2.519	31	0.081		
Conversion efficiencies					
Assimilation efficiency (%)					
Temperature	0.275	2	0.137	0.591	0.560
Salinity	0.750	2	0.375	1.614	0.215
Temperature × Salinity	6.470	4	1.617	6.961	<0.001***
Error	7.203	31	0.232		
Gross growth efficiency (%)					
Temperature	3.199	2	1.600	7.818	0.002***
Salinity	0.379	2	0.189	0.925	0.407
Temperature × Salinity	1.031	4	0.258	1.259	0.307
Error	6.343	31	0.205		
Net growth efficiency (%)					
Temperature	4.452	2	2.226	39.158	<0.001***
Salinity	0.050	2	0.025	0.442	0.647
Temperature × Salinity	0.130	4	0.033	0.573	0.684
Error	1.762	31	0.057		
Body water content (%)					
Temperature	0.008	2	0.004	27.968	<0.001***
Salinity	0.002	2	0.001	4.997	0.013***
Temperature × Salinity	0.002	4	0.001	3.841	0.012***
Error	0.005	31	0.0002		

Table 7. *Paralichthys californicus.* Tukey's multiple comparisons of treatment means of salinity effects on vital rates, conversion eficiencies and body water content in large juveniles. Continuous lines joining salinity levels indicate no significant differences between treatments ($p > 0.05$)

Parameter Temperature (°C)	Salinity (ppt)
Vital rates	
Food consumption rate (cal g^{-1} d^{-1})	
14	8 17 34
20	8 17 34
25	8 17 34
Metabolic rate (cal g^{-1} d^{-1})	
14	8 17 34
20	8 17 34
25	8 17 34
Growth rate (cal g^{-1} d^{-1})	
14	8 17 34
20	8 17 34
25	8 17 34
Conversion efficiencies	
Assimilation efficiency (%)	
14	8 17 34
20	8 17 34
25	8 17 34
Gross growth efficiency (%)	
14	8 17 34
20	8 17 34
25	8 17 34
Net growth efficiency (%)	
14	8 17 34
20	8 17 34
25	8 17 34
Body water content (%)	
14	8 17 34
20	8 17 34
25	8 17 34

Fig. 3A). At 14°C, halibut exposed to 8 ppt assimilated <15% of consumed food, far lower than 63 to 76% mean assimilation efficiencies measured at 17 and 34 ppt (Table 4, Fig. 3A). Conversely, between 20 and 28°C, assimilation efficiencies of small halibut did not differ significantly across salinities and averaged 89% (Table 4, Fig. 3A). At 8 ppt, assimilation efficiencies increased rapidly as water temperature increased from 14 to 20°C, but then leveled off between 20 and 28°C (Table 5, Fig. 3A). At 17 ppt, mean assimilation efficiencies did not vary significantly with water temperature and averaged 85.1% (Table 5, Fig. 3A). Conversely, at 34 ppt, mean assimilation efficiencies increased from 63% at 14°C to 98.6% at 20°C, but did not vary significantly between water temperatures of 14, 25 and 28°C (Table 5, Fig. 3A).

Significant interaction effects of water temperature and salinity on assimilation efficiencies of large halibut revealed that the main effects of these treatment variables were masked by data variability in the 2-way ANOVA (Table 6). Further analysis with 1-way ANOVAs and Tukey's multiple comparisons reveal that both salinity and water temperature had effects on assimilation efficiencies of large halibut (Tables 7 & 8). At 14°C, large halibut exposed to 8 ppt assimilated only 20% of the food consumed, significantly less than at 17 or 34 ppt (Table 7, Fig. 4A). Conversely, at 20°C, large halibut exposed to 8 and 17 ppt assimilated significantly more food than those at 34 ppt, but no significant differences in assimilation efficiencies were detected between any salinity at 25°C due to high data variability (Table 7, Fig. 4A). At 8 ppt, mean assimilation efficiencies increased significantly as water temperature increased from 14 to 20°C; however no significant differences were detected between assimilation efficiencies at 14 and 25°C, and 20 and 25°C (Table 8, Fig. 4A). At 17 ppt, mean assimilation efficiencies of large halibut at 14

Table 8. *Paralichthys californicus.* Tukey's multiple comparisons of treatment means of temperature effects on vital rates, conversion eficiencies and body water content in large juveniles. Continuous lines joining temperature levels indicate no significant differences between treatments ($p > 0.05$)

Parameter Temperature (°C)	Salinity (ppt)
Vital rates	
Food consumption rate (cal g^{-1} d^{-1})	
8	14 25 20
17	14 25 20
34	14 25 20
Metabolic rate (cal g^{-1} d^{-1})	
8	14 20 25
17	14 20 25
34	14 20 25
Growth rate (cal g^{-1} d^{-1})	
8	14 25 20
17	14 20 25
34	14 25 20
Conversion efficiencies	
Assimilation efficiency (%)	
8	14 25 20
17	14 20 25
34	20 14 25
Gross growth efficiency (%)	
8	14 25 20
17	20 14 25
34	14 20 25
Net growth efficiency (%)	
8	14 25 20
17	14 25 20
34	14 25 20
Body water content (%)	
8	14 20 25
17	14 20 25
34	14 20 25

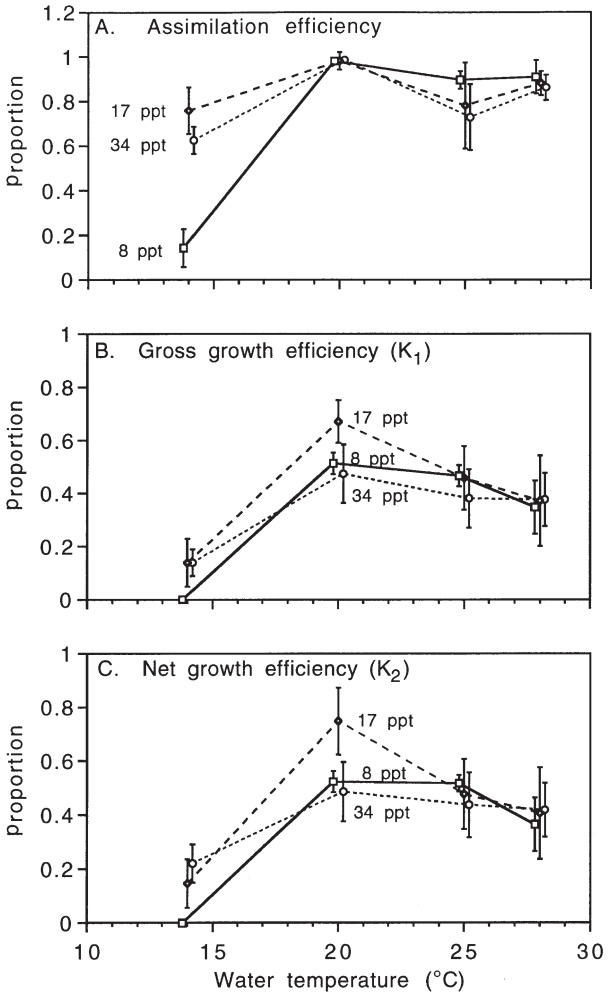

Fig. 3. *Paralichthys californicus*. (A) Assimilation efficiency, (B) gross growth efficiency, and (C) net growth efficiency of small juveniles at various combinations of water temperature and salinity. Rates are standardized to the mean halibut size of 6.6 g dry wt. Symbols are staggered to show SE bars

and 20°C were significantly higher than in fish at 25°C (Table 8, Fig. 4A). At 34 ppt, assimilation efficiency of large halibut did not vary significantly between 14 and 20°C, but it was significantly higher at 25°C (Table 8, Fig. 4A).

Gross growth efficiency (K_1)

Gross growth efficiencies of small halibut varied significantly with water temperature, but not with salinity, and no significant interactions between the 2 treatment variables were detected (Tables 3 & 4, Fig. 3B). Small halibut exposed to 8 ppt and 14°C did not use energy for growth (K_1 = 0), but K_1 > 0 at higher temperatures (Table 5, Fig. 3B). Conversely, at 17 and 34 ppt, K_1 of small halibut increased from 13.9% at 14°C, peaked at 47.4 to 67.0% at 20°C, but did not differ significantly between 14, 25, and 28°C (Table 5, Fig. 3B).

K_1 of large halibut varied with water temperature, and although 2-way ANOVA did not detect significant effects of salinity or interactions of the treatment variables (Table 6), 1-way ANOVA revealed that at 20°C, K_1 of large halibut exposed to 34 ppt was significantly lower than K_1 at 8 or 17 ppt (Table 7, Fig. 4B). At 8 ppt, K_1 of large halibut increased as temperatures increased from 14 to 20°C, but did not differ between 14 and 25°C (Table 8, Fig. 4B). At 17 ppt, K_1 of large halibut did not differ between 14 and 20°C, but declined significantly between 20 and 25°C (Table 8, Fig. 4B). K_1 of large halibut did not vary significantly with temperature at 34 ppt (Table 8, Fig. 4B).

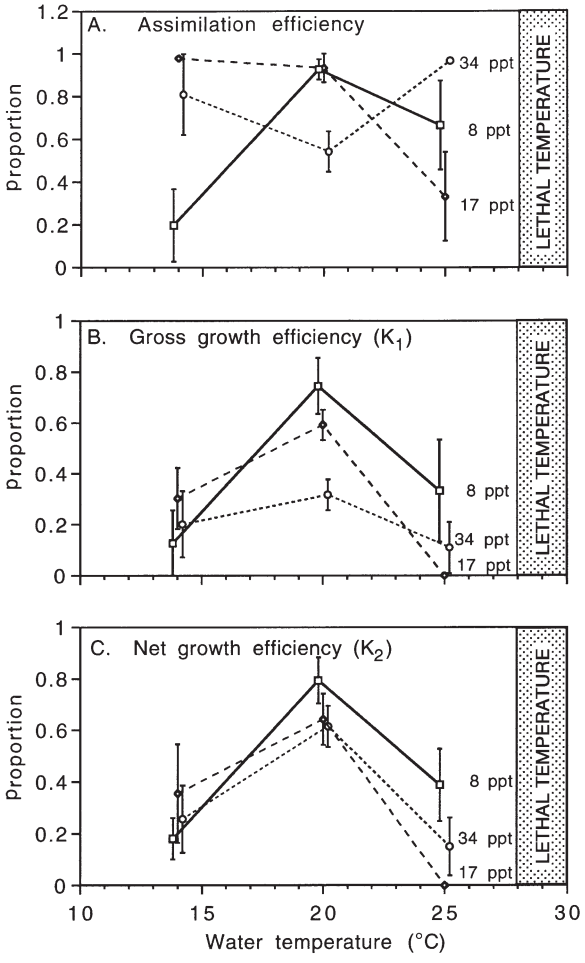

Fig. 4. *Paralichthys californicus*. (A) Assimilation efficiency, (B) gross growth efficiency, and (C) net growth efficiency of large juveniles at various combinations of water temperature and salinity. Rates are standardized to the mean halibut size of 50.4 g dry wt. Symbols are staggered to show SE bars. The shaded bar indicates the lethal temperature for large juveniles

Net growth efficiency (K_2)

Net growth efficiencies of small halibut varied with water temperature, and although 2-way ANOVA did not detect significant effects of salinity or interactions of the treatment variables (Table 3), 1-way ANOVA revealed that at 14°C, K_2 of small halibut exposed to 8 ppt was significantly lower than K_2 at 34 ppt (Table 4, Fig. 1C). Although K_2 of small halibut exposed to 34 ppt stayed relatively constant across all temperatures, K_2 in fish exposed to 8 and 17 ppt increased sharply between 14 and 20°C, and then leveled off between 20 and 28°C (Table 5, Fig. 3C).

K_2 of large halibut varied with water temperature but not with salinity, and no significant interactions were detected between the 2 treatments (Table 6 & 7, Fig. 4C). At all 3 salinities, K_2 of large halibut peaked at 20°C, while no differences were detected between K_2 at 14 and 25°C (Table 8, Fig. 4C).

Body water content

Body water content of small halibut varied with salinity but not with water temperature, and no significant interactions were detected between treatments (Tables 3 & 5, Fig. 5A). Small halibut exposed to 14°C water had higher body water content at 8 than at 34 ppt, but no salinity effects were detected in fish at 20 to 28°C (Table 4, Fig. 5A).

Both water temperature and salinity affected body water content in large halibut, and significant interactions were detected between the 2 treatments (Table 6, Fig. 5B). At 14°C, large halibut exposed to 8 ppt retained more water in their tissues than fish at 17 and 34 ppt (Table 7, Fig. 5B). No salinity effects were detected at 20°C; however, fish exposed to 25°C retained more water in their tissues at 8 and 17 than at 34 ppt (Table 7, Fig. 5B). Furthermore, mean body water content in large halibut exposed to 8 ppt was higher at 14 than at 20°C, and highest at 25°C (Table 8, Fig. 5B). At 17 ppt, mean body water content stayed relatively constant between 14 and 20°C, but increased sharply at 25°C (Table 8, Fig. 5B). At 34 ppt, body water content gradually increased with temperature from 14 to 25°C (Table 8, Fig. 5B).

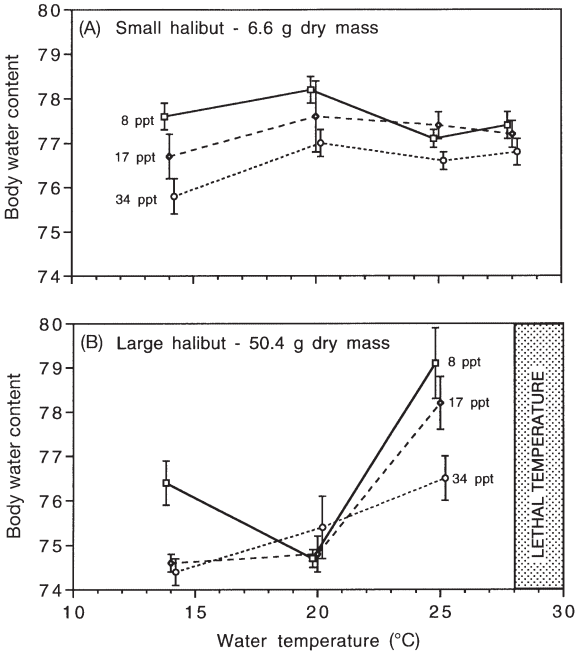

Fig. 5. *Paralichthys californicus*. Whole body water content of (A) small and (B) large juveniles at various combinations of water temperature and salinity. Data are standardized to the mean halibut sizes of 6.6 g (small) and 50.4 g (large) dry wt. Symbols are staggered to show SE bars. In (B), the vertically shaded bar indicates the lethal temperature for large juveniles

DISCUSSION

Acute environmental stress usually results in mortality, while subtle stress affects growth and reproduction (Adams 1990, Rice 1990). Manifestations of environmental stress are often stage-specific; that is, a specific level of a stressor with acute or pronounced effects on one life stage (e.g. larvae) might have little effect on another (e.g. juveniles). This is particularly true in fish that inhabit different environments during their life cycle. Changes in water temperature and salinity experienced by fish during migrations can affect growth rates due to the energy demands of ion exchange and osmoregulation. Habitat transitions can also depress energy intake, as appetite or ability to assimilate energy is reduced, or they can increase maintenance energy requirements (Brett 1979, Brett & Groves 1979). In either case, growth rate will decrease, unless the organism can compensate by increasing energy intake or reducing maintenance costs.

Changes in growth rate reflect changes in the food resource, habitat, or physiological condition of a fish, and are thus sensitive indicators of environmental stress (Rice 1990). Because growth integrates the effects of all biotic and abiotic factors influencing the fish, energy budget studies can be used to deconstruct the growth pattern and separately analyse the effects of environmental stress on energy intake and loss components. Thus, one can not only assess how specific stressors affect growth rate patterns, but also elucidate mechanisms and compensatory processes underlying the growth process.

Environmental effects on juvenile halibut

Ontogenetic differences were clearly evident in energetic and water balance responses of juvenile halibut to water temperature and salinity. These differences offer a physiological and energetic explanation for the estuarine dependence of small juvenile halibut, as well as for their need to emigrate to the open coast as they grow. Sharp changes in water temperatures and salinity caused by estuarine mouth closures can reduce growth, and in extreme cases, survival of both small and large juvenile halibut.

Small halibut were able to grow and osmoregulate over the entire range of water temperatures (14 to 28°C) and salinities (8 to 34 ppt) tested, except when exposed to the lowest set of temperature/salinity, i.e. 14°C and 8 ppt. As water temperatures increased from 14 to 28°C, small halibut at all salinities compensated for elevated metabolic rates by consuming more food. By maintaining food assimilation around 80%, small halibut were able to allocate significant proportions of ingested and assimilated energy towards growth at almost all temperature and salinity combinations tested in this study. However, small halibut experienced severe weight loss at 14°C and 8 ppt due to significantly lower food assimilation (14.3%) which proved insufficient for satisfying their metabolic needs. Teleosts are slightly hyperosmotic relative to their environment at 8 ppt and will gain water in their tissues unless they are able to osmoregulate effectively (Schmidt-Nielsen 1975). This ability to osmoregulate depends on water temperature (Schmidt-Nielsen 1975, Brett 1979). At 14°C, whole-body water content of small halibut exposed to 8 ppt was 2% higher than that of halibut at 34 ppt, indicating a breakdown in osmoregulatory function of individuals exposed to low salinity. Conversely, at higher water temperatures, there were no differences in body water content between halibut at any of the salinities tested, and thus no evidence of osmoregulatory breakdown. It is likely that osmoregulatory stress at the lowest temperature interfered with the halibut's ability to absorb nutrients. In estuarine and marine fish, including anadromous and catadromous species, intestinal nutrient transporters (protein carriers) are coupled to ionic gradients (particularly Na^+) in the intestinal lumen, and are thus affected by changes in salinity (Ferraris & Ahearn 1984, Collie 1985, Lionetto et al. 1996, Nordrum et al. 2000). From 28 to 64% of total absorption in the intestine may be accomplished by carrier-mediated transport which maintains an Na^+ gradient by directing the transport of Na^+ into the intestinal lumen and coupling this with nutrient transport from the lumen into the intestinal cells (Ferraris & Ahearn 1984, Collie 1985, Nordrum et al. 2000). In seawater, the Na^+ gradient needed for nutrient transport is provided without energetic cost, but at low salinities, the ion gradient may disrupt nutrient transport, and thus, food assimilation.

Energetic and osmoregulatory responses of large juvenile halibut to water temperature and salinity differed markedly from those of smaller juveniles. At all salinities, large halibut lost body mass at 25°C and experienced >90% mortality at 28°C. Even at 14°C, large halibut experienced slight weight loss at 17 and 34 ppt, but lost significantly more weight at 8 ppt. Consumption of food by large halibut was significantly depressed at 14 and 25°C and additionally, halibut exposed to 14°C and 8 ppt assimilated <20% of the energy they consumed. Under these conditions, energy intake was grossly insufficient for maintainance. Large halibut also experienced osmoregulatory stress in diluted seawater at 14 and 25°C, as indicated by sharp increases in body water content. Osmoregulatory stress in diluted seawater, coupled with the inability to balance energy intake with metabolic costs caused large halibut to lose body mass at 14 and 25°C.

Large halibut were able to grow only at 20°C, and growth rates at this temperature were not affected by salinity. At 20°C, large halibut exposed to diluted seawater treatments did not appear to be under osmoregulatory stress as whole-body water composition stayed near baseline levels (34 ppt). Large halibut exposed to 20°C consumed more food, but assimilated less, in full-strength seawater than in diluted seawater, yet metabolic costs did not vary with salinity. Thus, I did not observe the expected increase in growth of halibut in full-strength seawater compared to those reared in in diluted seawater, as the halibut at lower salinities compensated for reduced food intake by increasing food assimilation and allocating a larger proportion of consumed energy to growth.

Implications for halibut growth in southern California coastal wetlands

Coastal lagoons and estuaries in southern California are essentially urban wetlands that experience large seasonal and interannual variations in rainfall and streamflow, and hence in water temperature and salinity regimes. Additionally, anthropogenic disturbances can trigger episodic changes in water temperature, salinity and dissolved oxygen levels in the system (Zedler 2001). For example, the tidal prism in many of these wetlands is greatly reduced due to construction of roadways and rail lines that often bisect the wetland, and due to channelization and dredging of waterways for flood control, or port and marina construction (Zedler 2001). Consequently, sand, cobble, and debris occassionally accumulate near the mouth and close the

wetland to tidal action, leading to dramatic changes in environmental conditions within the impounded system (Nordby & Zedler 1991, Zedler 2001). Mouth closures are particularly common during winter (November to March), as offshore storms accumulate materials near the mouth, restricting tidal flow and causing reduced salinities, water temperatures and dissolved oxygen levels in wetlands (Nordby & Zedler 1991, Zedler 2001). Conversely, prolonged periods of mouth closure during the dry warm season (April to October) are marked by elevated water temperatures, salinity, and hypoxia (Nordby & Zedler 1991, Zedler 2001). However, dry season mouth closures are relatively rare due to the absence of large storm events. Using results from these experiments in conjunction with environmental patterns observed in coastal wetlands (Fig. 6), I was able to assess the suitability of these habitats for small and large juvenile halibut, and the emigration patterns exhibited by large juveniles.

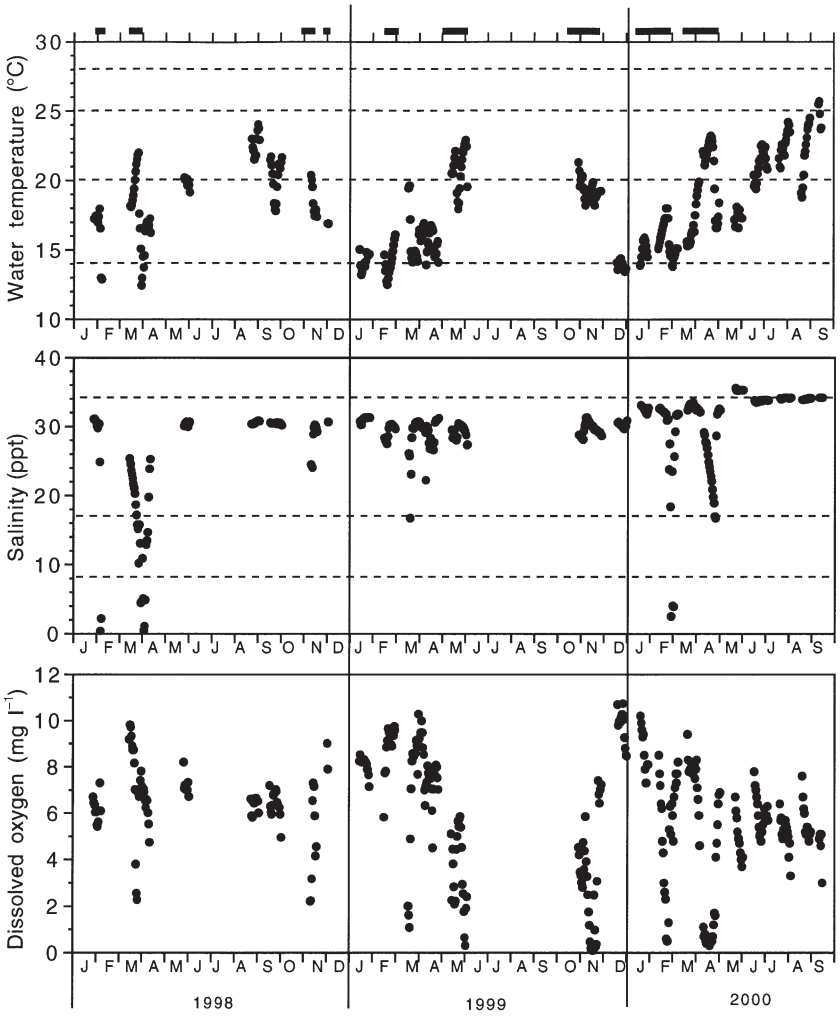

Fig. 6. Daily mean water temperature (top), salinity (center), and dissolved oxygen levels (bottom) measured with a YSI datalogger 0.3 m above the bottom in a large channel in Los Penasquitos Lagoon, San Diego county, CA. Each point represents the average of measurements taken every 15 min over 24 h. The horizontal broken lines indicate the experimental levels tested in this study. Bars at the top of the figure indicate closure of the lagoon mouth

Under the feeding conditions tested, small halibut were able to maximize their growth over almost the entire ranges of water temperature and salinity tested. Small juveniles can thus take full advantage of estuarine habitats where abundant food resources, warm temperatures and low abundance of predators will promote growth, fitness and survival. However, small halibut may still experience a potential growth bottleneck during winter, when mouth closures cause sudden declines in water temperature and salinity. For example, over a 3 yr period from January 1998 to September 2000, Los Penasquitos Lagoon experienced 9 mouth closure episodes, 8 of which occurred during the winter (Fig. 6). The mouth remained closed from several days to over a month, and water temperatures and salinity during this time frequently dropped below 14°C and 8 ppt, respectively (Fig. 6). Under these conditions, small halibut lose weight and experience a breakdown in osmoregulatory ability. In the lagoon, this effect would be even more severe as prey organisms for halibut are less abundant during the winter.

Large halibut are less tolerant of variable water temperature and salinity. Weight loss and a breakdown in water balance ability occurred at water temperatures lower and higher than 20°C, especially at diluted salinities, and large halibut suffered >90% mortality at 28°C at all salinities tested. During the summer, small creeks and channels in southern California estuaries typically exhibit water temperatures in the lethal range for large halibut. Larger channels provide thermal refuge, but occasionally exhibit summer temperatures that are suboptimal for large halibut (Fig. 6). During the winter, low water temperatures and salinities, especially during mouth closure events, can be particularly stressful, and the food resources (small gobiids) typically found in coastal wetlands might no longer be energetically beneficial to large halibut. Thus, large halibut prefer open coast habitats (Kramer 1991), where relatively stable water temperature and salinity regimes and an abun-

dant supply of large prey such as northern anchovies and mysids (Plummer et al. 1983) are more likely to ensure continued growth and fitness.

Hypoxia is another environmental factor that can limit growth of juvenile halibut, but was outside the scope of this study. Coastal wetlands in southern California often experience dramatic declines in dissolved oxygen levels during mouth closures and during warm summer nights. Sub-lethal levels of dissolved oxygen may limit growth of juvenile flatfish by restricting their feeding, decreasing food digestion and food conversion efficiency, and by increasing metabolic costs due to increased activity caused by avoidance behavior (Yamashita et al. 2001). Thus, hypoxia, water temperature and salinity interact to affect behavioral and physiological processes and may be particularly detrimental to large juvenile halibut with narrow tolerance ranges. Future work on the ecophysiology of juvenile California halibut should include an assessment of the effects of hypoxia.

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