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Abstract

Energetic responses of steelhead *Oncorhynchus mykiss* to climate-driven changes in marine conditions are expected to affect the species' ocean distribution, feeding, growth, and survival. With a unique 18-year data series (1991–2008) for steelhead sampled in the open ocean, we simulated interannual variation in prey consumption and growth efficiency of steelhead using a bioenergetics model to evaluate the temperature-dependent growth response of steelhead to past climate events and to estimate growth potential of steelhead under future climate scenarios. Our results showed that annual ocean growth of steelhead is highly variable depending on prey quality, consumption rates, total consumption, and thermal experience. At optimal growing temperatures, steelhead can compensate for a low-energy diet by increasing consumption rates and consuming more prey, if available. Our findings suggest that steelhead have a narrow temperature window in which to achieve optimal growth, which is strongly influenced by climate-driven changes in ocean temperature.

Steelhead *Oncorhynchus mykiss*, the anadromous form of rainbow trout, are declining throughout much of their endemic range in Asia and North America (Augerot 2005; Good et al. 2005). Major freshwater factors responsible for decreased survival of steelhead are relatively well known, i.e., mortality associated with hydroelectric dams, irrigation water withdrawal, degraded freshwater habitat and pollution, overharvest, and poor hatchery practices (e.g., Williams 2005), while marine factors remain largely unknown. However, about half of the total life cycle mortality of steelhead occurs in the marine environment, where smolt (ocean age-0)-to-adult survival rates typically range

from 2% to 10% (Quinn 2005). Furthermore, overall recruitment variations and trends of British Columbia steelhead populations between 1977 and 1999 appear to be related to variation in marine, not freshwater, survival (Ward 2000; Welch et al. 2000).

Climate-driven variation in the environment can result in energetic trade-offs that strongly influence marine distribution, feeding, growth, and survival of steelhead and other species of Pacific salmon *Oncorhynchus* spp. (e.g., Welch et al. 2000; Beauchamp et al. 2007). Prey availability, its energetic content, and water temperature have been identified as the most

important factors affecting growth, and ultimately survival, of salmon at sea (e.g., Quinn 2005; Seo et al. 2006; Beauchamp et al. 2007; Beauchamp 2009). Climate variations can influence the growth of salmon by affecting those factors directly or indirectly, e.g., directly through changes in ocean temperatures or indirectly through changes in prey abundance, distribution, or composition that affect energy consumed by salmon. The physiological response of salmon to changes in ocean temperature may result in altered metabolism, affecting the portion of energy allocated to somatic and gonadal growth. Faster growth leads to larger size at age, which reduces susceptibility to size-selective natural mortality (Ward et al. 1989; Moss et al. 2005; Cross et al. 2009; Duffy and Beauchamp 2011) and increases reproductive success (Quinn 2005). Successful growth during each marine life stage can enhance survival through subsequent life stages.

Steelhead habitats in the North Pacific Ocean are dynamic and can be influenced by climatic shifts such as those associated with variations in the Pacific Decadal Oscillation (Mantua and Hare 2002) and North Pacific Gyre Oscillation (Di Lorenzo et al. 2008). A mechanistic understanding of energetic responses by steelhead to factors limiting growth is needed to evaluate potential effects of future changes in climate and ocean conditions on steelhead populations. The objectives of this study were to simulate interannual variation in life-stage-specific consumption and growth efficiency of steelhead in North Pacific habitats, to evaluate temperature-dependent growth of steelhead during past climate events, and to model growth potential of steelhead in the North Pacific Ocean under future climate scenarios.

METHODS

Study Area

North American steelhead distributions in the North Pacific Ocean vary by life stage. Ocean age-0 steelhead begin leaving coastal waters over the continental shelf of North America soon after entering saltwater in the spring (Hartt 1980; Hartt and Dell 1986) and spend their first summer–fall at sea in the northeastern North Pacific Ocean and Gulf of Alaska (Burgner et al. 1992). At subsequent life stages, steelhead distribution during early spring is concentrated near the southern limit of their range in the North Pacific Ocean, between 42°N and 52°N latitude (Burgner et al. 1992; Welch et al. 1998). During the summer, steelhead distribution extends northward and westward, while remaining largely south of the Aleutian Islands (Hartt and Dell 1986; Burgner et al. 1992; Welch et al. 1998), and by August, North American steelhead are distributed as far west as North Pacific waters off the southern Kuril Islands, Russia (Kovalenko et al. 2005; Myers et al. 2005; Figure 1). Autumn and winter migrations are poorly understood due to low and sporadic sampling (Welch et al. 1998).

Steelhead samples and associated biological data used in our study were collected with research gill nets and longlines in late June and early July, during annual surveys of two Japanese research vessels (*Wakatake maru*, 1991–2009 and *Oshoro maru*, 1991–2002; Figure 1). Fishing stations for the *Wakatake maru* were located primarily along a 180°-longitude survey line that extended from the southern limit of salmon distribution in the central North Pacific Ocean (CNP) to the northern Bering Sea (38–58°N). Almost all steelhead caught along the 180° survey
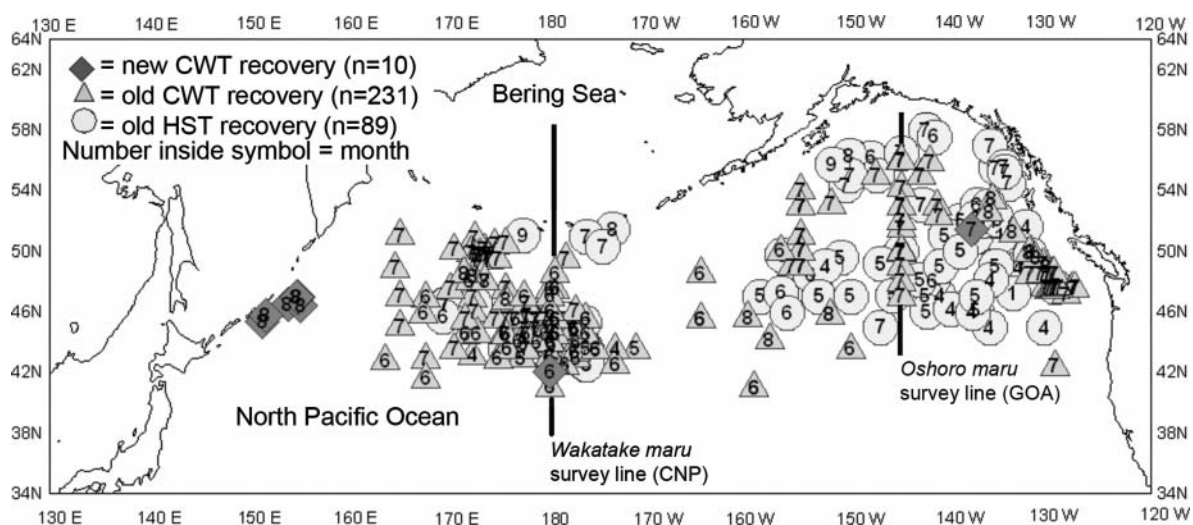

FIGURE 1. The known ocean distribution of North American steelhead as determined by high seas tagging experiments, 1955–2005 (Myers et al. 2005), and location of Japanese research vessel survey lines in the central North Pacific Ocean (CNP, *Wakatake maru*) and Gulf of Alaska (GOA, *Oshoro maru*). Coded-wire tag (CWT) recoveries of North American steelhead were used to calculate the number of days spent at sea since emigration from freshwater. New recoveries are those reported for the first time in 2005. High seas tags (HST) are external tags attached to salmon at sea and later recovered in North America. Month is high seas recovery month for CWT fish or high seas release month for HST fish and *n* = total number of tagged fish that were recovered.

line during June–July were distributed in the CNP between 45°N and 51°N (e.g., Fukuwaka et al. 2008). Fishing stations in the Gulf of Alaska (GOA) for the *Oshoro maru* were located primarily along a 145°W-longitude survey line from 44°N to 56°N, and most steelhead were caught from 49°N to 56°N (e.g., Myers et al. 2001). Gillnet operations of both vessels were conducted in international waters only.

Bioenergetics Model

Based on bioenergetics model simulations of an 18-year time series using annual growth increments, diets during the June–July growth period, and sea surface temperatures, we estimated and compared interannual, temperature-dependent differences in annual marine consumption and growth efficiency by different ages of steelhead in the GOA and CNP, then explored how future climate scenarios might affect growth. Bioenergetics models are useful tools for assessing how changes in feeding rate, thermal experience, and diet (prey availability) are ultimately expressed as net growth for different sizes of fish (McCarthy et al. 2009). We used the Wisconsin Bioenergetics model (Hanson et al. 1997), the most widely used such model (e.g., Ney 1990; Chipps and Wahl 2008; Hartman and Kitchell 2008), parameterized for steelhead (Rand et al. 1993). The model is an energy balance equation where the input in energy is equal to the output of energy in the form of waste, metabolism, and growth.

$$\text{Consumption} = \text{metabolism} + \text{waste} + \text{growth} \quad (1)$$

Simulation Model Inputs

Four factors play a major role in determining the growth of a fish in this model: (1) body mass, (2) feeding rate, (3) energetic content of the prey, and (4) temperature (Beauchamp 2009). The primary sources of bioenergetic variability, prey and temperature, can differ substantially from year to year. We used field-based estimates as inputs for each of the four factors in the model as described below, allowing us to determine their relative influence under empirically based growth scenarios.

Body mass.—Model inputs for body mass (initial and final weights at age) of steelhead were back-calculated from scale measurements of annual growth increments in length and length–weight relationships (Brodeur et al. 2004). Scales and associated fork length and whole body weight data were collected from individual fish sampled during Japanese research vessel fishing operations. Procedures for scale collection and aging followed Davis and Light (1985) and Davis et al. (1990). Ocean ages were designated by the number of ocean annuli on scales, e.g., an ocean age-0 fish (no ocean annulus) was in its first year at sea (SW1), an ocean age-1 fish (one ocean annulus) was in its second year at sea (SW2), etc. (Figure 2). Steelhead in the 1991–2008 samples ranged from ocean age 0 to ocean age 4, however, due to small sample sizes of ocean age-0, age-3, and age-4 fish, only ocean age-1 and age-2 fish were used to estimate body mass.

Procedures for measuring scales followed Hagen et al. (2001). All scales with a determinable ocean entry check and clean measurement axis (longest axis of the scale) were used. Scale images were digitized with a microfiche screen scanner and then measured using Optimus Imaging software (Optimus, Seattle, Washington). For ocean age-1 fish, three growth increments were measured: (1) scale focus to ocean entry (freshwater growth, FW), (2) ocean entry to end of first ocean annulus (first year of ocean growth, SW1), and (3) end of first ocean annulus to edge of scale (plus growth, SWPL) (Figure 2). For ocean age-2 fish, four growth increments were measured: FW, SW1, SW2 (second year of ocean growth), and SWPL (Figure 2).

The scale measurement data were used to back-calculate fork length (mm) of each fish (L_i, i = FW, SW1, or SW2; Figure 2) by the Fraser-Lee method (Francis 1990; Ricker 1992; Brodeur et al. 2004):

$$L_i = 30.1 + (L - 30.1) \cdot (S_i/S), \quad (2)$$

where L = fork length (mm) at capture, S_i = scale radius (units) at L_i, S = scale radius at capture, and 30.1 = fork length at scale formation for steelhead (Kesner and Barnhart 1972).

The estimated fork lengths (L_i) were used to back-calculate body weights (W_i; r^2 = 0.94238; N = 894):

$$W_i = 0.0000212 \cdot L_i^{2.8825}, \quad (3)$$

where W_i is the weight at annulus i for steelhead caught in conjunction with this study (Figure 3).

Growth rate in body mass (G) was calculated as (Brodeur et al. 2004)

$$G = (W_i - W_{i-1})/\Delta d, \quad (4)$$

where Δd = estimated number of days between ocean entry (FW) and capture. We calculated Δd for ocean age-1 and ocean age-2 fish separately using data from coded-wire tag (CWT) steelhead recovered during high seas research vessel operations (Figure 1). The release date of CWT fish was subtracted from the recovery date to estimate an average number of days at sea, assuming CWT steelhead emigrated from freshwater within 1 week of release.

Diet proportions.—Model inputs for prey consumed as proportions of the total diet were estimated from stomach content analysis of steelhead collected during Japanese research vessel fishing operations. Stomachs were weighed to the nearest gram before and after removal of the contents, and the weight of the stomach contents were obtained by subtraction. In most years, stomach contents were examined on board the survey vessels using a dissecting microscope. Prey were identified to the lowest taxon possible and grouped into 10 prey categories (euphausiid, copepod, amphipod, other crustacean [e.g., shrimp and crab larvae], squid, pteropod, fish, polychaete, chaetognath, and unidentified). The volumetric contribution of each prey category
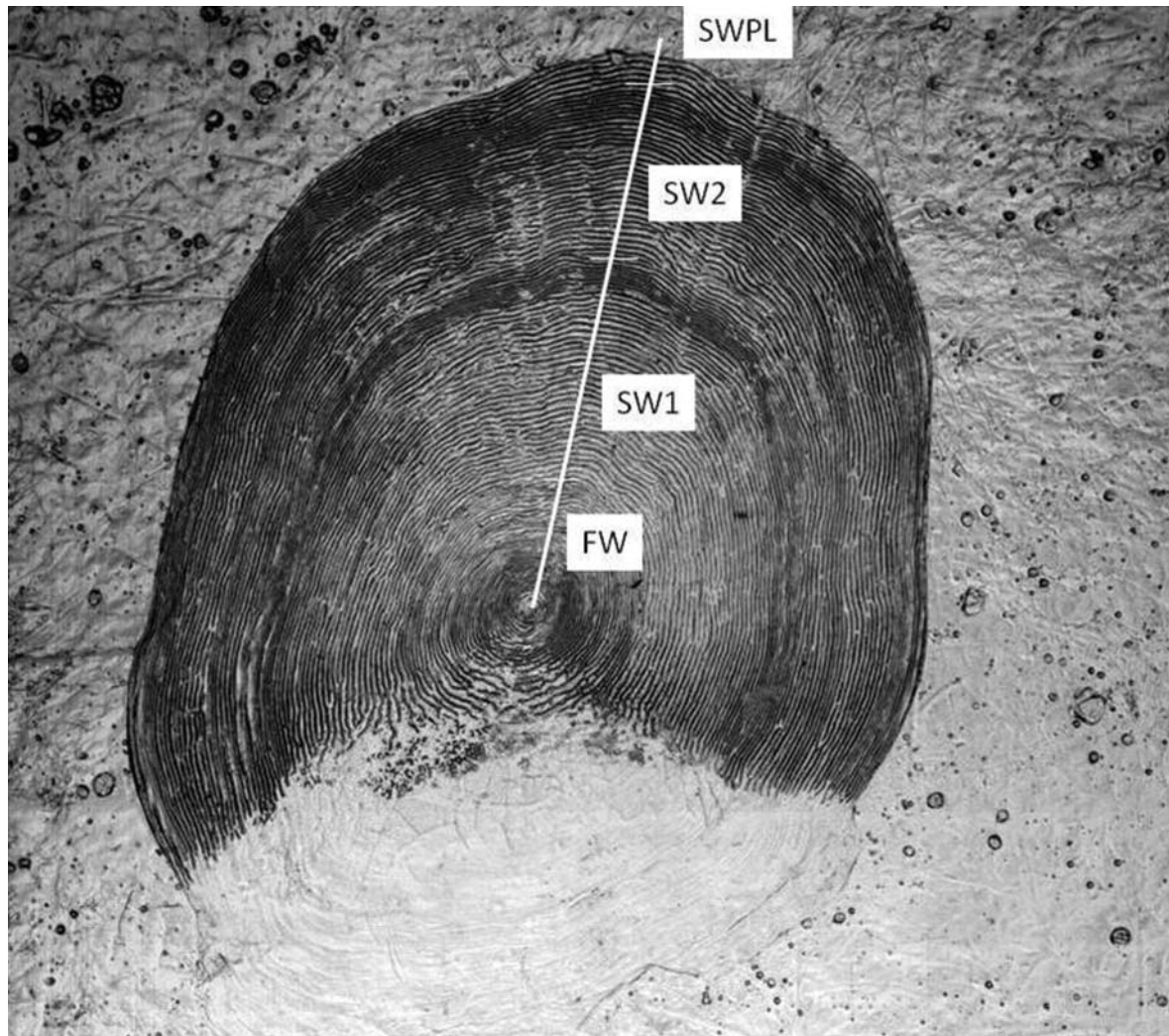
FIGURE 2. The scale of an ocean age-2 steelhead caught in the central North Pacific Ocean in summer 1999 showing the measurement axis and growth increments. For bioenergetics analysis all growth was lagged to the year in which it occurred. FW = freshwater growth; SW1 = first year of ocean growth (ocean age-0 fish in 1997); SW2 = second year of ocean growth (ocean age-1 fish in 1998), SWPL = plus growth, which is growth in the year that the fish was caught.

was estimated visually, and volumetric proportions of each were used as inputs for bioenergetics simulations. Diet proportions during June–July cruises were computed separately for each year (Table 1). For GOA steelhead, diets were stratified into two age groups: (1) ocean age 0 and (2) ocean age 1 and older, based on preliminary statistical analyses that showed diet proportions of these age groups were significantly different (Atcheson 2010). In the CNP there are no age-0 steelhead, so diet proportions were pooled across all ocean age groups (ocean age 1 and older) within each year. The diet composition calculated from June–July surveys was used to approximate the average diet through the entire year. Independent observations of mean monthly lengths of ocean-caught steelhead from 1956 to 1985 indicate growth is rapid and continuous through all months of the year (Burgner et al. 1992). Our scale samples indicate June–July is a period of rapid growth that contributed significantly to the

annual growth increment (e.g., see SWPL growth, Figure 2). For example, the average plus growth for ocean age-1 steelhead caught in June–July was 52.8% of the total annual ocean growth of an ocean age-2 fish caught in the GOA (1993–2001). Thus, we assumed that the corresponding diet was representative of the annual energy budget of steelhead.

Prey energy density.—Model inputs for prey energy density were calculated using the published caloric value (J/g) of each prey category based on the species that comprised that category (Davis et al. 1998; Davis 2003): squid (6,532 J/g), fish (5,119 J/g), polychaete (3,650 J/g), euphausiid (3,516 J/g), other crustacean (2,980 J/g), copepod (2,625 J/g), amphipod (2,466 J/g), pteropod (2,294 J/g), chaetognath (1,905 J/g), and unidentified (2,776 J/g). Unidentified material in stomach contents was assumed to be remnants of the other diet categories; therefore, the energy value for this prey category was an average of all
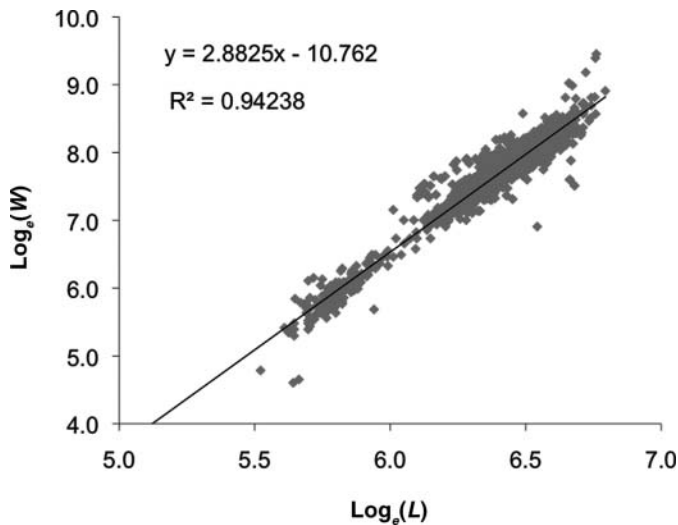
FIGURE 3. Regression of $\log_e(W)$ on $\log_e(L)$ of steelhead caught in the North Pacific Ocean during June–July 1991–2009. W = whole body wet weight, L = fork length (measured from tip of snout to fork of tail).

other categories. Prey density for "fish" was an average energy value of the top three species consumed: myctophids, Atka mackerel *Pleurogrammus monopterygius*, and threespine sticklebacks *Gasterosteus aculeatus*.

Temperature.—Model inputs for temperature were site- and time-specific. Steelhead are surface oriented and high seas catch data suggest that they remain in the upper 20 m of the ocean (Burgner et al. 1992), with relatively brief periodic dives of 40–60 m (Walker et al. 2000a, 2000b). Mixed-layer depths in the GOA during summer months are typically between 20 and 30 m allowing sea surface temperatures (SSTs) to be representative of steelhead's thermal experience. Monthly mean SST was calculated separately for the GOA and CNP regions using the National Centers for Environmental Predictions and National Center for Atmospheric Research reanalysis of monthly SST means (National Oceanic and Atmospheric Administration (NOAA), Earth Systems Research Laboratory, http://www.esrl.noaa.gov/psd/data/timeseries/) (Table 2).

Model Simulations

Interannual variation in consumption and growth efficiency.—Bioenergetic model simulations were used to estimate annual percentage of maximum consumption (% C_{max} = $C/C_{max} \cdot 100$), annual consumption of each prey category and total consumption (g/year), annual total energy consumed (kJ/year), and growth efficiency (GE = annual weight gain [g]/annual consumption [g/year]) of steelhead during the first year of ocean growth (SW1) in the GOA and second year of ocean growth (SW2) in both the GOA and CNP. The models were fitted to back-calculated estimates of initial (W_i) and final (W_f) body mass of ocean age-1 and age-2 steelhead in the GOA and CNP. All field-based inputs to the model, as described above, were spatially lagged to account for migration and

temporally lagged to match year of growth. We assumed that SW1 growth of steelhead occurred in the GOA and SW2 growth occurred in the region where fish were sampled. Consequently, SW1 growth for an ocean age-1 steelhead caught in the CNP during 1999 was paired with GOA diet and temperature data from 1998 in model simulations of SW1 consumption and growth efficiency. Time series varied for each of the inputs due to limitations of sample size, collection year, or lag to year of growth. The time series of model outputs was limited by the input variable with the fewest years of field data.

Temperature-dependent growth response.—Tropical El Niño events are a major source of interannual climate variation in the North Pacific. Our time series of field data included information collected during the strong El Niño of 1997 and La Niña of 1999. To help understand how interannual variation in climate affects steelhead growth and, ultimately, survival, we compared model outputs for temperature-dependent growth in the first ocean year (SW1) of steelhead in the GOA during the anomalously warm year of 1997 and anomalously cool year of 1999.

Model inputs included age-specific annual consumption rates, diet proportions, and the corresponding prey energy densities and were applied to a range of temperatures to identify the optimal temperature for growth, given those feeding conditions. Consumption rates were averages across ocean ages (age 1 and age 2) of model output from our previous simulations of SW1 growth of CNP steelhead in 1997 and 1999 (Table 3). Model inputs for 1997 were prey energy density (4,420 J/g), initial weight (49 g and 920 g), and mean feeding rate (55% C_{max}). Model inputs for 1999 were prey energy density (5,582 J/g), initial weight (58 g and 929 g), and mean feeding rate (46% C_{max}). Model inputs were applied to a range of temperatures (1–25°C) to identify optimal temperatures for growth.

We evaluated whether growth would be reduced by deviations from the optimal temperature for growth during the warmest months (June–October). If the mean thermal experience deviated from the optimal temperature for growth, we estimated the percentage reduction G_{red} in daily growth that would result by

$$G_{red} = (G_{exp} - G_{opt})/G_{opt} \cdot 100, \qquad (5)$$

where G_{exp} = daily growth at the mean thermal experience during June–October and G_{opt} = daily growth at the optimal growth temperature.

Growth based on future climate scenarios.—As inputs for baseline simulations, we calculated mean annual initial body weights, composite energy densities of diets, and consumption, based on the mean annual %C_{max} for SW1 growth of CNP, age-1 steelhead and SW2 growth of CNP, age-2 steelhead from our previous simulations (Tables 3, 4) and mean monthly temperatures for the study period (1993–2002 for SW1 growth in the GOA; 1991–2008 for SW2 growth in the CNP; Table 2). Model inputs for baseline simulations of SW1 growth were 69.7 g initial body weight, 4,963 J/g composite energy density,

TABLE 1. Annual mean proportions (by volume) of each prey category in the stomach contents of steelhead in summer (June–July) samples from the North Pacific Ocean by region and two ocean age categories, ocean age-0 and older fish (≥ ocean age 1). GOA = Gulf of Alaska, CNP = central North Pacific Ocean, n = sample size, SQ = squid, FI = fish, PT = pteropod, AM = amphipod, PO = polychaete, EU = euphausiid, CO = copepod, CR = other crustaceans, primarily crab larvae and shrimp, CH = chaetognath, UN = unidentified. A blank cell indicates that prey was not present.

Region, age	Year	n	SQ	FI	PT	AM	PO	EU	CO	CR	CH	UN
GOA, age 0	1994	11	0.51	0.29	0.13							0.07
	1995	10	0.14	0.64	0.14	0.01				0.06		0.01
	1996	29	0.39	0.40	0.15	0.01	0.05					
	1997	17		0.71	0.17					0.04		0.08
	1998	24	0.27	0.42	0.19	0.03		0.04				0.05
	1999	9	0.37	0.60		0.01						0.02
	2000	27	0.23	0.49	0.07	0.15	0.02	0.02	0.01			0.01
	2001	2		0.99					0.01			
	2002	21	0.36	0.31	0.01	0.20		0.05		0.07		
GOA, ≥ age 1	1993	23	0.33	0.27	0.16	0.09		0.02		0.03		0.10
	1994	28	0.65	0.25	0.05	0.05						
	1995	58	0.48	0.30	0.04	0.07	0.09			0.01		0.01
	1996	24	0.55	0.29	0.10	0.01	0.03					0.02
	1997	31	0.26	0.60	0.06	0.02	0.04			0.01		0.01
	1998	49	0.56	0.27	0.10	0.01	0.04	0.01				0.01
	1999	92	0.31	0.47	0.02	0.04	0.10		0.01			0.05
	2000	60	0.48	0.28	0.05	0.11	0.06	0.01	0.01			
	2001	75	0.47	0.28	0.07	0.08	0.02		0.02	0.02		0.04
	2002	21	0.34	0.27	0.03	0.16	0.01	0.10		0.09		
CNP, ≥ age 1	1991	12	0.70	0.11	0.02	0.15				0.02		
	1992	8	0.49	0.23	0.01	0.13		0.14				
	1993	4	0.60		0.03	0.35		0.02				
	1994	18	0.62	0.29	0.04	0.04						0.01
	1995	10	0.33	0.51	0.01	0.07				0.07		0.01
	1996	21	0.44	0.49		0.07						
	1997	54	0.20	0.38	0.02	0.11	0.23	0.03	0.01	0.02		
	1998	21	0.76	0.22	0.01	0.01						
	1999	9	0.13	0.81	0.01	0.04			0.01			
	2000	28	0.54	0.31			0.14		0.01			
	2001	25	0.27	0.51		0.03	0.16					0.03
	2002	23	0.86	0.12			0.01					0.01
	2003	12	0.76	0.24								
	2004	26	0.74	0.18		0.02	0.05	0.01				
	2005	50	0.33	0.47	0.01	0.01	0.15	0.03				
	2006	38	0.53	0.20	0.06	0.11	0.04		0.01	0.02		0.03
	2007	29	0.70	0.25		0.04			0.01			
	2008	15	0.39	0.29	0.07	0.11	0.08	0.02	0.01	0.02	0.01	
	2009	15	0.33	0.40	0.01	0.06	0.08	0.09		0.03		

4,197 g/year consumption, and 49.7% C_{max} (Table 3). Model inputs for baseline simulations of SW2 growth were 824 g initial body weight, 5,492 J/g composite energy density, 10,922 g/year consumption, and 44.0% C_{max} (Table 4). Baseline temperature inputs were 5.8°C in January and 10.8°C in July for the GOA and 6.7°C in January and 11.0°C in July for the CNP (Table 2).

Under the A1B greenhouse gas emissions scenario, the SSTs from multimodel average climate change scenarios in the GOA are projected to increase approximately 1.4°C in July and 1.2°C in December by the 2040s and approximately 2.4°C in July and 2.2°C in December by the 2080s (Trenberth et al. 2007). Similarly, these scenarios suggest temperatures in the CNP will increase approximately 1.4°C in both July and December in the 2040s and 2.8°C in July and 2.6°C in December in the 2080s (Overland and Wang 2007). Model simulations were run for 2040 and 2080 with the corresponding projected temperature

TABLE 2. Temporal thermal experience (mean monthly sea surface temperature, °C) used as inputs to bioenergetic models by ocean region and year. GOA = Gulf of Alaska, CNP = central North Pacific Ocean. Source: NOAA Earth Systems Research Laboratory (http://www.esrl.noaa.gov/psd/data/timeseries/).

Region	Year	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
GOA	1993	5.8	5.3	5.3	5.7	6.8	8.9	11.5	13.3	13.3	11.9	9.7	7.7
	1994	6.7	6.1	5.8	6.0	6.8	8.7	11.2	13.8	12.8	10.3	7.9	6.5
	1995	5.8	5.4	5.2	5.1	6.4	7.8	10.5	12.3	13.0	10.7	8.5	7.1
	1996	6.4	5.7	5.6	5.9	6.9	8.6	10.7	13.1	12.8	10.5	8.7	7.1
	1997	6.1	5.7	5.5	5.7	7.0	9.4	12.1	14.2	14.0	11.6	9.3	7.0
	1998	5.6	5.3	5.3	5.6	6.4	8.4	10.9	12.7	11.7	10.6	8.6	6.6
	1999	5.8	4.9	4.3	4.5	5.4	7.4	9.9	12.7	12.2	10.4	7.6	5.9
	2000	4.8	4.4	4.5	4.8	6.0	8.0	10.7	13.2	13.8	11.7	8.6	7.0
	2001	5.9	5.3	5.2	5.2	5.9	7.7	10.7	12.9	12.1	10.2	7.6	6.2
	2002	5.3	4.6	4.6	5.0	6.9	8.6	10.8	13.3	13.4	12.2	9.7	7.6
Mean ($n = 10$)		5.8	5.3	5.1	5.4	6.5	8.4	10.8	13.2	12.9	11.0	8.6	6.9
CNP	1991	8.2	7.3	6.9	6.8	6.9	8.8	11.4	13.6	12.5	10.5	9.0	7.5
	1992	6.1	5.8	5.7	6.2	6.8	8.1	9.6	12.3	12.6	11.3	9.0	7.3
	1993	6.5	6.0	5.6	5.8	6.4	8.2	10.2	13.3	12.3	11.0	9.1	7.4
	1994	6.2	5.9	5.8	6.1	6.6	7.8	11.5	14.7	15.1	12.2	10.6	8.8
	1995	6.9	6.0	6.2	6.3	6.6	8.0	10.1	13.3	13.6	11.6	9.7	8.6
	1996	7.7	6.8	6.4	6.5	7.2	9.0	11.1	14.7	14.5	12.3	10.5	9.0
	1997	7.5	6.4	6.1	6.1	6.7	8.1	10.7	13.0	13.5	10.8	9.2	7.9
	1998	6.8	5.9	5.4	5.7	6.3	7.7	10.9	14.8	14.7	12.2	9.6	7.5
	1999	6.7	5.9	5.5	5.5	6.5	7.6	9.9	12.3	12.8	11.6	9.9	7.8
	2000	7.0	5.8	5.3	5.6	6.3	7.5	10.1	13.7	14.0	11.0	8.7	6.5
	2001	5.4	4.9	4.8	5.4	6.4	8.1	12.1	14.4	14.6	12.2	10.0	7.8
	2002	6.2	5.8	5.5	6.0	7.0	8.1	11.0	12.7	13.2	11.5	9.1	7.1
	2003	5.7	5.3	5.4	5.8	6.7	8.0	11.6	14.3	14.5	11.9	9.5	7.8
	2004	6.7	5.6	5.4	5.7	6.5	7.9	10.8	13.8	14.0	12.4	10.0	7.7
	2005	6.6	5.9	5.5	5.6	6.4	7.7	10.6	13.5	15.0	12.3	10.5	8.9
	2006	6.9	5.9	5.7	6.0	6.7	8.8	11.7	15.0	15.9	12.1	10.5	8.4
	2007	6.6	5.7	5.9	5.9	7.0	8.8	12.0	13.5	13.6	12.3	9.7	7.8
	2008	6.5	5.7	5.2	5.8	6.7	9.0	12.3	15.8	14.4	13.2	10.2	8.0
Mean ($n = 18$)		6.7	5.9	5.7	5.9	6.7	8.2	11.0	13.8	13.9	11.8	9.7	7.9

increase, and the resulting projected growth was compared with our calculated baseline.

RESULTS

Field-Based Input Data

Body mass input data (back-calculated from scales) showed some consistent within-year patterns that need to be considered when interpreting our bioenergetic model results. In most years, initial SW1 body mass (except 1997) and final SW1 body mass (except 2001) of ocean age-1 CNP steelhead were larger than those of ocean age-1 GOA steelhead (paired t-test, initial Wt: $t = 4.33$, df = 7, $P < 0.01$; final Wt: $t = 3.61$, df = 7, $P < 0.01$; Table 3). We attributed this to size-related differences in migration of ocean age-1 steelhead, i.e., larger fish migrated farther westward (to the CNP or beyond) than smaller fish,

which remained in the GOA. In addition, in most years (except 1994) final SW1 weights of ocean age-2 GOA steelhead were larger than those of ocean age-2 CNP steelhead. We attributed this to regional differences in steelhead maturation schedules, i.e., a higher proportion of maturing and mature (postspawn) steelhead were distributed in the GOA than in the CNP, and mature fish had larger final SW1 weights than immature fish of the same ocean age-group.

The most pronounced negative and positive deviations from observed average SW1 weight gain (837 g, SD = 150 g; $n = 33$) during our study period occurred in the same year (1995), i.e., –253 g for GOA, age-1 fish and 274 g for GOA, age-2 fish. Model inputs for diet and thermal experience were the same for both age groups, demonstrating the effect of back-calculated initial and final body weights on model output.

TABLE 3.   Bioenergetic model estimates of consumption (*C*) and growth efficiency (GE) during the first year of ocean growth (SW1; Figure 2) of steelhead in the Gulf of Alaska (GOA), 1994–2002. E = mean composite energy density of stomach contents, based on diets of age-0 steelhead sampled in the GOA (Table 1); W_i = initial body weight at ocean entry and W_f = final body weight at the end of SW1 (Figure 2) for ocean age-1 and age-2 steelhead sampled in the GOA and central North Pacific Ocean (CNP). C_{max} = feeding rate as a percentage of maximum consumption.

Sample region, age	Growth year	Model input			Model output			
		E (J/g)	W_i (g)	W_f (g)	% C_{max}	C (g/yr)	C (kJ/yr)	GE (%)
GOA, age 1	1994	5,356	39	680	40.9	2,671	14,308	24.0
	1995	4,750	54	638	44.9	2,820	13,398	20.7
	1996	5,147	60	797	42.8	3,238	16,663	22.8
	1997	4,420	53	801	51.2	3,967	17,535	18.9
	1998	4,737	40	737	49.3	3,213	15,219	21.7
	1999	5,582	59	684	40.4	2,485	13,871	25.1
	2000	4,745	47	783	50.8	3,449	16,369	21.3
	2001	5,095	54	859	48.1	3,455	17,601	23.3
Mean (*n* = 8)		4,979	51	747	46.1	3,162	15,621	22.2
CNP, age 1	1994	5,356	64	1,121	47.0	4,360	23,354	24.2
	1995	4,750	75	890	49.2	3,903	18,540	20.9
	1996	5,147	75	945	44.6	3,831	19,714	22.7
	1997	4,420	52	994	55.9	4,868	21,518	19.3
	1998	4,737	81	1,020	51.5	4,467	21,159	21.0
	1999	5,582	69	1,134	48.7	4,051	22,613	26.3
	2000	4,745	64	1,045	55.0	4,590	21,779	21.4
	2001	5,095	72	721	43.0	2,946	15,008	22.0
	2002	4,839	71	1,085	52.3	4,758	23,026	21.3
Mean (*n* = 9)		4,963	70	995	49.7	4,197	20,746	22.1
GOA, age 2	1994	5,356	49	861	43.7	3,362	18,008	24.2
	1995	4,750	71	1,182	55.8	5,126	24,352	21.7
	1996	5,147	87	1,023	45.1	4,149	21,353	22.6
	1997	4,420	53	856	52.6	4,224	18,672	19.0
	1998	4,737	61	1,117	55.4	4,845	22,950	21.8
	1999	5,582	52	789	43.6	2,837	15,837	26.0
	2000	4,745	56	1,064	56.3	4,654	22,086	21.7
Mean (*n* = 7)		4,962	61	985	50.4	4,171	20,465	22.4
CNP, age 2	1994	5,356	66	1,167	47.6	4,536	24,297	24.3
	1995	4,750	61	741	46.9	3,260	15,486	20.9
	1996	5,147	45	776	43.9	3,129	16,103	23.4
	1997	4,420	46	845	53.1	4,153	18,357	19.2
	1998	4,737	72	965	51.1	4,223	20,003	21.1
	1999	5,582	47	724	42.6	2,607	14,554	26.0
	2000	4,745	63	876	51.3	3,871	18,372	21.0
	2001	5,095	62	819	46.3	3,313	16,877	22.9
	2002	4,839	55	872	49.4	3,831	18,537	21.3
Mean (*n* = 9)		4,963	57	865	48.0	3,658	18,065	22.2

Interannual Variation in Prey Consumption and Growth Efficiency

In model simulations from field-based data, the range of annual feeding rates was narrower (40% to 56% C_{max}) for steelhead in their first year of ocean growth (Table 3) than in their second year (38% to 59% C_{max}; Table 4). The range of modeled annual growth efficiencies (GEs) was considerably higher for steelhead in their first year of ocean growth (19% to 26%) than for ocean age-2 steelhead in their second year of ocean growth (14% to 20%).

For ocean age-1 steelhead, average annual SW1 feeding rates were lower in GOA fish (46% C_{max}) than in CNP fish (49% C_{max}) during 1994–2000 (Table 3). For ocean age-2 steelhead, average annual SW1 feeding rates were higher (50% of C_{max} in

TABLE 4. Bioenergetic model estimates of consumption rate (C) and growth efficiency (GE) during the second year of ocean growth (SW2; Figure 2) of steelhead in the Gulf of Alaska (GOA) in 1993–2001 and central North Pacific Ocean (CNP) in 1991–2008. E = mean composite energy density of stomach contents, based on diets of ≥ age-1 steelhead sampled in the GOA and CNP (Table 1). W_i = initial body weight at ocean entry and W_f = final body weight at the end of SW2 for ocean age-2 fish sampled in the GOA and CNP. C_{max} = feeding rate as a percentage of maximum consumption.

Sample region, age	Growth year	Model input			Model output			
		E (J/g)	W_i (g)	W_f (g)	% C_{max}	C (g/yr)	C (kJ/yr)	GE (%)
GOA, age 2	1993	4,621	707	3,102	59.2	14,763	68,225	16.2
	1994	5,764	890	3,804	49.8	14,167	81,658	20.6
	1995	5,329	861	2,421	42.4	9,177	48,898	17.0
	1996	5,510	1,182	3,539	45.8	13,397	73,819	17.6
	1997	5,167	1,023	3,291	49.2	13,978	72,230	16.2
	1998	5,510	856	3,446	50.5	12,930	71,243	20.0
	1999	5,140	1,117	2,847	46.6	10,793	55,472	16.0
	2000	5,235	789	2,643	48.1	10,485	54,891	17.7
	2001	5,185	1,064	3,289	50.7	12,938	67,078	17.2
Mean ($n = 9$)		5,273	943	3,154	49.1	12,514	65,946	17.6
CNP, age 2	1991	5,611	681	2,544	41.6	9,877	55,419	18.9
	1992	5,214	587	2,288	46.2	9,249	48,225	18.4
	1993	4,921	851	2,689	49.0	11,611	57,142	15.8
	1994	5,760	735	2,864	44.0	11,146	64,197	19.1
	1995	5,205	1,167	3,051	44.1	12,581	65,486	15.0
	1996	5,555	741	2,666	42.4	10,951	60,838	17.6
	1997	4,600	776	2,256	46.4	10,332	47,524	14.3
	1998	6,138	845	2,583	37.9	9,135	56,075	19.0
	1999	5,144	965	2,681	44.5	10,883	55,981	15.8
	2000	5,655	724	2,665	43.7	9,805	55,452	19.8
	2001	5,136	876	3,389	53.1	14,397	73,948	17.5
	2002	6,303	819	2,918	39.2	9,713	61,224	21.6
	2003	6,193	872	2,715	38.3	9,436	58,440	19.5
	2004	6,022	750	2,642	39.9	9,419	56,723	20.1
	2005	5,262	786	2,568	44.2	10,582	55,688	16.8
	2006	5,230	903	3,346	50.4	14,672	76,737	16.7
	2007	5,977	1,001	3,411	42.7	12,478	74,583	19.3
	2008	4,931	754	2,243	45.2	10,321	50,896	14.4
Mean ($n = 18$)		5,492	824	2,751	44.0	10,922	59,699	17.8

1994–2000) for fish in the GOA than in CNP (48% of C_{max}). Average annual GE was similar for SW1 in fish from both regions (22% in 1994–2000). All region-age groups exhibited the lowest SW1 GE in 1997 (range 18.9–19.3%) and the highest in 1999 (range 25.1–26.3%), as illustrated by GE anomalies, which shifted from strongly negative in 1997 to strongly positive in 1999 (Figure 4). Mean composite prey energy density (E) used to model SW1 growth was substantially lower in 1997 (4,420 J/g) than in 1999 (5,582 J/g; Table 3), primarily due to the absence of energy-dense squid in stomach contents of ocean age-0 steelhead sampled in the GOA in 1997 (Table 1). However, the total mass and energy of prey consumed during SW1 was higher in 1997 than in 1999 for all region-age groups except CNP, ocean age-1 steelhead (Table 3). For CNP steelhead, total mass of prey and energy consumed during SW1 was higher for

ocean age-1 fish than ocean age-2 fish in all years except 1994 and 2001 (Figure 5).

For ocean age-2 steelhead, the average annual feeding rates during SW2 were higher in GOA (48% C_{max} in 1994–2000) than in CNP (43% C_{max}) steelhead (Table 4). Average annual GE was lower in both the GOA (18% in 1994–2000) and CNP (17%) during SW2 (Table 4) than during SW1 (Table 3). For steelhead in the GOA during SW2, GE was similar in 1997 (16.2%) and 1999 (16.0%), whereas in the CNP, GE was lowest in 1997 (14%), midrange in 1999 (16%), and highest in 2002–2004 (20–22%) (Table 4). The GE anomalies for SW2 in both GOA and CNP steelhead were negative during 1997 and 1999 (Figure 4). The GOA steelhead consumed more prey biomass and total energy in 1997 than in 1999 (Table 4). In the CNP, prey energy density during SW2 was lower in 1997 (4,600 J/g) than
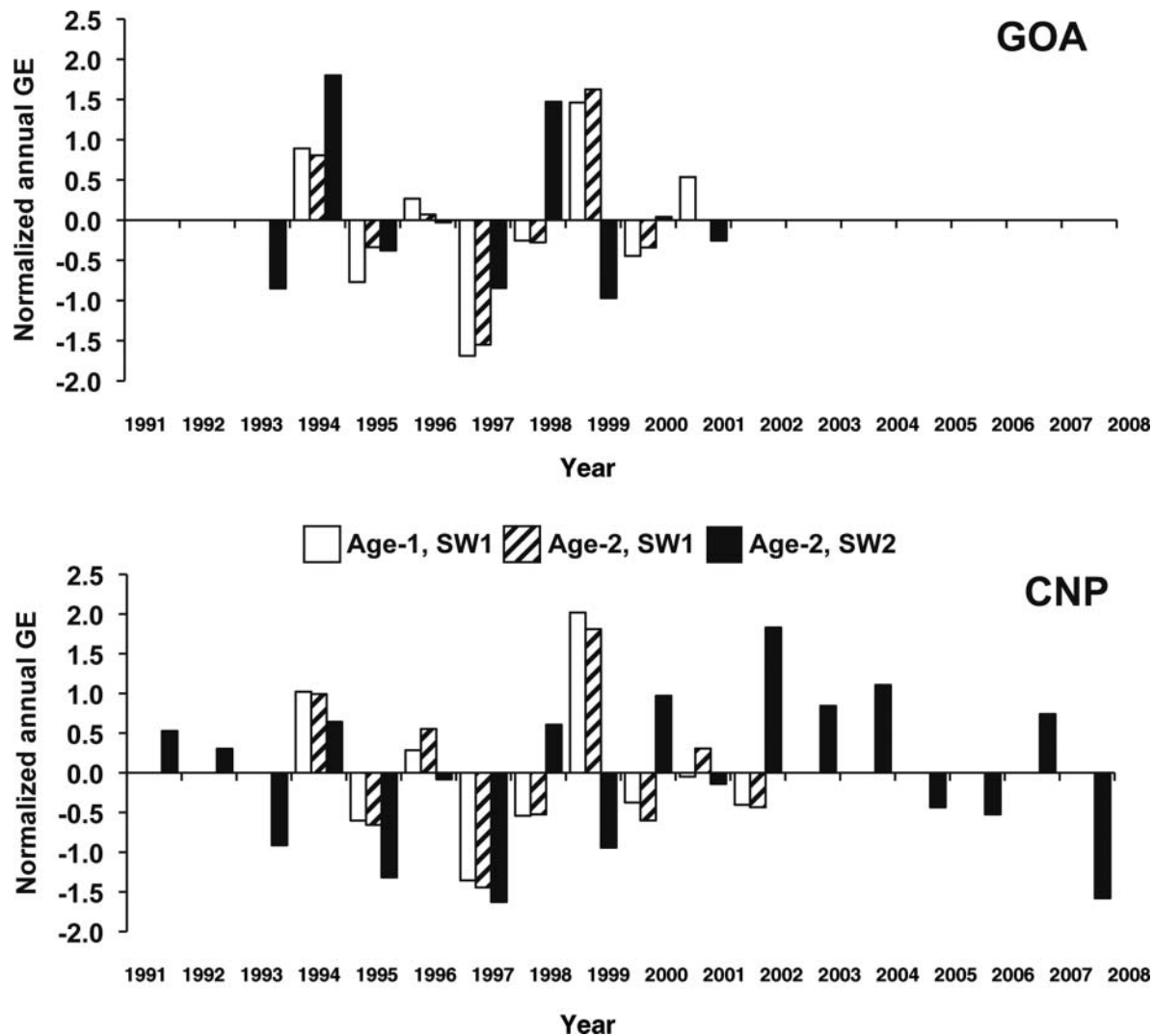
FIGURE 4. Annual growth efficiency (GE) of steelhead for each ocean age at capture and each growth year normalized to means specific to region and age: Gulf of Alaska (GOA; top panel) – ocean age 1, SW1 (1994–2001), ocean age 2, SW1 (1994–2000) and ocean age 2, SW2 (1993–2001); central North Pacific Ocean (CNP; bottom panel) – ocean age 1, SW1 (1994–2002), ocean age 2, SW1 (1994–2002) and ocean age 2, SW2 (1991–2008). SW1 = first year of ocean growth, SW2 = second year of ocean growth.

in 1999 (5,144 J/g), but since steelhead consumed similar total biomass of prey both years, total annual energy consumption was lower in 1997 than 1999 (Figure 6).

Temperature-Dependent Growth Response

The results from the previous section identified 1997 and 1999 as the years with the lowest and highest GE during SW1. We explored this further by simulating temperature-dependent growth in those 2 years using the composite prey energy densities and the fitted feeding rates from the simulations for the CNP as inputs to model simulations applied to a range of temperatures. During 1997, the optimal temperature for growth for steelhead feeding at 55% C_{max} on a composite diet of 4,420 J/g was 14.0°C for a 49-g (ocean age-0) steelhead and 12.0°C for a 920-g (ocean age-1) steelhead, whereas the mean temperature during

the warmest months (June–October) was 12.2°C (Figure 7). The resulting change in daily growth due to the difference between the optimal growth temperature and the mean June–October thermal experience was –2.9% for ocean age-0 steelhead and 0.0% for ocean age-1 steelhead during 1997. During 1999, the optimal temperature for growth for steelhead feeding at 46% C_{max} on a composite diet of 5,582 J/g was 14.0°C for a 58-g (ocean age-0) steelhead and 12.5°C for a 929-g (ocean age-1) steelhead, whereas the mean June–October temperature was 10.5°C (Figure 7). The difference between the optimal growth temperature and the mean June–October thermal experience resulted in a –11.8% change in daily growth for ocean age-0 steelhead and –5.8% for ocean age-1 steelhead during 1999. Despite large differences in C_{max} and energy density of the diet between 1997 and 1999, the temperature-dependent response
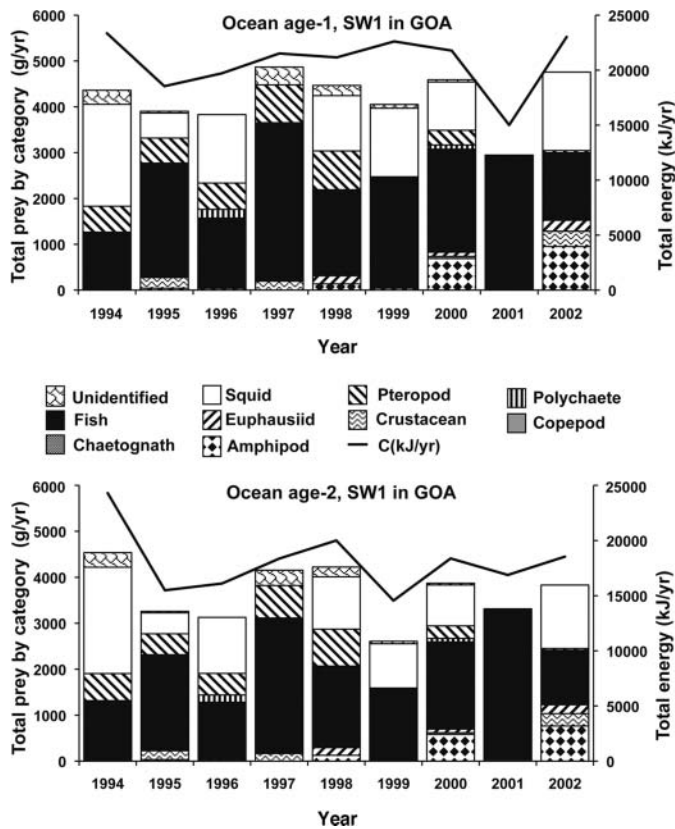
FIGURE 5. Grams of prey consumed per year by prey category (bar graph) and total energy consumed per year (line graph) during the first year of ocean growth (SW1) in the Gulf of Alaska (GOA) for ocean age-1 (top panel) and ocean age-2 (bottom panel) steelhead caught in the Central North Pacific Ocean.
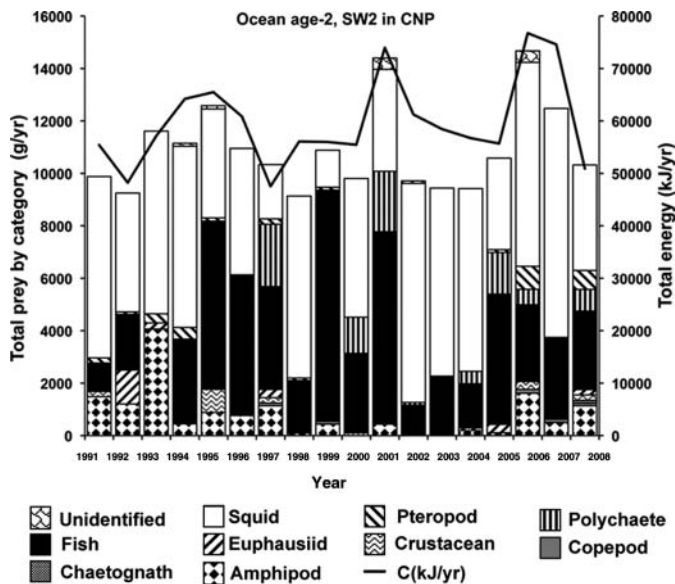

FIGURE 6. Grams of prey consumed per year by prey category (bar graph) and total energy consumed per year in kJ (line graph) during the second year of ocean growth of ocean age-2 steelhead caught in the central North Pacific Ocean (CNP).
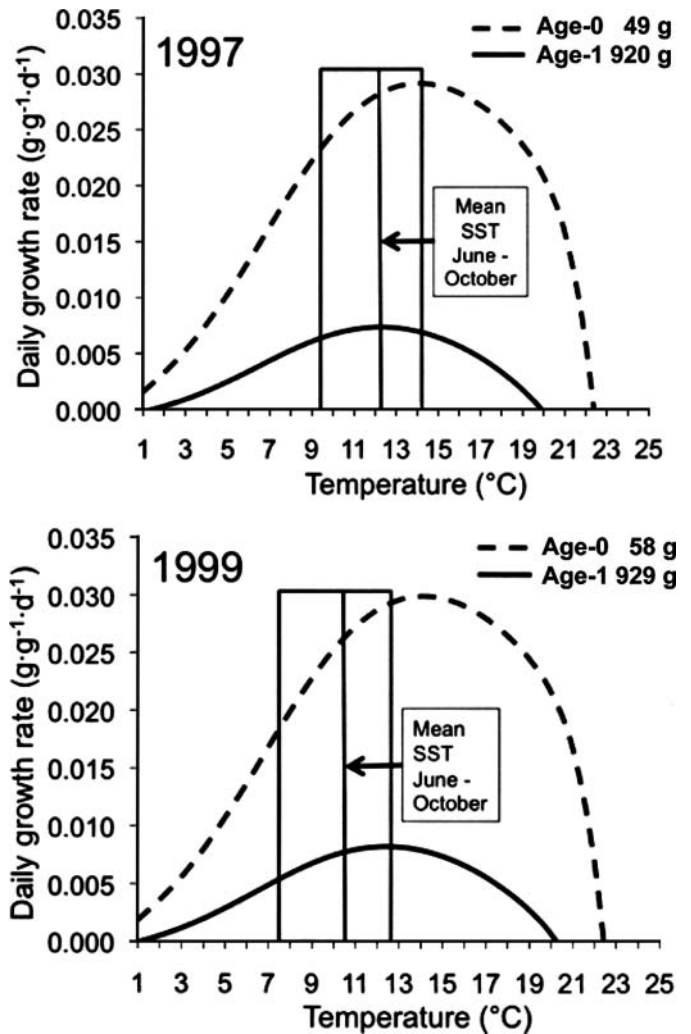
FIGURE 7. Temperature-dependent daily growth responses for steelhead of two different body masses (ocean age 0 and age 1) using field-based prey energy density and estimated consumption rates for the Gulf of Alaska (GOA) in 1997 (top panel: 4,420 J/g diet, 55% C_{max}) and 1999 (bottom panel: 5,582 J/g, 46% C_{max}). The rectangle enclosing the GOA mean sea surface temperature (SST) line (12.2°C) includes the minimum–maximum range of GOA monthly mean SSTs during 1997 (9.4–14.2°C) and 1999 (7.4–12.6°C) (Table 1).

curves appeared similar; however, this resulted from the compensatory effects of lower energy density–higher feeding rate in 1997 versus higher energy density–lower feeding rate in 1999.

Growth and Future Climate Scenarios

The baseline growth potential (final body weight) for ocean age-1 CNP steelhead during the first ocean year of growth (SW1) in the GOA was 1,001 g compared to 943 g for the 2040s and 894 g for the 2080s temperature scenarios (Figure 8). The baseline growth potential for ocean age-2 CNP steelhead in their second year of growth (SW2) was 2,853 g compared with 2,627 g for the 2040s and 2,397 g for the 2080s scenarios, respectively.
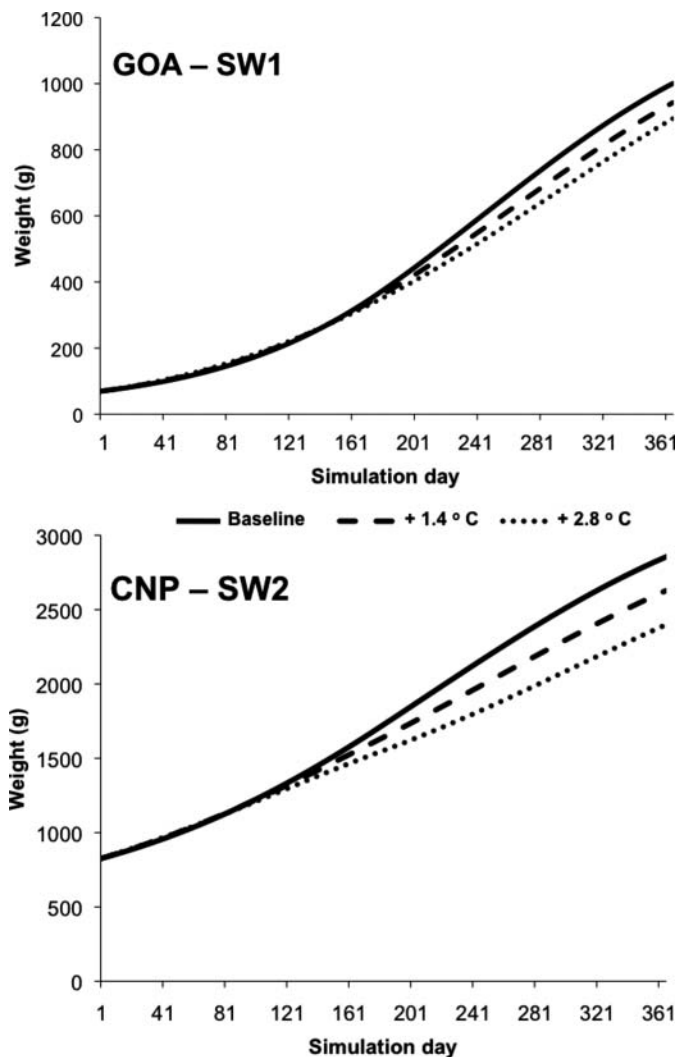
FIGURE 8. Simulated growth response of steelhead to climate change in the North Pacific Ocean. Bioenergetics model output of daily growth of steelhead during the first year of ocean growth (SW1) in the Gulf of Alaska (GOA; top panel) and second year of ocean growth (SW2) in the central North Pacific Ocean (CNP; bottom panel). Growth was estimated using the average consumption (g) and average temperature from the initial (baseline) modeling effort for steelhead sampled in the CNP (Tables 3, 4). Model simulations were run for 2040 ($+1.4°C$) and 2080 ($+2.8°C$) predicted temperature scenarios.

DISCUSSION

Our bioenergetics model simulations suggested that steelhead growth in the North Pacific Ocean was highly variable depending on prey quality, consumption rates, total consumption, and thermal experience. Higher consumption rates sometimes compensated for low-energy diets. Growth was higher in years when the thermal experience was close to optimal, whereas more pronounced declines in growth occurred when thermal experience deviated substantially from the optimum. Our findings suggest that steelhead have a narrow temperature window in which to achieve optimal growth, which is strongly influenced by changes in ocean temperature.

Steelhead that migrate to the open ocean are the most highly migratory of all salmonid species (Quinn and Myers 2004), and their response to climate change can vary; growth potential may decrease with increasing temperatures or steelhead may migrate to more conducive temperatures (either vertically or horizontally). For example, annual (1992–2005) trends in Japanese research gillnet catch-per-unit-effort data show that the relative abundance of steelhead during the 1997 El Niño decreased in the eastern North Pacific and increased the western North Pacific (Nagasawa et al. 2005), perhaps indicating a westward shift in ocean distribution of steelhead. Our estimates of initial body weights of ocean age-1 steelhead that migrated to the CNP were usually larger than those of ocean age-1 steelhead sampled in the GOA. This might have important implications for the energetic response of steelhead to climate change, because SSTs differed between the GOA and CNP. For example, the CNP might provide a cool thermal refuge for steelhead during El Niño years, when GOA SSTs exceed the thermal optimum for SW2 growth. This also has important implications for hatchery management practices, as hatchery steelhead are typically released to the ocean at a larger size than naturally produced steelhead and might have a greater tendency to migrate to the CNP, where growth potential tends to be lower than the GOA during the second year of ocean growth. An important topic for future bioenergetics modeling research is to evaluate whether energetic responses to variation in diet, thermal habitat, and climate differ between hatchery and wild steelhead in the North Pacific Ocean.

We speculate that initial body size plays an important role in ocean growth and survival of ocean age-0 steelhead in some years. Previous studies using scale back-calculation procedures indicated smolt-to-adult survival of Keogh River, British Columbia, steelhead was positively correlated with smolt (ocean age-0) size (Ward and Slaney 1988; Ward et al. 1989). Starting in 1990, however, Keogh River steelhead experienced a sharp drop in smolt-to-adult survival from an average of 15–16% to 4% and marine survival of Keogh River steelhead was no longer strongly related to smolt size (Welch et al. 2000). The SSTs in the GOA during most years of our study were cool relative to our estimated threshold for optimum growth of ocean age-0 steelhead. Cool SSTs and associated growth reductions might increase size-selective mortality of steelhead, particularly at the initial growth (ocean age-0) stage, as our models indicated the optimal temperature for steelhead growth decreased with increasing body size.

While SST has a direct metabolic impact on growth, it may also contribute to indirect effects that are difficult to quantify. For example, SSTs probably influence prey composition, distribution, recruitment, and productivity, ultimately affecting prey quality and availability. During 1997 we found lower prey quality but higher quantity in stomach contents.

Steelhead feed on a variety of prey including zooplankton, fish, and squid, many of which may be temperature-dependent species. Mackas et al. (2007) found changes in latitudinal

distribution and life cycle timing of zooplankton in response to temperature changes. Pearcy et al. (1988) found that gonatid squids were very important in the diets of most salmonids in the region of the Subarctic Current but not farther to the north. Aydin et al. (2000) found a latitudinal cutoff for gonatid squid in stomach contents of salmon in certain years, suggesting gonatid squid are also a temperature sensitive species. Kaeriyama et al. (2004), who analyzed 1994–2000 steelhead food habits data from the *Oshoro maru*, found a large decrease in gonatid squid in steelhead stomach contents in 1997, specifically in the Alaska Gyre (145°W, 52–56°N), in agreement with our study, but not in the Subarctic Current (145°W, 50–51°N).

During *Oshoro maru* surveys in the GOA, ocean age-0 steelhead were distributed along the entire 145°W survey line (49–56°N), but catches were highest between 51°N and 53°N, particularly at 52°N (Myers et al. 2001). Mesoscale (200–300 km) and smaller (<2 km) eddies, observed every year in this region, may affect primary productivity and distribution of preferred prey of steelhead and other species (Onishi et al. 2000; Myers et al. 2001). In the Great Lakes, steelhead feed very close to the surface under scum lines of insects and debris concentrated by thermal fronts in spring and summer (Haynes et al. 1986). While feeding behavior of steelhead has not been directly observed in the North Pacific Ocean, high seas catch data suggest that they remain in the upper 20 m of the ocean (Burgner et al. 1992), with periodic dives of 40–60 m (Walker et al. 2000a, 2000b). A vertical shift in squid distribution, reducing the availability of energy-dense prey to steelhead feeding at the surface, could be one explanation for lower growth efficiency of ocean age-0 steelhead in the GOA in 1997.

One temperature data storage tag (DST) was recovered from an ocean age-3 steelhead captured, tagged, and released in the GOA (49°58′N, 145°00′W) on July 9, 1998, and recovered 36 d later in a northern GOA (60°13′N, 144°40′W) coastal fishery (Walker et al. 2000a, 2000b). This is the only such record of daily thermal experience for a steelhead tagged on the high seas. These data reveal vertical migrations for steelhead throughout full 24-h periods (both daytime and nighttime). Minimum DST temperature was 6.4°C (Walker et al. 2000a). Peak DST temperature (15.5°C), recorded in early August, was similar to peak SST input to our bioenergetics model (15.9°C in 2006). This information, in conjunction with our temperature-dependent growth curves, suggested that steelhead during our study period were well within the thermal tolerance for positive growth. However, steelhead undergo vertical migrations that might keep them out of this temperature range for long periods. The question then arises: should vertical migrations of steelhead be considered in bioenergetic simulations? Thirty-day bioenergetic simulations of steelhead growth using these DST data found that the final weights of steelhead modeled with constant actual SST at the release site (10.9°C) versus daily range of DST temperatures (6.4°C–15.6°C) were 1.5% less (Walker et al. 2000a). Previous studies examining other species that exhibit daily vertical migrations estimated thermal experience as a time–depth weighted average (Beauchamp et al. 2007).

Archival tag data (temperature and depth) recovered from two northern GOA (Ninilchik River) postspawn steelhead, tagged in 2002 and recovered in 2004 (16 months at sea), showed that both fish spent 97% of their time near the ocean surface (<6 m depth during day and night, most frequently at depths of 3–4 m), suggesting a time–depth averaged thermal experience would be very similar to SST (Nielsen et al. 2010). Activity at depth was greatest during late summer, when sea temperatures were highest. However, it was not clear from the data whether these steelhead remained in coastal habitats adjacent to the Ninilchik River (Cook Inlet) or migrated to the open ocean, as sea temperatures in both habitats were similar. An increase in steelhead tagging with DSTs would be beneficial in determining year round thermal experience (minimum and maximum temperatures) and the extent to which steelhead experience varying temperatures due to vertical migrations in both coastal and high seas habitats.

The first summer in the ocean is considered the most critical period for ocean survival of Pacific salmon (e.g., Hartt 1980; Hartt and Dell 1986; Beamish and Mahnken 2001; Farley et al. 2007). Our study indicated some fundamental differences between steelhead and other species of Pacific salmon in their bioenergetic strategies during this critical period. While salmon spend most or all of their first ocean summer foraging in productive coastal and continental shelf habitats, ocean age-0 steelhead quickly exit predator- and prey-dense marine coastal and shelf habitats for less productive epipelagic waters over the deep ocean basin (Burgner et al. 1992). Ocean age-0 steelhead in the GOA consumed relatively high-energy diets (annual average 4,967 J/g) at relatively moderate consumption rates (48.5%), compared with low-energy (2,800 J/g) and high-energy (5,000 J/g) diets of other species of ocean age-0 (10–100 g) salmon feeding at high rates (50–100% C_{max}) in epipelagic coastal and shelf waters (Beauchamp et al. 2007). While open-ocean GOA habitats are less productive than coastal habitats, by consuming high-energy prey (fish and squid) steelhead gained final SW1 body weights not achieved by other species of Pacific salmon until SW2. These interspecific differences in size-at-age might increase the potential for competitive interactions between ocean age-0 steelhead and older age groups of other salmon species, e.g., maturing pink salmon *O. gorbuscha*. Ocean age-0 steelhead, however, might successfully avoid trophic interactions with older age-groups of salmon by spatial (vertical) partitioning of foraging habitats, feeding at or closer to the surface than other species.

The number of tropical El Niño events since 1977 has increased and may be linked to observed increases in atmospheric greenhouse gasses (Trenberth and Hoar 1996). The 1997 El Niño event, which was the strongest on record, was associated with widespread warming in the GOA (Trenberth et al. 2007). This was followed by a major tropical cooling (La Niña) event in 1999, which in turn was associated with anomalously cool SSTs in the GOA. Our field-based diet data and bioenergetic

model simulations indicated that ocean age-0 steelhead in the GOA had the least energy-dense diet and lowest growth efficiency in 1997, compared with other years in our time series. Alternatively, ocean age-0 steelhead in the GOA had the most energy-dense diet and highest growth efficiency in 1999. Despite these differences, the final SW1 body weights of ocean age-1 and age-2 GOA steelhead, as back-calculated from scale growth, were higher in 1997 than in 1999. Feeding rate was lower in 1999, and mean SST was lower than the optimal growth temperature, given the estimated feeding rate and energy content of food. As a result, growth in 1999 was reduced by both a lower feeding rate and suboptimal SST despite a more energy-dense diet. Conversely, feeding rates were higher in 1997, and the mean SST was within the range of peak growth for ocean age-0 steelhead.

While SST in most years of our study (1991–2008) did not reach optimal temperatures for steelhead growth (including 1999), it did during the 1997 El Niño event. Ward et al. (1989) observed higher smolt-to-adult survival of smaller size classes of Keogh River, British Columbia, steelhead smolts during the 1982–1983 El Niño event compared with other (non-El Niño) years. One might conclude that rising SST would, at least up to a point, benefit steelhead, but the results of modeled growth potential under future SST scenarios suggested otherwise. The results of growth potential under future SST scenarios show that growth will be reduced under these temperatures, because temperatures continued to warm beyond the optimum growth temperature for a given feeding rate and body mass of the consumer. One caveat is that this modeled growth potential does not account for the increased C_{max} observed in our field-based simulations. However, as the temperatures increase along the right-hand descending limbs of the daily growth curves in Figure 7, the combined reduction in physiological maximum feeding rate and increasing metabolic costs quickly overwhelm the ability for any potential increases in feeding rate or energetic prey quality to sustain historic growth rates. The resulting growth decline would probably become a strong selective force in shifting the geographic distribution for steelhead in the ocean and perhaps for freshwater life stages as well.

Using published reference SSTs (6–12.5°C) for high seas distribution of steelhead, Abdul-Aziz et al. (2011) estimated potential reductions in July thermal habitat throughout the North Pacific Ocean and adjacent seas under A1B greenhouse emissions scenarios relative to a 30-year (1970–1999) historical reference period (8–10% reduction for the 2020s, 16–19% for the 2040s, and 24–43% for the 2080s). Projected habitat losses were largest in the GOA and subarctic (western and central) North Pacific. These results are important because the GOA is primary rearing habitat for U.S. West Coast steelhead populations listed under the Endangered Species Act. Our bioenergetics model simulations indicated that optimal temperatures for ocean growth of steelhead varied by life history stage, and potential reductions in ocean growth potential by the 2080s were substantial. Bioenergetics models can serve as tools to further investigate potential responses of steelhead to climate-driven changes in ocean thermal habitats, information that is needed to develop alternative strategies for sustainable management of steelhead.

In conclusion, our study showed that ocean growth of steelhead might be limited by either temperature or prey availability. The results of bioenergetic models with field-based inputs indicated that under baseline conditions in the 1990s and 2000s steelhead were able to compensate for low prey quality by increasing consumption rate and thus total consumption if temperature was in the optimal range. However, interannual variation in SST and related oceanographic conditions probably influence (or are correlated with) prey availability and prey quality, exerting both a direct and indirect effect on ocean growth of steelhead. Modeling of future climate-change scenarios indicated substantial reductions (~10% declines for the 2040s and 20% declines for the 2080s) in ocean growth potential of steelhead by the 2080s.

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