Temperature and prey quality effects on growth of juvenile walleye pollock *Theragra chalcogramma* (Pallas): a spatially explicit bioenergetics approach

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A bioenergetics model for juvenile age-0 year walleye pollock *Theragra chalcogramma* was applied to a spatially distinct grid of samples in the western Gulf of Alaska to investigate the influence of temperature and prey quality on size-specific growth. Daily growth estimates for 50, 70 and 90 mm standard length (L_S) walleye pollock during September 2000 were generated using the bioenergetics model with a fixed ration size. Similarities in independent estimates of prey consumption generated from the bioenergetics model and a gastric evacuation model corroborated the performance of the bioenergetics model, concordance correlation (r_c) = 0·945, lower 95% CL (transformed) (L_1) = 0·834, upper 95% CL (transformed) (L_2) = 0·982, $P < 0·001$. A mean squared error analysis (M_{SE}) was also used to partition the sources of error between both model estimates of consumption into a mean component (M_C), slope component (S_C), and random component (R_C). Differences between estimates of daily consumption were largely due to differences in the means of estimates ($M_C = 0·45$) and random sources ($R_C = 0·49$) of error, and not differences in slopes ($S_C = 0·06$). Similarly, daily growth estimates of 0·031–0·167 g day^{-1} generated from the bioenergetics model was within the range of growth estimates of 0·026–0·190 g day^{-1} obtained from otolith analysis of juvenile walleye pollock. Temperature and prey quality alone accounted for 66% of the observed variation between bioenergetics and otolith growth estimates across all sizes of juvenile walleye pollock. These results suggest that the bioenergetics model for juvenile walleye pollock is a useful tool for evaluating the influence of spatially variable habitat conditions on the growth potential of juvenile walleye pollock.

Key words: bioenergetics; energy budgets; food consumption; model evaluation; prey energy
content; spatially explicit growth.

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INTRODUCTION

Body size often mediates predator-prey interactions (Brooks & Dodson, 1965; Persson *et al.*, 1996) and thus may have important influences on the survival and future recruitment of juvenile fishes to adult life stages (Sogard, 1997). Similarly, it appears that many species of fishes in temperate boreal climates need to reach a critical size prior to the end of their first summer to survive through the following winter (Toneys & Coble, 1980; Shuter & Post, 1990; Sogard & Olla, 2000). The relationship between body size and predator vulnerability, energy storage and metabolic demand of juvenile fishes is thought to generally favour the survival of larger, faster growing individuals during winter (Sogard, 1997; Pangle *et al.*, 2004). If size and rapid growth is important to juvenile fish survival and recruitment, then measurements of habitat characteristics that influence juvenile fish growth could help explain recruitment variability. Because growing conditions in large aquatic systems are not homogeneous (Lasker, 1978) and juvenile fishes are highly mobile, they could experience wide ranges of growing conditions. Therefore, a better understanding of how juvenile fishes of different sizes grow in response to a spatially-diverse range of environmental conditions should increase understanding of how spatially variable conditions influence growth, and ultimately the recruitment dynamics of size-structured juvenile fish populations.

For walleye pollock *Theragra chalcogramma* (Pallas) in the western Gulf of Alaska (GOA), control of recruitment since the 1980s appears to have shifted from environmental constraints on larval survival to predator-induced mortality occurring during the juvenile (25–150 mm standard length, L_S) life stage (Bailey, 2000). Temporally, autumn water temperatures and predator abundance appears to interact and influence survival from the age-0 to the age-1 year life stage (Ciannelli *et al.*, 2004*a*). These broader scale patterns in survival and recruitment of walleye pollock result from the accumulation of finer scale processes that occur at spatial scales relevant to individuals. Therefore, to understand how body size and temperature influence survival and recruitment of walleye pollock to the adult life stage, it is informative to explore growth at spatial scales relevant to individuals, in regions where these interactions take place (Wellborn *et al.*, 1996).

Bioenergetics models are powerful tools for isolating and exploring the non-linear effects of temperature, prey quality, prey quantity and predator size on the growth of fishes (Madenjian *et al.*, 2004). A bioenergetics model for juvenile walleye pollock was developed by Ciannelli *et al.* (1998) and has been extensively used to investigate the foraging impact of walleye pollock on their prey (Sturdevant *et al.*, 2001; Duffy-Anderson *et al.*, 2002; Ciannelli *et al.*, 2004*b*). Attempts to corroborate the walleye pollock model using field data and alternate models have produced mixed results, with both comparable (Ciannelli *et al.*, 1998) and dissimilar (Ciannelli *et al.*, 2004*b*) consumption estimates among models. Both of these corroboration attempts, however, consisted of single point estimates of consumption from a restricted size range of fish.

As with any model, the performance and utility of bioenergetics models are greatly influenced by the precision and quality of environmental and biological information collected and used within the model. Bioenergetics models from

a variety of species have performed inconsistently when compared to field derived estimates of consumption or growth across broad temporal scales (Ney, 1993). The inconsistencies have often been attributed to inaccuracies in field measurements of bioenergetics parameters, primarily centreing on unknown activity costs (Ney, 1993). Similarly, many applications of bioenergetics models, out of necessity, use literature values of whole body energy densities for prey and predators. The energy content of both predators and prey, however, can vary spatially and temporally due to variable environmental conditions (Hartman & Brandt, 1995). Energy density estimates for the whole assemblage of possible prey species and predators rarely exist in the literature at the appropriate taxonomic resolution and for the desired spatial-temporal scales. Erroneous energy density values for some or all of the prey groups could lead to misinterpretations of the level of predator demand for specific prey or contribution of that prey group to the growth of the modelled fish.

In this study the variation in growth of juvenile (age-0 year) walleye pollock was measured across an important nursery area (Wilson *et al.*, 1996) in the western Gulf of Alaska during September of 2000. A bioenergetics model was used to isolate environmental influences on growth and to investigate which components exerted the most influence on the observed variability in juvenile walleye pollock growth across this area. Because the approach relies on the performance of the walleye pollock model, it was also necessary to corroborate the model in the field using independent estimates of consumption across a broad size range of juvenile fish. Measurements of the energy content of prey groups found in the juvenile walleye pollock diet were also used to investigate the contribution of each prey group to the size-specific growth of juvenile fish.

MATERIALS AND METHODS

Biological information was collected across a grid of stations in the western GOA to facilitate bioenergetics modelling of juvenile walleye pollock growth. Samples were collected to identify fish diet, prey energy content and otolith growth. Comparisons between estimates of size-specific consumption generated from the walleye pollock bioenergetics model and a gastric evacuation approach were used to corroborate the performance of the bioenergetics model. Spatially explicit estimates of size-specific walleye pollock growth were then estimated across the sample grid using a fixed ration size in the bioenergetics model.

STUDY SITE

Study samples were collected from 14 to 19 September 2000 in the western GOA from the southern end of the Shelikof Strait to the north-eastern edge of the Shumagin Islands (Fig. 1). This area is thought to be an important rearing area for juvenile walleye pollock that recruit to the Shelikof spawning population (Wilson *et al.*, 1996). The rearing area is primarily contained over the shelf of the Alaska Peninsula with water depth generally <200 m. The Alaska Coastal Current (ACC) is an important feature in this area. The ACC follows the Shelikof Sea Valley, joining the Alaska Stream in the south-eastern edge of the sampling grid (Schumacher & Reed, 1986). Some water from the ACC flows across the shelf and into the walleye pollock rearing area (Schumacher & Reed, 1986). Variable freshwater input from snowmelt contributes to a large range of temperatures (6·0–13·5° C) and salinities (30–33) (Lanksbury *et al.*, 2005).
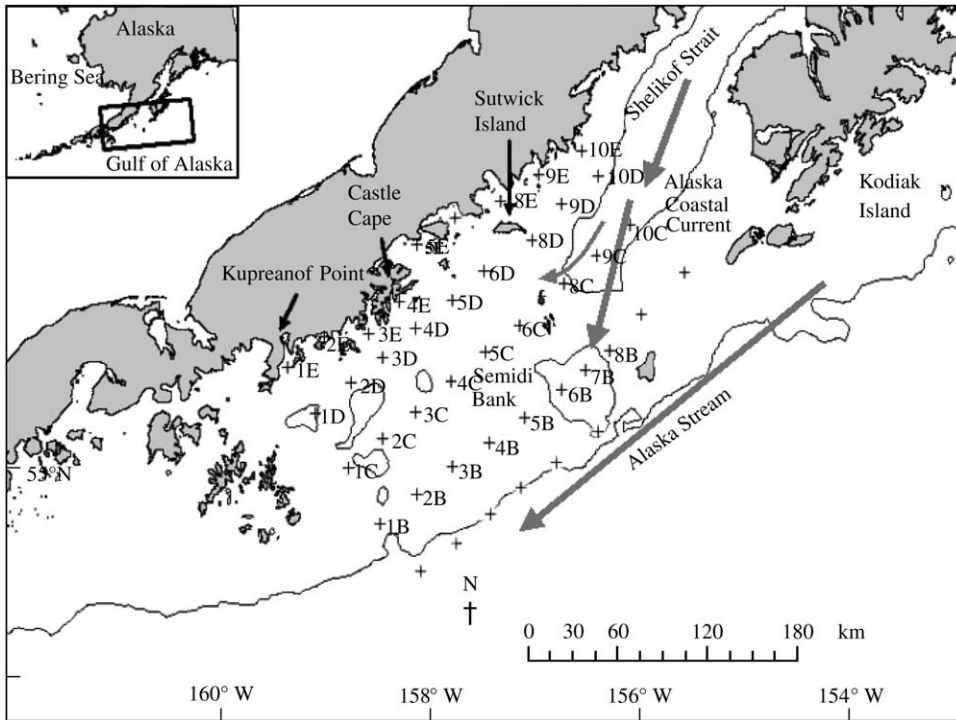
FIG. 1. Study area and sampling stations (+) in the western Gulf of Alaska. Stations where juvenile walleye pollock were captured in midwater trawl hauls during September 2000 are indicated with a station label.

SAMPLE COLLECTION

Day and night paired tows for forage fishes, plankton and oceanographic conditions were conducted at 42 stations along a grid across the rearing area from the NOAA Ship *Miller Freeman*. Juvenile walleye pollock were captured in the water column using an anchovy trawl equipped with 568 kg, steel-v doors, and a 3 mm mesh codend liner (Wilson *et al.*, 1996). The trawl was fished from 200 m depth to the surface or 10 m off the bottom, if the bottom was shallower than 200 m, with a warp retrieval of 10 m min^{-1} and ship speed of 4·6–5·6 km h^{-1} (2·5–3 knots). Effective net mouth for the anchovy trawl was previously estimated at *c.* 100 m^2 (Wilson *et al.*, 1996). Plankton were sampled using a Tucker trawl with a 1 m^2 net opening and two 333 μm mesh sequential closing nets. The first net was opened at 200 m or 10 m off the bottom and fished at a 45° wire angle during retrieval (20 m min^{-1}) until the bottom of the thermocline was reached. The second net was then fished from the bottom of the thermocline to the surface. Measurements of net depth, temperature and salinity were collected using a Sea-Bird SeaCat profiler attached to the lead wire of the Tucker trawl.

Juvenile walleye pollock captured in the anchovy trawl were weighed and enumerated on deck with up to 50 individuals randomly selected for preservation. Age-0 year walleye pollock were differentiated from older fish using the previously identified body length threshold of <130 mm fork length (L_F) (Brodeur & Wilson, 1996). The subsamples of walleye pollock were either flash frozen at −80° C or preserved in 10% buffered formalin for gut content analysis at the NOAA AFSC in Seattle, WA, U.S.A. (Buchheister & Wilson, 2005). Zooplankton collected in the Tucker trawl was preserved in 5% buffered formalin and sent to the Poland Plankton Sorting and Identification Center (Szczecin, Poland) for identification and enumeration.

DIET ANALYSIS

Preserved juvenile walleye pollock were thawed in sea water or removed from the formalin solution and rinsed in sea water for analysis in the laboratory. Individual fish were blotted dry, measured to the nearest mm standard length (L_S), and weighed (0·001 g). Individual L_S and mass were corrected for shrinkage due to preservation (Buchheister & Wilson, 2005) prior to use in any analysis. Stomachs were dissected and prey items removed. Prey items were identified to the lowest possible taxonomic level under a dissecting microscope, sorted, counted, blotted and weighed (wet mass). Otoliths were removed from up to 20 thawed fish selected to represent the available size range, cleaned and stored in 95% ethanol for later analysis.

Diet data were analysed by grouping prey into broad taxonomic groups (Ciannelli *et al.*, 2004b) and calculating the mean proportional diet content, by mass, of each prey group for size-specific fish diet. Because body size strongly influences fish consumption and to parallel the temporal and spatial extent of gastric evacuation estimates, walleye pollock diet estimates were grouped into 5 mm size classes and pooled from across the sampling grid to ensure adequate sample sizes and a frequent diel-sampling interval for all size classes for the comparison between bioenergetics and gastric evacuation models. To account for potential diel and spatial influences on ration size, bioenergetics model runs used 5 mm size classes for diet pooled across 24 h sampling events to estimate the mean and variance of size-specific ration sizes for the entire sample grid. By fixing the ration size of each size class of walleye pollock it was possible to isolate thermal and energy density influences on bioenergetics model estimates of station-specific growth. Diets for juvenile walleye pollock used to estimate station-specific diets and growth estimates were grouped into three size classes (35–59, 60–85 and >85 mm L_S) to ensure adequate sample sizes at each independent station.

PREY ENERGY DENSITY ESTIMATES

For estimates of prey energy densities, zooplankton and ichthyoplankton samples were collected from the study area in September 2003 from the NOAA ship *Miller Freeman*. Samples were collected using the Tucker trawl using the same procedures outlined above. Prey groups commonly found in the diets of juvenile walleye pollock from 2000 were sorted from the samples into broad taxonomic groupings, including gammariid and hyperiid amphipods, chaetognaths, copepods, crab megalopae, euphausiids, fish larvae, larvaceans and pteropods. Sorted samples were frozen (−80° C) in vials with sea water and thawed *c.* 5 months later in the laboratory. Additional sorting of samples using dissecting microscopes was used to verify that other prey groups had not contaminated the samples. Due to the prevalence of two major species of euphausiids in the diets of juvenile walleye pollock, euphausiid samples were separated by species, resulting in four groups: *Thysanoessa inermis* (Hansen), *Thysanoessa spinifera* (Holmes), *Thysanoessa raschii* (Hansen) and *Euphausia pacifica* (Hansen). Euphausiids were further differentiated by size, either > or <15 mm total length. Copepods found in the diets of the fish from this study were not identified to species but rather distinguished by size, therefore copepod samples were also divided by size groups using 2 mm, 850 μm and 48 μm sieves. The resultant copepod groups were *c.* 0·5–1·5 mm (small), 1·5–4·0 mm (medium) and 3·0–6·5 mm (large) in prosome length. Most fish larvae were *Mallotus villosus* (Müller). All samples were gently blotted, weighed to the nearest 0·1 mg and dried at 65° C until a stable mass was reached (±0·01 g). Once dry, each prey group was ground to a homogenous mixture using a mortar and pestle, and energy densities were measured using a Parr 1425® semi-micro bomb calorimeter. When enough dry material was available, two replicates of a sample weighing between 0·04 and 0·16 g (dry mass) were combusted. Differences between the two replicates were minimal (coefficient of variation, CV ≤1%). Prey energy density values were converted to kJ g^{-1} wet mass for use in the bioenergetics model using the ratio of wet to dry mass for each of the samples.

OTOLITH GROWTH

Otoliths for age and growth analysis were selected from the size range of available age-0 year walleye pollock captured (45–104 mm L_S) and were stratified across the sample grid (Fig. 1). Otoliths from 139 juvenile walleye pollock were processed following the methods of Brown & Bailey (1992). Measurements of the ventral radius and outer growth increments for the last 5 days were identified and recorded. Lengths were back-calculated using an equation relating the ventral radius of the otolith to L_S ($r^2 = 0.88$): $L_S = 16.14 + 88.08 \, O_{VR}$, where O_{VR} is the ventral radius of the otolith. Separate length and mass regressions were derived for the north-east, south-east, north-west and south-west sections of the sample grid and were used to convert backcalculated L_S estimates into mass: $M = aL_S^b$, where M is the estimated wet mass, L_S the preservative-corrected standard length, with area-specific intercepts a and slopes b (Table I). Daily growth, in mass, was estimated by subtracting the backcalculated mass 5 days before capture from the estimated capture mass and dividing by 5 days, producing an individual daily average for the 5 day period prior to capture. Individual estimates were then averaged to produce daily growth estimates for each sample station and 5 mm size class.

BIOENERGETICS AND GASTRIC EVACUATION MODELS

The Wisconsin bioenergetics model, version 3.0 (Hanson *et al.*, 1997) was used to estimate both the daily growth of juvenile walleye pollock and the size-specific consumption for model corroboration. This model, parameterized for juvenile walleye pollock (Ciannelli *et al.*, 1998), uses a balanced energy budget where energy available for growth equals the total energy consumed minus the energy lost to waste, activity and respiration (Hanson *et al.*, 1997). The bioenergetics model operates on a daily time step and incorporates allometric mass-dependent and temperature-dependent functions for maximum consumption and metabolism (Hanson *et al.*, 1997).

To corroborate the walleye pollock model, estimates of consumption from the walleye pollock model were compared with independent estimates from an *in situ* gastric evacuation model, similar to the methods used by Arrhenius & Hansson (1994) for young-of-the-year (YOY) herring *Clupea harengus* L. Because consumption is dependent on fish size, estimates from both models were generated for 5 mm size classes of walleye pollock from across the sampling grid. Size-specific bioenergetics model inputs were averaged from across the grid for thermal experience (8·6° C), proportional diet content (Table II), growth (Table III) and prey energy content (Table IV) to parallel the temporal and spatial extent of gastric evacuation estimates. Juvenile walleye pollock whole body energy contents (WBEC) were measured previously (Buchheister *et al.*, 2006) and the mean WBEC for each 10 mm size class was applied as the predator energy density within the pollock model (Table III). The prey energy density for the euphausiid prey group was modelled using one energy value estimated by multiplying the proportion of each identified euphausiid species in the diet of juvenile walleye pollock by the species-specific wet WBEC and summing. The diets of walleye pollock contained 900 euphausiids, 488 were unidentifiable and another 171 were only broadly

TABLE I. The sample stations contained in each habitat area and area-specific intercepts (*a*) and slopes (*b*) of standard length and mass equations for juvenile walleye pollock used to estimate daily growth (g) for bioenergetics model runs

Habitat area	Sample stations	a	b	r^2	n	P
South-west	1-4B, 1-4C	6·7E-06	3·06	0·98	322	<0·001
North-west	1-4D, 1-4E	5·1E-06	3·12	0·97	245	<0·001
South-east	5-8B, 5-10C	7·7E-06	3·03	0·98	199	<0·001
North-east	5-10D, 5-10E	4·4E-06	3·16	0·98	353	<0·001

TABLE II. Proportional diet composition of prey for size-specific groups of juvenile walleye pollock from all stations sampled in the grid (see Fig. 1). Proportional diet content was determined from the wet masses of prey items identified in stomach samples

L_S class (mm)	n	Amphipods and shrimp	Copepods ≤2 mm	Copepods >2 mm	Chaetognaths and larvaceans	Crab larvae	Euphausiids	Fish larvae	Pteropods
40–44	4	0·00	0·49	0·03	0·02	0·00	0·20	0·00	0·25
45–49	33	0·01	0·49	0·27	0·09	0·01	0·07	0·00	0·06
50–54	104	0·00	0·53	0·17	0·13	0·01	0·09	0·00	0·07
55–59	164	0·01	0·43	0·15	0·15	0·02	0·16	0·00	0·08
60–64	159	0·02	0·29	0·13	0·11	0·04	0·31	0·00	0·09
65–69	194	0·01	0·24	0·12	0·10	0·08	0·36	0·01	0·07
70–74	157	0·01	0·14	0·08	0·08	0·15	0·49	0·02	0·03
75–79	109	0·03	0·14	0·07	0·09	0·12	0·47	0·06	0·03
80–84	100	0·05	0·11	0·09	0·04	0·12	0·54	0·03	0·03
85–89	61	0·05	0·07	0·09	0·10	0·10	0·55	0·03	0·01
90–94	44	0·07	0·07	0·07	0·02	0·13	0·61	0·01	0·02
95–99	25	0·03	0·04	0·08	0·01	0·27	0·55	0·02	0·00
100–105	9	0·02	0·00	0·01	0·20	0·29	0·49	0·00	0·00

L_S, standard length.

TABLE III. Mean size-specific estimates of daily growth rate in wet mass and the corresponding 95% CI. Growth was estimated using sectioned otoliths from juvenile walleye pollock captured across all stations and was used in bioenergetics model runs to predict prey consumption for model corroboration. The whole body energy content (WBEC) of juvenile walleye pollock was altered in bioenergetics model runs to correspond with observed WBEC measured in the western Gulf of Alaska (Buchheister *et al.*, 2006)

L_S class (mm)	n	Wet mass (g day^{-1})	95% CI	WBEC (J g wet^{-1} mass)
40–44	1	0·029		3506
45–49	2	0·033	0·010	
50–54	32	0·042	0·003	
55–59	27	0·047	0·004	
60–64	14	0·048	0·006	
65–69	10	0·062	0·010	3862
70–74	29	0·087	0·007	
75–79	16	0·093	0·011	4389
80–84	4	0·078	0·039	
85–89	2	0·090	0·022	4490
100–105	2	0·178	0·055	

L_S, standard length.

identifiable as being *Thysanoessa* sp. Of the 241 remaining identifiable euphausiid, 2% (5) were *T. raschii*, 12% (29) *E. pacifica*, 42% (102) *T. spinifera* and 44% (105) *T. inermis*. The size structure of consumed copepods was only roughly estimated from the diets of juvenile walleye pollock, so the energy content of small copepods was modelled by taking the mean of the 0·5–1·5 mm (small) and 1·5–4·0 mm (medium) energy estimates. Copepods >2 mm were modelled using the energy estimate obtained from the 3·0 to 6·5 mm (large) size group.

For the gastric evacuation estimate, fish diets were pooled across the 15 day cruise to ensure adequate sample sizes for all size classes and a frequent diel-sampling interval necessary for gastric evacuation estimates. Differences in the stomach fullness of the size-specific diet and diel variation were negligible across the 15 day sampling event. Therefore, gastric evacuation estimates of consumption were modelled using a Bajkov equation (Ney, 1990) modified by Eggers (1979) to fit an exponential evacuation rate without applying a correction for differences in diet at the beginning and end of model estimates (Boisclair & Marchand, 1993; Richter *et al.*, 2004): $C_D = 24S_{median}R$. Daily consumption C_D (g day^{-1}) was estimated for each size class from S_{median}, the median amount of food in the stomach over all diel sample periods and R, the gastric evacuation rate assuming a simple exponential evacuation rate (Eggers, 1979). We applied the evacuation rate of 0·25 day^{-1} estimated by Merati & Brodeur (1996) using the MAX-IMS programme (Jarre-Teichmann *et al.*, 1993) generated from samples collected during September of 1990 from the same juvenile walleye pollock nursery area. To reduce the influence of several very large individual stomach contents and to maintain comparability with previous studies conducted on juvenile walleye pollock, median stomach content was used rather than the geometric mean (Cochran & Adelman, 1982; Merati & Brodeur, 1996).

To compare model (gastric evacuation *v.* bioenergetics) estimates of daily consumption, concordance correlation analysis (Zar, 1996) was used in conjunction with a partitioned mean squared error (M_{SE}) analysis (Rice & Cochran, 1984; Yang & Arritt, 2002). The concordance correlation analysis is most commonly used to assess the reproducibility of measurements made using two independent techniques. The partitioned-M_{SE} analysis technique was used to identify the degree and source of error associated with the deviation between predicted values: $M_{SE} = \sum_{i=1}^{n} (P_i - A_i)^2 = (\overline{P} - \overline{A})^2 +$

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TABLE IV. The whole body energy content (WBEC), wet mass, dry mass, per cent dry mass and bioenergetics modelled energy values of juvenile walleye pollock prey groups collected in September of 2003 from the western Gulf of Alaska sampling grid (see Fig. 1). WBEC was estimated for size- and species-specific differences when feasible

Prey group	Species	Size (mm L_T)	Wet mass (g)	Dry mass (g)	Per cent dry mass	kJ dry g^{-1}	kJ wet g^{-1}	Modelled J wet g^{-1}
Chaetognaths		15–30	10·954	1·092	10·0	20·692	2·062	2062
Crab larvae	*Cancer* spp.	4·5–5·5	5·551	1·428	25·7	17·330	4·458	4458
Fish larvae	*Mallotus villosus*	23–52	11·402	2·053	18·0	20·880	3·760	3760
Gammariids		1·0–13·5	3·469	0·926	26·7	21·522	5·747	5747
Hyperiids		0·9–15·4	3·421	0·543	15·9	17·575	2·787	2787
Pteropods		0·25–2·75	0·415	0·092	22·1	11·880	2·630	2630
Larvaceans		8*	0·550	0·053	9·6	14·990	1·434	1434
Copepods	*Calanoid* spp.	3·0–6·5**	1·563	0·297	19·0	28·039	5·319	5319
	Calanoid spp.	1·5–4·0**	3·449	0·508	14·7	24·554	3·616	3040
	Calanoid spp.	0·5–1·5**	2·841	0·331	11·7	21·128	2·463	
Euphausiids	*Euphausia pacifica*	≥15	3·195	0·662	20·7	19·290	3·999	5949
	Thysanoessa inermis	≥15	0·951	0·267	28·1	25·190	6·824	
	Thysanoessa inermis	<15	0·274	0·062	22·7	19·975	4·685	
	Thysanoessa raschii	13–20	0·184	0·043	23·2	20·347	4·714	
	Thysanoessa spinifera	≥15	2·605	0·701	26·9	21·753	5·577	
	Thysanoessa spinifera	<15	0·607	0·139	22·9	18·738	4·259	

*Mean lengths for the prey group.
**Indicates prosome length for copepods.
L_T, total length.

$(S_P - S_A)^2 + 2(1 - r)S_P S_A$, where P_i and A_i are the series of predicted and actual values with mean values $\overline{P}$ and $\overline{A}$, standard deviations S_P and S_A, and correlation coefficient r. The M_{SE} analysis partitions the sources of error between the mean component (M_C), slope component (S_C) and the random error component (R_C) based on the proportional contribution of each to the observed deviations in the relationship between model estimates: $1 = M_C + S_C + R_C = (\overline{P} - \overline{A})^2 M_{SE}^{-1} + (S_P - S_A)^2 M_{SE}^{-1} + 2(1 - r) \ S_P S_A M_{SE}^{-1}$.

SPATIAL GROWTH PREDICTIONS

Daily growth for juvenile walleye pollock was estimated using the walleye pollock model at every sample station in the western Gulf of Alaska where fish of that size were captured and diet information was available. Bioenergetics model inputs of proportional diet content, thermal experience and size-specific growth from otoliths (Table V) were estimated for each sample station in the grid. Station-specific growth estimated from otoliths was used to estimate ration size (P-value) using the walleye pollock model with station-specific inputs for each 5 mm size class (Table V). Mean P-values for each size class were then calculated and assigned as the fixed rations for each size class of walleye pollock modelled to estimate growth across the sample grid (Table VI). By fixing the ration size for each size class of walleye pollock, any unknown errors associated with the bioenergetics model in estimating growth induced by altering the ration size would be fixed at a consistent level within size classes (Bajer *et al.*, 2004). A multiple linear regression was used to investigate the relative contribution of temperature and prey quality to the estimated growth of juvenile walleye pollock.

RESULTS

PREY ENERGY DENSITY

Prey WBEC collected during September of 2003 in the western GOA varied by prey group and body size (Table IV). Larvaceans and chaetognaths had the lowest specific WBEC while large euphausiids, gammariids and large copepods contained the highest WBEC. Energy densities may have been slightly underestimated for larvaceans because it was only possible to measure the energy contained in their body and not their 'house'. The amount of water in prey tissue was more correlated with wet energy content ($r = 0.85$, $P < 0.001$), than were estimates of joules in a gram of dry tissue ($r = 0.60$, $P < 0.01$). *Euphausia pacifica* contained the lowest energy content observed among the euphausiid prey group (WBEC $= 3.999$ kJ wet g^{-1}), whereas large *T. inermis* contained 1.7 times higher energy content (WBEC $= 6.824$ kJ wet g^{-1}). Similarly, the specific energy content of large bodied (≥ 15 mm L_T), euphausiids of the species *T. inermis* and *T. spinifera* were 1.3 and 1.5 times greater, respectively, than smaller (< 15 mm L_T) individuals of the same species.

MODEL CORROBORATION

Size-specific consumption estimates for juvenile walleye pollock using the bioenergetics model and the gastric evacuation rate model were correlated ($r_c = 0.945$, transformed 95% confidence limits $L_1 = 0.834$, $L_2 = 0.982$; Fig. 2) and highly significant ($P < 0.001$). Both estimates of daily consumption (g day^{-1}) consistently fell below the theoretical level of maximum consumption (C_{max}) for walleye pollock (Fig. 3) with no apparent trend associated with body size.

TABLE V. Station-specific thermal exposure and size-specific otolith growth (g wet mass day^{-1}) used in the bioenergetics model to estimate ration sizes (*P*-value)

Station	Temperature (° C)	L_S (mm)	Otolith growth (g day^{-1})	Ration
1B	7·1	45–49	0·029	0·25
		50–54	0·033	0·24
		55–59	0·045	0·22
		60–64	0·056	0·26
1C	7·9	40–44	0·029	0·27
		45–49	0·038	0·25
		50–54	0·037	0·24
		55–59	0·044	0·22
		60–64	0·053	0·26
		65–69	0·067	0·28
		70–74	0·062	0·35
2B	8·4	50–54	0·043	0·26
		55–59	0·058	0·31
		65–69	0·069	0·37
		70–74	0·091	0·48
2C	8·5	50–54	0·047	0·31
		70–74	0·075	0·39
		75–79	0·099	0·50
2D	9·4	50–54	0·043	0·21
		55–59	0·038	0·19
		60–64	0·044	0·19
		65–69	0·059	0·24
		75–79	0·080	0·33
		80–84	0·057	0·26
		85–89	0·095	0·27
2E	8·5	50–54	0·026	0·15
		60–64	0·044	0·20
		65–69	0·046	0·21
		70–74	0·058	0·26
		75–79	0·076	0·33
		80–84	0·077	0·33
3B	8·4	50–54	0·039	0·27
		55–59	0·036	0·24
3C	8·2	50–54	0·042	0·27
		70–74	0·134	0·55
3D	9·1	50–54	0·047	0·28
		70–74	0·092	0·43
		75–79	0·092	0·45
3E	9·0	55–59	0·053	0·18
		70–74	0·105	0·34
		75–79	0·114	0·37
5C	8·8	50–54	0·038	0·14
		55–59	0·054	0·18
		70–74	0·108	0·31
		75–79	0·107	0·31
5D	8·8	50–54	0·052	0·17

TABLE V. Continued

Station	Temperature (° C)	L_S (mm)	Otolith growth (g day^{-1})	Ration
5E	7·6	55–59	0·040	0·21
6B	8·0	55–59	0·039	0·12
		70–74	0·109	0·29
6C	9·5	50–54	0·076	0·40
6D	8·8	55–59	0·056	0·17
7B	8·6	50–54	0·040	0·18
		70–74	0·094	0·29
		75–79	0·132	0·39
8B	8·8	50–54	0·039	0·17
		55–59	0·053	0·20
		75–79	0·107	0·36
8D	8·8	55–59	0·051	0·23
		70–74	0·098	0·41
		75–79	0·108	0·45
8E	8·9	55–59	0·055	0·27
		70–74	0·084	0·29
		75–79	0·071	0·27
9D	8·2	70–74	0·079	0·26
		75–79	0·075	0·26
9E	8·4	65–69	0·054	0·21
		70–74	0·087	0·31
		75–79	0·083	0·31
		80–84	0·099	0·35
		85–89	0·085	0·25
		100–104	0·178	0·41
10D	9·0	75–79	0·085	0·34

The partitioned-M_{SE} analysis indicated that the slight differences between consumption estimates were primarily associated with the random R_C (0·49) and mean M_C (0·45) components, while the slope component S_C (0·06) had little influence. The M_C error identified the systematic difference between model estimates where the walleye pollock model consistently estimated a larger amount of consumption than the gastric evacuation model. The lack of error associated with the S_C illustrated that the difference between estimates was consistent across the size range of walleye pollock in this analysis. Similarly, the strong correlation of the consumption estimates indicates that the systematic error was small and would not produce significantly different estimates from those expected from a null model (Rice & Cochran, 1984).

WALLEYE POLLOCK GROWTH

Growth estimates generated from otoliths for all size classes of juvenile pollock for September 2000 in the sample grid ranged between 0·03 and 0·19 g day^{-1} with a mean of 0·06 g day^{-1}. The corresponding specific growth rates ranged from 0·01 to 0·06 g g^{-1} day^{-1} with a mean of 0·03 g g^{-1} day^{-1}. Mean size-specific ration sizes generated from otolith-based growth increments in the

TABLE VI. Size-specific rations sizes (*P*-value) used to estimate station- and size-specific growth in the bioenergetics model

L_S class (mm)	*n*	Mean *P*-value	Range	S.E.
40–44	1	0·27		
45–49	2	0·25	0·19–0·31	0·06
50–54	14	0·24	0·14–0·40	0·02
55–59	13	0·22	0·12–0·31	0·02
60–64	4	0·26	0·19–0·38	0·04
65–69	5	0·28	0·21–0·37	0·03
70–74	14	0·35	0·26–0·55	0·02
75–79	13	0·36	0·26–0·50	0·02
80–84	3	0·31	0·26–0·35	0·03
85–89	2	0·26	0·25–0·27	0·01
100–105	1	0·41		

walleye pollock model ranged from 22 to 41% (*P*-value = 0·22–0·44) of the theoretical maximum daily consumption rate (C_{max}). The resulting area- and size-specific estimates of growth from the walleye pollock model using the fixed ration sizes (*P*-value) compared reasonably well with the otolith-based estimates (Fig. 4).

To investigate the potential influence of temperature and prey quality on walleye pollock growth, the fixed rations were used to estimate growth across the sample grid for 50, 70 and 90 mm L_S fish at every sample station where fish of that size were captured and diet information was available (Fig. 5). Estimates of growth for the selected sizes of juvenile walleye pollock ranged between 0·03 and 0·08 g day^{-1} for 50 mm, 0·06 and 0·12 g day^{-1} for 70 mm, and 0·07 and 0·11 g day^{-1} for 90 mm L_S walleye pollock. The spatial plots
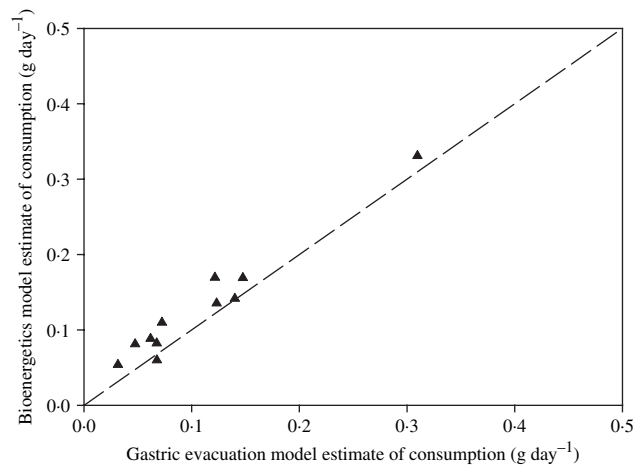
FIG. 2. Comparison of gastric evacuation rate model estimates of consumption and bioenergetics model estimates of consumption for size-specific groups of walleye pollock in the western Gulf of Alaska, September 2000. The dashed line represents the 1:1 line used for comparison.
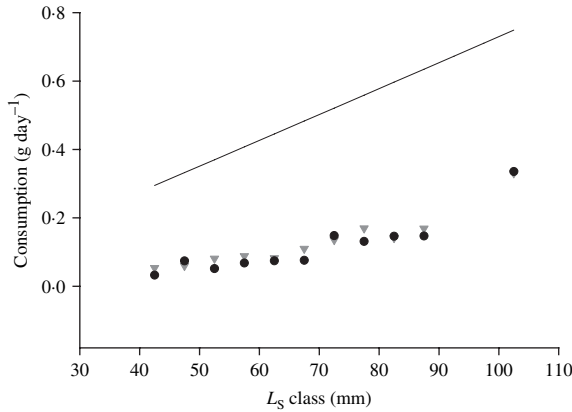
FIG. 3. Standard length class consumption estimates from bioenergetics (▼) and gastric evacuation models (●) with the theoretical maximum daily consumption (C_{max}) estimated by the bioenergetics model (—) for comparison.

of growth for all three sizes of walleye pollock (Fig. 5) indicated that the best areas for growth were generally located in the central sections of the sample area (Semidi Bank) while the areas in the south-west section had the lowest amounts of growth. The 70 and 90 mm L_S pollock were additionally estimated to grow well in stations adjacent to the ACC in both the north-east and south-east sections of the grid.

Areas of higher growth for 70 and 90 mm L_S juvenile walleye pollock contained significantly higher proportions of euphausiids in captured fish diets than areas of lower growth ($r^2 = 0.72$ and 0.74, $P < 0.001$). The multiple
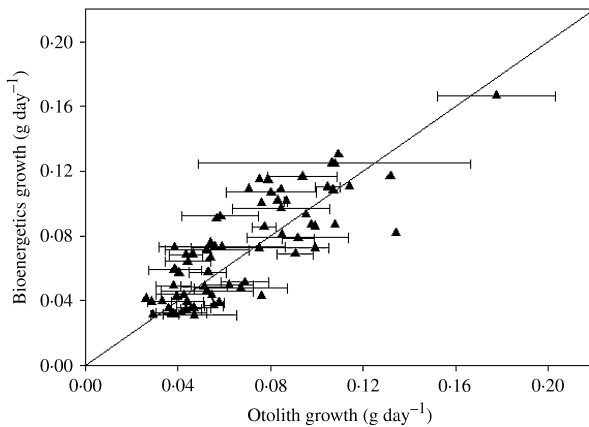
FIG. 4. Comparison of otolith and bioenergetics model daily growth estimates for walleye pollock during September 2000. Otolith growth represents the mean daily growth of the last 5 days observed in the structure of the otolith. Error bars are ± 2 S.E. around station-specific otolith growth estimates. Symbols without error bars consist of only one otolith estimate for growth. The solid line represents the 1:1 line used for comparison.
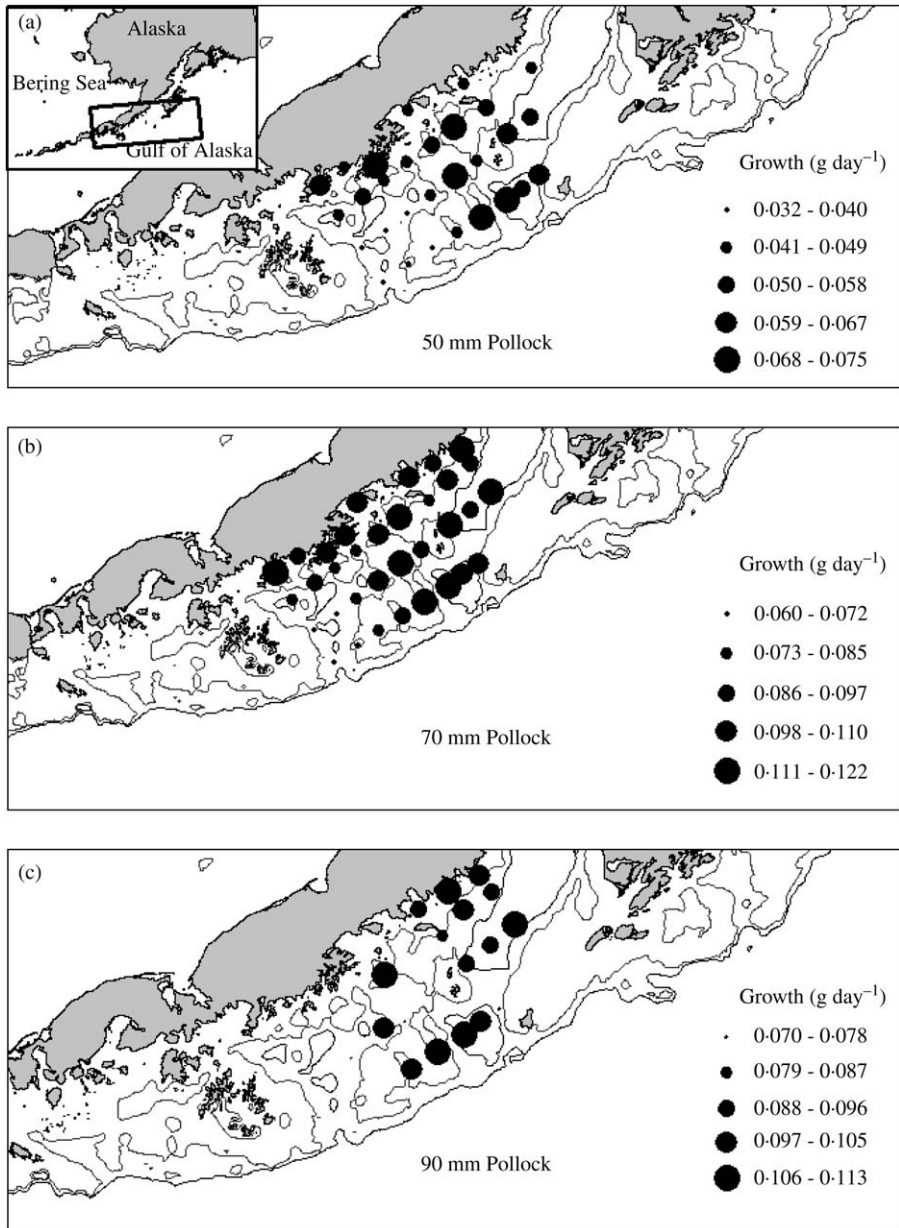
FIG. 5. Bioenergetics model estimates of daily growth for (a) 50, (b) 70 and (c) 90 mm standard length walleye pollock in the western Gulf of Alaska for September 2000. Estimates were calculated using a fixed ration size for each size class to illustrate the influence of temperature and prey quality on the size-specific growth of walleye pollock at each station. Depth contours in grey are 100 m and in black are 200 m.

regression analysis indicated that the proportion of euphausiids in the diet explained 85–86% of the variation observed in estimates of growth across the sample grids for both 70 mm ($r_a^2 = 0.83$, $P < 0.001$) and 90 mm pollock

$(r_a^2 = 0.72, P < 0.001)$. In contrast, differences in thermal exposure among sample stations had little effect on estimates of growth for 70 mm L_S walleye pollock ($P > 0.05$) and a slightly negative relationship for 90 mm L_S walleye pollock ($P = 0.05$).

DISCUSSION

The bioenergetics estimates of growth for juvenile walleye pollock indicated that the quality of available prey, in terms of wet WBEC, influenced walleye pollock growth more than the range of temperature available in September 2000. Growth for juvenile fish under the most extreme temperature observed in the sample area (13·5° C) was only 32% lower than the growth experienced at the preferred temperature (10° C). The presence of low quality prey (larvaceans) in the diet, however, depressed growth by as much as 67% when compared to estimates for fish consuming primarily high quality (euphausiid) prey. The relative importance of prey quality (WBEC) to walleye pollock growth in the western GOA suggests that the availability of high WBEC prey in the autumn, prior to the onset of winter, could have important ramifications for juvenile walleye pollock body condition and survival through the winter.

For juvenile walleye pollock, high proportions of euphausiids in the diet with high WBEC explained most of the variations between otolith and walleye pollock model growth estimates when ration sizes for each 5 mm size class were held constant. The ration sizes generated by the model from otolith growth estimates showed modest variability (*P*-value range 0·22–0·41). The remaining variability in growth estimates between otoliths and bioenergetics model runs was within the 95% CI of the otolith estimates of growth. Fixed ration sizes encompassed much of the variability observed in growth, which suggests that spatial differences in ration size should be less important in explaining differences in juvenile walleye pollock growth than the overall quality or type of the prey consumed at different stations. The influence of spatially heterogeneous prey availability on juvenile walleye pollock growth, however, was not explicitly tested or resolved in this analysis. The limited number of otoliths used to estimate station- and size-specific growth at each sample station and the variability associated with these estimates probably accounts for the majority of the remaining differences observed between daily growth estimates. It is important to note that some variability among growth estimation techniques is inherent, because bioenergetics and otoliths estimate daily growth at different temporal scales and require different assumptions. The bioenergetics model estimates represent the potential daily growth given a mean thermal exposure, diet and ration size for an individual. Otoliths produce an estimate of past growth experienced by a limited number of captured individuals, integrated across a 5 day period and averaged to produce daily growth.

The strong correlation between independent estimates of consumption from both the bioenergetics and gastric evacuation models, while not a validation of either model, provides some confidence and support for estimates made using either approach for juvenile walleye pollock. The consistency in daily

consumption estimates across the juvenile walleye pollock sizes and environmental conditions examined in this study suggests that the walleye pollock model is a robust estimator and provides reasonable estimates of consumption. This analysis, however, does not constitute a validation of the walleye pollock model and should not supplant efforts for a directed laboratory validation (Bajer *et al.*, 2004; Madenjian *et al.*, 2004). Attempts to corroborate energetic models in the field are problematic due to difficulties in estimating either consumption or growth of fishes in the field and have been found to occasionally result in misleading results (Bajer *et al.*, 2003). The short temporal scale and fixed low to moderate ration sizes used in this analysis, however, should have minimized the potential for errors identified in some bioenergetics model applications (Ney, 1993; Bajer *et al.*, 2004).

Similar to other applications of bioenergetics models the present results are vulnerable to potential biases associated with any simplified model representation of an energy budget for a free ranging wild organism. The use of a constant activity multiplier to represent the energetic cost of fish activity has previously been suggested as a potential bias for bioenergetics model estimates of fish species that display highly variable spatial and temporal activity levels (Ney, 1993). Walleye pollock, however, are a cruising fish with a relatively constant base activity level. The use of a constant activity multiplier when modelling on a daily or longer time scale was found to closely approximate daily activity costs for rainbow trout *Oncorhynchus mykiss* (Walbaum) a cruising forager (Briggs & Post, 1997). Similarly, no statistical difference was observed in spatial or diel feeding activity that would lead to the conclusion that activity costs due to foraging varied widely across the sampling area or 24 h modelled period. In accordance with previous applications of the juvenile walleye pollock model an activity multiplier of 2·0 was used (Ciannelli *et al.*, 1998, 2004*b*; Duffy-Anderson *et al.*, 2002) which has recently been supported for a North Sea pollock species, the saithe *Pollachius virens* (L.), whose activity multiplier was found to range between 2·0 and 2·5 at optimum cruising speeds (Andersen & Riis-Vestergaard, 2004; Steinhausen *et al.*, 2005).

The accuracy of the juvenile walleye pollock bioenergetics model has previously been supported by its ability to produce estimates of consumption and growth that are consistent with estimates derived using alternate techniques (Ciannelli *et al.*, 1998, 2004*b*). The walleye pollock model's estimates of growth and consumption for September 2000 were also comparable to previous estimates derived for juvenile walleye pollock in the western GOA. Gastric evacuation model estimates of consumption for an average sized juvenile walleye pollock during September of 1990 in the western GOA were between 7·4 and 8·5% body mass (BM) per day (Merati & Brodeur, 1996). Gastric evacuation model estimates from this study were slightly lower, ranging between 2·4 and 7·9% BM per day across the size range of juvenile walleye pollock in the present study. The present bioenergetics estimates of consumption were similar, with an average of 6·0% BM per day and a range of 3·2–10·6% BM per day for September of 2000. Similarly, the growth rate estimates of 1·5–6·9% BM per day from the walleye pollock model were comparable to the 1·3–7·4% BM per day from the otolith analysis in this study and the 2·0–6·8% BM per day estimates of otolith growth for August to September 1987 (Brown & Bailey,

1992). Previous application of the bioenergetics model for juvenile walleye pollock in the western GOA estimated growth at 2·4–9·3% BM per day for the 1990 year class (Ciannelli *et al.*, 1998).

The spatial application of the bioenergetics model in the western GOA for September 2000 indicated that growth favourable habitat conditions, in terms of areas where temperature and prey quality interacted to produce the highest growth rates for juvenile walleye pollock, was in the south-east corner of the grid along the eastern edge of the Semidi Bank. Additional areas of high growth were located near shore in the vicinity of Castle Cape, Kupreanof Point and south-west of Sutwik Island for 50 and 70 mm L_S walleye pollock, and east of Sutwik Island over the Shelikof Sea Valley for 70 and 90 mm L_S walleye pollock. Areas of the sampling grid where the model estimated high growth were often associated with catches of larger body sized juvenile fish with a higher mean condition factor (M. Wilson, unpubl. data). No statistically significant relationship, however, existed between walleye pollock condition and areas estimated to have increased growth rates. The lack of a statistically significant relationship between high growth habitat and high fish condition indices was not surprising given that the present analysis estimated growing conditions on a finite daily scale, whereas fish condition is an integrated measure of growth history over a longer time scale.

The relative importance of large euphausiid prey observed in this study to the autumn growth of juvenile walleye pollock prior to winter conditions in the western GOA, highlights a potentially important link to the growth, survival and ultimate recruitment of juvenile walleye pollock to adult life stages. Previous studies have highlighted the importance of euphausiids as prey in terms of their contribution to the diet of juvenile walleye pollock (Merati & Brodeur, 1996). The high euphausiid WBEC observed in this study further emphasizes the importance of large euphausiids to the overall energy budget and growth efficiency of juvenile walleye pollock in the autumn, contributing substantially to the observed spatial variability in walleye pollock growth. Interspecific and spatial differences in WBEC of euphausiid species have been documented before (Davis, 2003) with *T. spinifera* and *T. inermis* from the Gulf of Alaska containing higher WBEC than similar sized individuals from across the North Pacific and Bering Sea (Davis *et al.*, 1998). Similarly, the comparatively low WBEC observed for *E. pacifica* and smaller body sized individuals of all euphausiid species in this study and referenced in the Davis (2003) study suggests that interspecific, seasonal and size-specific differences among euphausiids should be accounted for when attempting to balance energy budgets.

Accounting for how spatially variable habitats influence the size-specific growing conditions of juvenile fishes may provide a link between observed environmental conditions and realized fish growth. The ability to quantify differences in potential fish growth among habitats and identify which attributes are most influential to fish growth improves the understanding of, and ability to manage, large pelagic ecosystems. The present results illustrate that this modelling approach has merit as a tool to identify and investigate how differences among habitats may influence the size-specific growth of highly mobile juvenile fishes. Future applications of this modelling approach may provide insights into

how the spatial variability of growing conditions inherent in pelagic environments influences the recruitment of juvenile fishes into adult populations.

References

Andersen, N. G. & Riis-Vestergaard, J. (2004). Alternative model structures for bioenergetics budgets of a cruising predatory gadoid: incorporating estimates of food conversion and costs of locomotion. *Canadian Journal of Fisheries and Aquatic Sciences* **61,** 2413–2424.

Arrhenius, F. & Hansson, S. (1994). In-situ food-consumption by young-of-the-year Baltic Sea herring *Clupea harengus*: a test of predictions from a bioenergetics model. *Marine Ecology Progress Series* **110,** 145–149.

Bailey, K. M. (2000). Shifting control of recruitment of walleye pollock *Theragra chalcogramma* after a major climatic and ecosystem change. *Marine Ecology Progress Series* **198,** 215–224.

Bajer, P. G., Whitledge, G. W., Hayward, R. S. & Zweifel, R. D. (2003). Laboratory evaluation of two bioenergetics models applied to yellow perch: identification of a major source of systematic error. *Journal of Fish Biology* **62,** 436–454. doi: 10.1046/j.0022-1112.2003.00040.x

Bajer, P. G., Whitledge, G. W. & Hayward, R. S. (2004). Widespread consumption-dependent systematic error in fish bioenergetics models and its implications. *Canadian Journal of Fisheries and Aquatic Sciences* **61,** 2158–2167.

Boisclair, D. & Marchand, F. (1993). The guts to estimate fish daily ration. *Canadian Journal of Fisheries and Aquatic Sciences* **50,** 1969–1975.

Briggs, C. T. & Post, J. R. (1997). In situ activity metabolism of rainbow trout (*Oncorhynchus mykiss*): estimates obtained from telemetry of axial muscle electromyograms. *Canadian Journal of Fisheries and Aquatic Sciences* **54,** 859–866.

Brodeur, R. D. & Wilson, M. T. (1996). Mesoscale acoustic patterns of juvenile walleye pollock (*Theragra chalcogramma*) in the western Gulf of Alaska. *Canadian Journal of Fisheries and Aquatic Sciences* **53,** 1951–1963.

Brooks, J. L. & Dodson, S. I. (1965). Predator, body size, and composition of plankton. *Science* **150,** 28–35.

Brown, A. L. & Bailey, K. M. (1992). Otolith analysis of juvenile walleye pollock *Theragra chalcogramma* from the western Gulf of Alaska. *Marine Biology* **112,** 23–30.

Buchheister, A. & Wilson, M. T. (2005). Shrinkage correction and length conversion equations for walleye pollock (*Theragra chalcogramma*), capelin (*Mallotus villosus*), and eulachon (*Thaleichthys pacificus*). *Journal of Fish Biology* **67,** 541–548. doi: 10.1111/j.1095-8649.2005.00741.x

Buchheister, A., Wilson, M. T., Foy, R. J. & Beauchamp, D. A. (2006). Seasonal and geographic variation in condition of juvenile walleye pollock in the western Gulf of Alaska. *Transactions of the American Fisheries Society* **135,** 897–907.

Ciannelli, L., Brodeur, R. D. & Buckley, T. W. (1998). Development and application of a bioenergetics model for juvenile walleye pollock. *Journal of Fish Biology* **52,** 879–898.

Ciannelli, L., Chan, K. S., Bailey, K. M. & Stenseth, N. C. (2004*a*). Nonadditive effects of the environment on the survival of a large marine fish population. *Ecology* **85,** 3418–3427.

Ciannelli, L., Brodeur, R. D. & Napp, J. M. (2004*b*). Foraging impact on zooplankton by age-0 walleye pollock (*Theragra chalcogramma*) around a front in the southeast Bering Sea. *Marine Biology* **144,** 515–526.

Cochran, P. A. & Adelman, I. R. (1982). Seasonal aspects of daily ration and diet of largemouth bass, *Micropterus salmoides*, with an evaluation of gastric evacuation rates. *Environmental Biology of Fishes* **7,** 265–275.

Davis, N. D. (2003). Feeding ecology of Pacific salmon (*Oncorhynchus* spp.) in the central North Pacific Ocean and Central Bering Sea, 1991–2000. PhD, Hokkaido University, Hakodate, Japan.

Davis, N. D., Myers, K. W. & Ishida, Y. (1998). Caloric value of high-sea salmon prey organisms and simulated salmon ocean growth and prey consumption. *North Pacific Anadromous Fish Commission Bulletin* **1,** 146–162.

Duffy-Anderson, J. T., Bailey, K. M. & Ciannelli, L. (2002). Consequences of a superabundance of larval walleye pollock *Theragra chalcogramma* in the Gulf of Alaska in 1981. *Marine Ecology Progress Series* **243,** 179–190.

Eggers, D. M. (1979). Some recent methods for estimating food-consumption by fish – reply. *Journal of the Fisheries Research Board of Canada* **36,** 1018–1019.

Hanson, P. C., Johnson, T. B., Schindler, D. E. & Kitchell, J. F. (1997). *Fish Bioenergetics 3.0.* Madison, WI: University of Wisconsin Sea Grant.

Hartman, K. J. & Brandt, S. B. (1995). Estimating energy density of fish. *Transactions of the American Fisheries Society* **124,** 347–355.

Jarre-Teichmann, A. M., Palomares, L. D., Soriano, M., Sambilay, V. C. & Pauly, D. (1993). A draft user's manual for MAXIMS. A computer program for estimating the food consumption of fishes from diel stomach contents data and population parameters. *ICLARM Software No. 4.* Manila: ICLARM.

Lanksbury, J. A., Duffy-Anderson, J. T., Mier, K. L. & Wilson, M. T. (2005). Ichthyoplankton abundance, distribution, and assemblage structure in the Gulf of Alaska during September 2000 and 2001. *Estuarine Coastal and Shelf Science* **64,** 775–785.

Lasker, R. (1978). The relation between oceanographic conditions and larval anchovy food in the California Current: identification of factors contributing to recruitment failure. *Rapports et Proces-Verbaux des Reunions Conseil Permanent International pour l'Exploration de la Mer* **173,** 212–230.

Madenjian, C. P., O'Connor, D. V., Chernyak, S. M., Rediske, R. R. & O'Keefe, J. P. (2004). Evaluation of a chinook salmon (*Oncorhynchus tshawytscha*) bioenergetics model. *Canadian Journal of Fisheries and Aquatic Sciences* **61,** 627–635.

Merati, N. & Brodeur, R. D. (1996). Feeding habits and daily ration of juvenile walleye pollock, *Theragra chalcogramma*, in the western Gulf of Alaska. In *Ecology of Juvenile Walleye Pollock*, Theragra chalcogramma (Brodeur, R. D., Livingston, P. A., Loughlin, T. R. & Hollowed, A. B., eds). *U.S. Department of Commerce, NOAA Technical Report* **NMFS 126,** 65–79.

Ney, J. J. (1990). Trophic economics in fisheries – assessment of demand-supply relationships between predators and prey. *Reviews in Aquatic Sciences* **2,** 55–81.

Ney, J. J. (1993). Bioenergetics modeling today: growing pains on the cutting edge. *Transactions of the American Fisheries Society* **122,** 736–748.

Pangle, K. L., Sutton, T. M., Kinnunen, R. E. & Hoff, M. H. (2004). Overwinter survival of juvenile lake herring in relation to body size, physiological condition, energy stores, and food ration. *Transactions of the American Fisheries Society* **133,** 1235–1246.

Persson, L., Andersson, J., Wahlstrom, E. & Eklov, P. (1996). Size-specific interactions in lake systems: predator gape limitation and prey growth rate and mortality. *Ecology* **77,** 900–911.

Rice, J. A. & Cochran, P. A. (1984). Independent evaluation of a bioenergetics model for largemouth bass. *Ecology* **65,** 732–739.

Richter, H., Luckstadt, C., Focken, U. & Becker, K. (2004). Some mathematical considerations in estimating daily ration in fish using food consumption models. *Ecological Modelling* **171,** 381–393.

Schumacher, J. D. & Reed, R. K. (1986). On the Alaska Coastal Current in the western Gulf of Alaska. *Journal of Geophysical Research-Oceans* **91,** 9655–9661.

Shuter, B. J. & Post, J. R. (1990). Climate, population viability, and the zoogeography of temperate fishes. *Transactions of the American Fisheries Society* **119,** 314–336.

Sogard, S. M. (1997). Size-selective mortality in the juvenile stage of teleost fishes: a review. *Bulletin of Marine Science* **60,** 1129–1157.

Sogard, S. M. & Olla, B. L. (2000). Endurance of simulated winter conditions by age-0 walleye pollock: effects of body size, water temperature and energy stores. *Journal of Fish Biology* **56,** 1–21.

Steinhausen, M. F., Steffensen, J. F. & Andersen, N. G. (2005). Tail beat frequency as a predictor of swimming speed and oxygen consumption of saithe (*Pollachius virens*) and whiting (*Merlangius merlangus*) during forced swimming. *Marine Biology* **148,** 197–204. doi: 10.1007/s00227-005-0055-9

Sturdevant, M. V., Brase, A. L. J. & Hulbert, L. B. (2001). Feeding habits, prey fields, and potential competition of young-of-the-year walleye pollock (*Theragra chalcogramma*) and Pacific herring (*Clupea pallasi*) in Prince William Sound, Alaska, 1994–1995. *Fishery Bulletin* **99,** 482–501.

Toneys, M. L. & Coble, D. W. (1980). Mortality, hematocrit, osmolality, electrolyte regulation, and fat depletion of young-of-the-year fresh-water fishes under simulated winter conditions. *Canadian Journal of Fisheries and Aquatic Sciences* **37,** 225–232.

Wellborn, G. A., Skelly, D. K. & Werner, E. E. (1996). Mechanisms creating community structure across a freshwater habitat gradient. *Annual Review of Ecology and Systematics* **27,** 337–363.

Wilson, M. T., Brodeur, R. D. & Hinckley, S. (1996). Distribution and abundance of age-0 walleye pollock, *Theragra chalcogramma*, in the western Gulf of Alaska during September 1990. In *Ecology of Juvenile Walleye Pollock*, Theragra chalcogramma (Brodeur, R. D., Livingston, P. A., Loughlin, T. R. & Hollowed, A. B., eds). *U.S. Department of Commerce, NOAA Technical Report* **NFMS 126,** 11–24.

Yang, Z. & Arritt, R. W. (2002). Tests of a perturbed physics ensemble approach for regional climate modeling. *Journal of Climate* **15,** 2881–2896.

Zar, J. H. (1996). *Biostatistical Analysis*, 3rd edn. Upper Saddle River, NJ: Prentice Hall.