Season variation in nutrient composition of Alaskan walleye pollock

David D. Kitts, Minh Dieu Huynh, Chun Hu, and Andrew W. Trites

Abstract: A popular hypothesis for the noted steady decline in the population of Steller sea lions, *Eumetopias jubatus* (Schreber, 1776), in the regions from Prince William Sound through the Aleutian Islands relates to their nutritional status. Sea lion diets appear to have shifted from primarily small schooling fatty fishes to low-fat fish such as walleye pollock, *Theragra chalcogramma* (Pallas, 1814). We examined the seasonal changes in proximate nutrients of pollock collected in the Bering Sea. Mean energy density (dry mass) of pollock peaked in October then declined and remained low throughout winter. Energy recovery occurred in the summer months with strong recovery observed in female fish caught in July. Contrary to whole fish carcass energy contents, both total protein and moisture contents were at their highest levels in winter (January) when total crude lipid content was at its lowest ($p < 0.05$). This trend gradually declined to its lowest levels in the fall when lipid content was high. The decline in total lipids during winter seasons appeared to parallel gonad development during the prespawning period. Sex differences in energy densities were not found. Proximate analysis data for moisture, protein, ash, and lipid content also did not show any significant variation between males and females. Protein digestibility of pollock was higher ($p < 0.05$) in the summer than in the spring, but not different for winter or fall. We concluded that the nutrient content of walleye pollock may have some impact on the Steller sea lions that feed on them, particularly the energetic value that appears to be low during important feeding periods for this marine mammal.

Résumé : Une hypothèse retenue communément pour exper le déclin persistant observé chez les populations de lions de mer de Steller, *Eumetopias jubatus* (Schreber, 1776), dans les régions allant du détroit du Prince William aux îles aléoutiennes inclusivement se base sur leur statut alimentaire. Le régime alimentaire des lions de mer semble avoir changé d'une prédominance de petits poissons riches en gras et vivant en bancs à une prépondérance de poissons maigres, tels que les goberges de l'Alaska, *Theragra chalcogramma* (Pallas, 1814). Nous avons examiné les changements saisonniers de la composition nutritionnelle en éléments nutritifs des goberges de la mer de Béring. La densité énergétique moyenne (masse sèche) de la goberge atteint un sommet en octobre pour ensuite décliner et demeurer basse pendant tout l'hiver. La récupération de l'énergie se fait pendant les mois d'été et une forte récupération s'observe chez les poissons femelles capturés en juillet. Contrairement au contenu total en énergie de la carcasse entière du poisson, les contenus totaux en protéines et en humidité sont tous deux à leur maximum en hiver (janvier), au moment où le contenu global total en lipides est à son minimum ($p < 0{,}05$). Cette tendance décline graduellement vers son minimum à l'automne, quand le contenu lipidique est élevé. Le déclin des lipides totaux durant l'hiver semble coïncider avec le développement des gonades durant la période qui précède la fraye. Il n'y a pas de différence de densité énergétique entre les mâles et les femelles. Les données de contenus d'humidité, de protéines et de lipides de l'analyse nutritionnelle ne montrent pas non plus de différence entre les sexes. La digestibilité des protéines de la goberge est plus élevée ($p < 0{,}05$) en été qu'au printemps, mais elle n'est pas différente en hiver, ni à l'automne. Nous concluons que le contenu en éléments nutritifs de la goberge peut avoir un impact sur les lions de mer de Steller qui s'en nourrissent, particulièrement la valeur énergétique qui semble être basse durant des période d'alimentation importantes pour ce mammifère marin.

[Traduit par la Rédaction]

Introduction

A dramatic decline in Steller sea lion, *Eumetopias jubatus* (Schreber, 1776), populations west of Prince William Sound, Alaska, began in the late 1970s (Trites and Larkin 1996; Loughlin 1998). In addition to potential environment-related factors influencing sea lion populations, there is an equally important theory that Steller sea lion health may have been negatively affected by an increase in dietary gadid consumption, such as walleye pollock (*Theragra chalcogramma* (Pallas, 1814)) in the Gulf of Alaska and Eastern Aleutian Islands, and a corresponding decline in the small, fatty

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D.D. Kitts,[1] M.D. Huynh, and C. Hu. Food, Nutrition and Health, Faculty of Agricultural Sciences, University of British Columbia, Food Sciences Building, 6640 Northwest Marine Drive, Vancouver, BC V6T 1Z4, Canada.
A.W. Trites. Marine Mammal Research Unit, Fisheries Centre, University of British Columbia, Vancouver, BC V6T 1Z4, Canada.

[1]Corresponding author (e-mail: ddkitts@interchange.ubc.ca).

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schooling fish such as sand lance (*Ammodytes hexapterus* Pallas, 1814) (Alverson 1992; Merrick et al. 1997; Trites and Donnelly 2003). Changes in the nutrient composition of these species and abundance of forage fish in Alaska occurred rapidly in the late 1970s, possibly as a result of long-term environmental changes and the unusual mortality of juvenile and adult fish owing to disease (Van Pelt et al. 1997; Paul et al. 1998*b*; Anderson and Piatt 1999; Trites et al. 1999; Benson and Trites 2002).

Estimates from 1973 to 1978 indicated that 58.3% of the Steller sea lion population in the Gulf of Alaska had diets that predominantly contained walleye pollock (Brodeur and Wilson 1996). Other studies have shown that diets of stable and increasing populations of Steller sea lions were more diverse, thus implying that diets dominated by pollock may have played role in their decline (Merrick et al. 1997). A captive feeding study found that juvenile Steller sea lions lost mass when fed exclusively pollock. This observation was not apparent when sea lions were fed Pacific herring (*Clupea pallasii* Valenciennes in Cuvier and Valenciennes, 1847) (Rosen and Trites 2000). Other known adverse changes in physiological status, including induced anemia attributed to decreased erythrocyte counts, have been attributed to the high consumption of gadoid fish such as pollock (Merrick et al. 1997). A former study from our laboratory concluded that the energy content was a primary factor limiting the nutritional value of pollock (Donnelly et al. 2003).

Dietary feeding patterns and prey consumption by Steller sea lions vary seasonally, and likely coincide with the breeding behavior of males and the pregnancy and lactation demands of females. Changes in environmental temperature also influence the demand for body fat stores for insulation, with colder temperatures of winter months resulting in greater food consumption. Longer durations of time that sea lions spend in the water will result in increased body heat losses. Collectively, behavior and physiological demands require an adequate nutritional status to build up body fat stores and insulate against loss of body heat (Kastelein et al. 1990).

The following study examined seasonal variation in the proximate composition and energy content of whole walleye pollock that are eaten by Steller sea lions. This information is useful for understanding, in part, the magnitude of energy transfer and essential nutrients from prey sources, such as pollock, to sea lions.

Materials and methods

Physical measurements

Walleye pollock were caught in the Bering Sea, Alaska, during September and October 1998, and for 7 months in 1999 (January, February, March, July, August, October, and November). Some months were missing owing to periods when no fishing occurred. Pollock were frozen on the fishing boats (At-sea Processors Association, Seattle, Washington) in boxes after catch and transported to the University of British Columbia or the Vancouver Aquarium Marine Science Centre where they were stored at –18 °C prior to processing. Fish were thawed overnight and only good-quality uniform whole fish samples were selected for analysis.

Fish morphology was evaluated using mass, girth, length (standard length), and mass of gonads. A gonadosomatic index was determined based on the formula of (gonad mass / total body mass) × 100. Subsequently, the fish were ground in a Hobart silent cutter, mixed, and bagged under a vacuum seal. Subsamples (n = 3–4) of the mixed ground fish (15 g) were collected and refrozen in vacuum-sealed bags until ready for analysis.

Proximate analysis

Moisture content, crude protein, total crude lipids, and ash content were measured. Moisture determinations were made on 3–5 g wet fish samples, dried at 80 °C in a vacuum oven for 12 h (AOAC 950.46; AOAC International 1995). Dried samples were ashed in a muffle furnace heated at 550 °C for 32 h to determine the percentage of crude ash (AOAC 920.153; AOAC International 1995). Crude protein was determined using the Leco method (AOAC 992.15; AOAC International 1995). Air dried samples (0.25 g) were combusted in an automated Leco FP-328 nitrogen analyser (Leco Corp., Joseph, Michigan). Nitrogen values were multiplied by 6.25 to obtain crude-protein values. Total crude lipid content was determined on ground fish using the Folch's double phase method (Folch et al. 1957). Fish homogenate sample (2 g) was mixed with 50 mL Folch's solution (2:1 solution of chloroform–methanol), filtered, and left standing for phase separation. An aliquot (5.0 mL) of the chloroform layer was removed and evaporated to dryness to determine total crude lipid content, using the gravimetric method.

Gross energy analysis

Energy density was determined using an adiabatic bomb calorimeter on vacuum-dried samples. The results were reported as kiloJoule per gram dry mass.

Protein digestibility analysis (in vitro)

In vitro digestibility of fish sample was determined according to the method of Yuan et al. (1991). Briefly, ground fish samples were suspended in distilled water and the pH adjusted to 1.9 using hydrochloric acid. Pepsin (porcine stomach mucosa 1 : 10 000; catalogue no. p-6887; Sigma Chemical, St. Louis, Missouri) was added to the suspended fish solution, and samples were placed in a shaking water bath at 37 °C for 30 min. Samples were then adjusted to a pH of 8.0 and incubated with pancreatin (porcine pancrease; Sigma Chemical) and incubated again at 37 °C in a shaking water bath. At defined 1-min intervals, aliquots were removed over a 30-min period and deproteinized with 20% *m*/*v* trichloroacetic acid. TNBS (2,4,6-trinitrobenzene sulfonic acid) was added to each sample to measure protein digestion products. Protein digestibility was determined from the initial slope (e.g., 0–10 min) using linear regression analysis of TNBS absorption-time data. Relative digestability of different fish protein sources was made in comparison with a casein protein standard (sodium salt; ICN Nutritional Biochemicals, Cleverland, Ohio).

Fatty-acid analysis

Fatty acids were measured from the chloroform layer by evaporating aliquots (10 mL, in duplicate) under a stream of nitrogen gas in a warm water bath. Lipid extracts were

Table 1. Summary of morphological data of walleye pollock (*Theragra chalcogramma*) collected from the Bering Sea, Alaska.

Catch month and year	Season	Sex	Mass (g)	Length (cm)	Girth (cm)	Gonad mass (g)	GSI*	*n*
Sept. 1998	Fall	Male	674.2±29.75	42.1±0.55	19.7±0.33	13.7±2.00	1.94±0.213	33
		Female	683.5±36.33	42.3±0.82	19.7±0.34	19.8±4.27	2.78±0.582	30
Oct. 1998	Fall	Male	643.5±19.75	40.4±0.42	19.5±0.24	12.9±1.58	1.93±0.218	30
		Female	696.0±37.10	41.6±0.75	19.9±0.34	14.7±2.63	2.08±0.370	44
Jan. 1999	Winter	Male	523.2±12.06	38.6±0.28	18.4±0.17	18.7±1.37	3.51±0.234	46
		Female	530.6±20.01	38.8±0.49	18.1±0.41	34.3±5.50	5.90±0.754	36
Feb. 1999	Winter	Male	643.9±15.28	40.9±0.42	19.9±0.21	24.6±2.76	3.67±0.354	30
		Female	697.1±25.12	42.1±0.39	20.4±0.31	64.8±6.87	9.16±0.826	29
Mar. 1999	Spring	Male	597.4±14.05	40.5±0.33	18.9±0.18	25.7±1.55	4.31±0.244	33
		Female	631.1±23.46	41.0±0.50	19.2±0.25	52.5±5.03	8.04±0.653	28
July 1999	Summer	Male	490.7±26.96	38.6±0.87	18.2±0.32	3.1±0.64	0.46±0.102	30
		Female	564.5±34.42	40.3±0.85	18.7±0.32	8.5±1.20	1.46±0.173	30
Aug. 1999	Summer	Male	272.6±7.90	32.5±0.38	15.1±0.20	2.6±0.31	0.65±0.104	30
		Female	261.8±11.08	31.5±0.46	14.9±0.29	1.8±0.20	0.64±0.055	30
Oct. 1999	Fall	Male	876.4±30.92	46.5±1.01	22.0±0.33	17.9±2.30	1.91±0.247	26
		Female	951.5±33.36	48.4±0.55	23.0±0.34	26.7±5.24	2.85±0.318	31
Nov. 1999	Fall	Male	728.6±37.77	43.9±0.81	21.2±0.41	29.9±4.96	3.77±0.520	30
		Female	689.5±31.05	44.3±0.73	21.1±0.46	40.7±10.22	5.56±1.449	30

*Gonadosomatic index (GSI) = gonad mass/body mass × 100.

saponified with 0.5 mol/L of methanol – potassium hydroxide (2.5 mL) in a 50 °C shaking water bath for 1 h. The nonsaponifiable materials were removed using petroleum ether. The saponifiable lipids were derivatized with 5.0 mL of boron triflouride in methanol (Sigma Chemical) in a boiling water bath. After cooling, hexane (2.5 mL) was added to extract the fatty acid methyl esters. Fatty acid methyl esters were analyzed by gas chromatograph (Shimadzu GC-17A; Shimadzu Scientific Instruments Inc., Columbia, Maryland) equipped with a flame ionization detector and an AOC 1400 auto injector (Shimadzu Scientific Instruments Inc.). Samples were injected onto a silicone fused Omegawax™-320 capillary column (30 m × 0.32 mm inner diameter, 0.25 µm film thickness) (Supelco Inc., Bellefonte, Pennsylvania). Helium was used as the carrier gas. Injector and detector temperatures were 200 and 220 °C, respectively. The column temperature was set at 220 °C and the column flow rate was kept at 1.9 mL/min. Identification of fatty acids was determined from known standard mixtures (fatty acid methyl ester mixture #189-19, Sigma lipid standard; Sigma Chemical).

Statistical analysis

All analyses were conducted in triplicate samples and the results are expressed as means ± SD. Statistical analysis was conducted using analysis of variance (ANOVA) with Tukey's post hoc tests performed on individual treatment means to determine statistical difference. Kruskal–Wallis and Mann–Whitney tests were used on results that required a nonparametric ANOVA. Logarithmic transformation was used to normalize data that exhibited heteroscedasticity prior to performing parametric tests (one-way ANOVA) (Zar 1974).

In this study, walleye pollock were divided and reported by seasons based on the months in which they were caught. These included winter (January and February), spring (March), summer (July and August), and fall (September, October, and November). Some months were missing owing to periods when no pollock fishing occurred.

Results

The morphological data of walleye pollock samples collected from the Bering Sea are shown by the month of catch (Table 1 and Fig. 1). Samples collected in the summer of 1999 (July and August) exhibited a marked reduction in body mass compared with fish collected in the winter and spring of 1999 (February and March). This mass reduction coincided with the decline in gonad mass in the summer, following a peak increase seen in the prespawning months of February and March (Table 1). The August 1999 samples appeared to comprise mostly younger class fish (averaging 270 g in both males and females), which were smaller ($p < 0.05$) than the average mass (over 500 g) of fish collected in other months. The mean standard length of these fish was 32 cm, which indicated that these fish had attained maturity (Smith 1981). One possible explanation for this mass discrepancy likely involves the limitations of sampling fish from commercial fisheries.

Seasonal changes in total energy density of both male and female walleye pollock are shown in Tables 2 and 3. Gross energy values were lowest during the winter months and highest during the fall in both males and females ($p < 0.05$). The maximum energy content occurred in October, but declined in November and remained low throughout the winter. Some return of total energy recovery was seen in the summer months for both males and females, with a strong recovery observed in females caught in July. Although the energy data displayed some variation between males and females in some months, there was no statistically significant difference in energy density between genders in this study.

Changes in proximate analysis for both male and female walleye pollock at specific seasons are presented in Table 3. Peak moisture contents occurred in January (winter), but slightly declined afterwards, in both sexes. The moisture content remained relatively stable during the spring and summer months but declined markedly in fall (September–

Fig. 1. Whole body mass of walleye pollock (*Theragra chalcogramma*) sampled from September 1998 to November 1999. Values are means ± SD, with the sample sizes given beneath the lower SD.

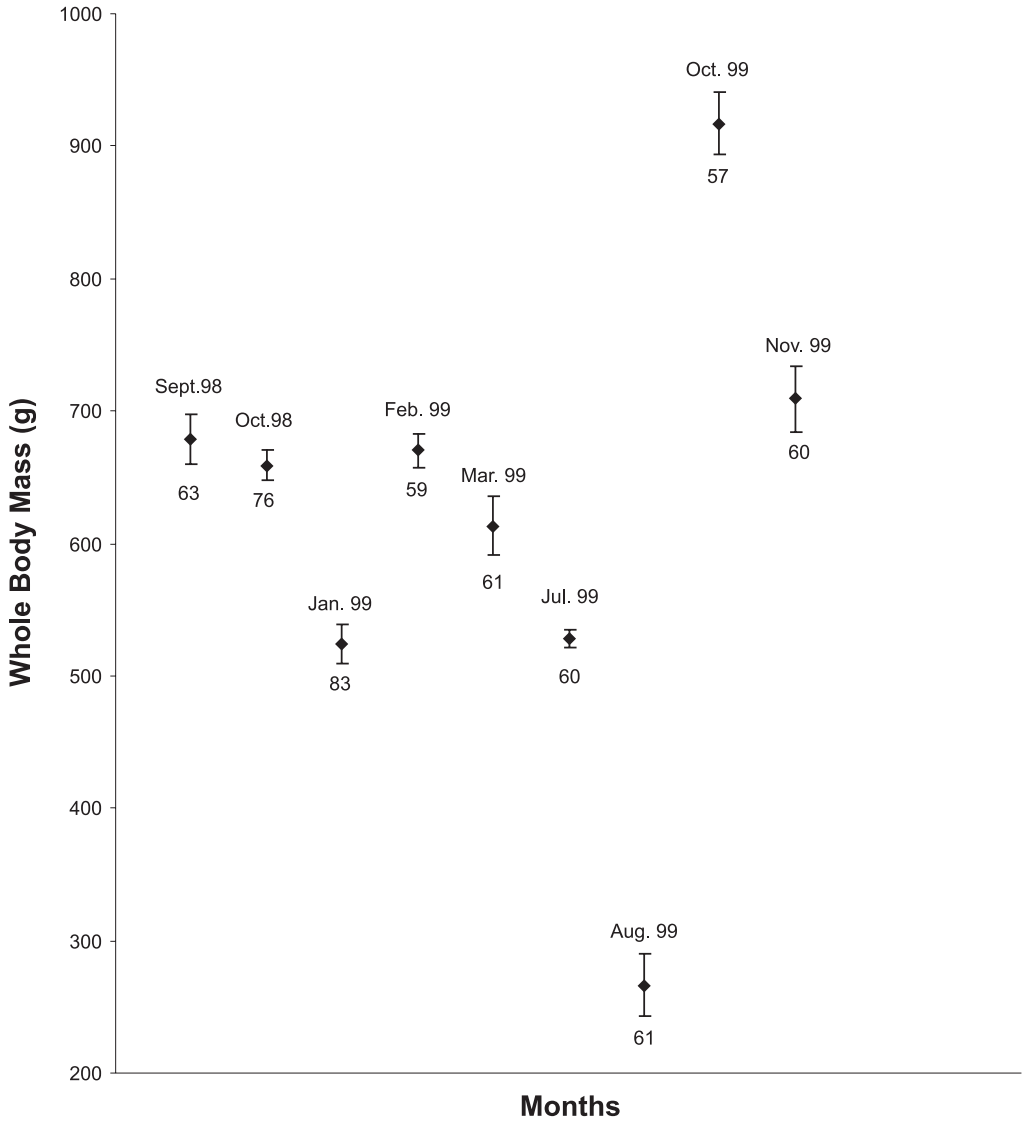


Table 2. Seasonal changes in proximate composition and energy content of walleye pollock.

	Winter	Spring	Summer	Fall	df	*F*	Kruskal–Wallis	*p*
n	140	60	120	256				
Moisture (% wet mass)	77.0±0.1a	76.7±0.2a	75.9±0.2b	74.3±0.1c	3,576	68.82		<0.001
Ash* (% dry mass)	11.9±0.3a	11.7±0.4a	10.6±0.3b	10.8±0.2b	3,576	6.77		<0.001
Lipid* (% dry mass)	15.4±0.3a	17.0±0.7b	22.0±0.5c	21.3±0.4c	3,576	56.03		<0.001
Protein (% dry mass)	66.3±0.5a	62.7±1.1b	62.2±0.5b	60.8±0.4c	3		82.91	<0.001
Energy (kJ/g dry mass)	21.27±0.13a	21.60±0.17a	22.23±0.21b	22.65±0.13b	3		53.57	<0.001

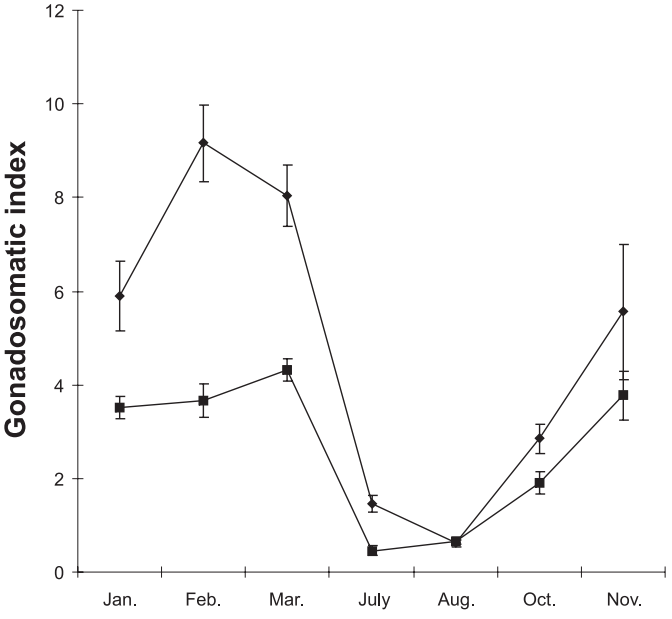
November) months ($p < 0.05$). Similarly, the protein content remained relatively constant during the spring and summer months before declining to the lowest level during fall, losing about 9% of the peak level seen in the winter months. Contrary to the moisture content, the total crude lipid content of fish carcass peaked ($p < 0.05$) in summer (July and August) and gradually declined in fall, to a minimal level in winter, with the lowest content observed in January ($p < 0.05$). Fish carcass lipid decline paralleled gonad development as maximum lipid loss occurred during prespawning months when gonad mass increased rapidly before spawning (Table 1 and Fig. 2). The proximate analyses data for mois-

Table 3. Sex differences in proximate composition and energy content of walleye pollock.

	Winter		Spring		Summer		Fall	
	Male	Female	Male	Female	Male	Female	Male	Female
n	76	65	33	28	60	60	133	121
Moisture (% wet mass)	77.2±0.2	76.7±0.2	76.7±0.2	76.7±0.3	75.9±0.3	75.9±0.2	75.6±0.2	74.0±0.2
Ash* (% dry mass)	12.3±0.4	11.4±0.4	12.1±0.5	11.2±0.7	11.0±0.5	10.2±0.4	10.9±0.3	10.8±0.3
Lipid* (% dry mass)	15.0±0.5	16.0±0.5	17.5±1.1	16.5±0.7	22.2±0.6	21.8±0.8	21.4±0.5	21.2±0.6
Protein (% dry mass)	66.4±0.8	66.1±0.7	61.3±1.6	63.8±1.5	61.0±0.6	62.3±0.8	61.0±0.5	60.5±0.7
Energy (kJ/g dry mass)	21.35±0.13	21.23±0.17	21.39±0.21	21.86±0.21	22.23±0.25	22.27±0.38	22.73±0.17	22.52±0.17

Note: Significance of season, sex, and season × sex according to the p values from parametric (ANOVA) and nonparametric (Kruskal–Wallis) tests.
*Data for these variables were log-transformed to determine their significance.

Fig. 2. Gonadosomatic index of walleye pollock sampled from January to November 1999. Values are means ± SD (■, male; ◆, female).



ture, protein, ash, and lipid contents of whole fish carcass were not significantly different between fish gender.

The relative difference in protein digestibility of whole walleye pollock (combined sexes) during different seasons is shown in Fig. 3. Pollock caught in the summer displayed higher protein digestibility relative to fish caught in the spring (Fig. 3). A large variation in the estimates of in vitro protein digestibility was also found for whole fish caught in the summer months. It is noteworthy that the relative differences in seasonal protein digestibility of pollock were not related to the seasonal essential or nonessential amino-acid composition of these fish (Table 4). The results of this study indicated less than half of the amino acids in pollock constituted essential amino acids (37%–39%). Predominate essential amino acids were leucine, lysine, threonine, and valine, while the nonessential amino acids included glutamate, aspartate, and glycine. There were also no significant seasonal differences in the amounts of individual essential or nonessential amino acids in whole fish (Table 4).

Fatty-acid composition of walleye pollock is presented in Table 5. We identified and quantified only 11 fatty acids; the most abundant fatty acids included palmitic, palmitoleic, linoleic, timnodonic, and cervonic acids. The concentration of long-chain omega-3 fatty acids appeared to be highest during the summer, owing to a significant increase of timnodonic acid ($p < 0.05$). The other omega-3 acids (α-linolenic and cervonic acids) showed no significant variation, although the concentration of both dropped slightly from spring to summer.

Discussion

The total energy values of whole pollock carcass we measured were consistent with those previously reported for pollock and other gadids. Total gross energy values for adult pollock reported by Smith et al. (1997) were 3.3–5.8 kJ/g wet mass and were dependent on the reproductive cycle. In comparison, Pacific cod (*Gadus macrocephalus* Tilesius, 1810) have energy content values of 3.8–4.1 kJ/g wet mass (Smith and Paul 1990). Our pollock samples had mean energy values varying from 21.27 kJ/g in winter fish to 22.65 kJ/g in fall fish, based on the dry mass of the combined sexes (or 4.86 kJ/g in winter fish to 5.82 kJ/g in fall fish, based on wet mass).

Seasonal differences in walleye pollock carcass were noted for total gross energy and crude lipid contents. The variation pattern in energy density appeared to parallel those in the crude lipid content. In both instances, male and female pollock contained greater energy reserves in the form of lipid during the summer (July and August) and early fall (September and October), indicating that the energy intake was larger than the energy expenditure in those months. One explanation for these differences likely involves the feeding behavior of pollock, which changes with the season (Ciannelli et al. 1998). Gross energetic values that peaked during summer and fall have also been reported in other species like capelin, *Mallotus villosus* (Müller, 1776), and Pacific herring (Montevecchi and Piatt 1984; Lawson et al. 1998; Paul et al. 1998*a*). Pacific herring and capelin are also seasonal feeders that accumulate fat stores to sustain themselves during winter temperatures (Robards et al. 1999). This similarity in feeding behavior may be related to their spring-spawning nature, as walleye pollock also spawn in spring (March).

While the energy density in walleye pollock was highest in the fall, the energy values in winter and spring were lower, corresponding to the declined lipid content found in the winter and spring months. These changes can be explained partly by a food shortage, or lack of prey availability during winter seasons, when lipid reserve is used for energy. Although feeding may be reduced during winter, energy ex-

Season				Sex				Season × sex			
df	*F*	Kruskal–Wallis	*p*	df	*F*	Kruskal–Wallis	*p*	df	*F*	Kruskal–Wallis	*p*
3,568	67.4		<0.001	1,568	1.69		0.2	3,568	0.62		0.602
3,568	6.45		<0.001	1,568	3.01		0.1	3,568	1.01		0.389
3,568	55.4		<0.001	1,568	0		0.93	3,568	1.22		0.302
3		82.91	<0.001	1		13 013.5	0.41	7		86.91	<0.001
3		53.57	<0.001	1		40 067.5	0.51	7		53.54	<0.001

Fig. 3. Seasonal changes in protein digestibility of walleye pollock. Values with different letters are statistically different (Kruskal–Wallis = 8.356, df = 3,28, p = 0.039).

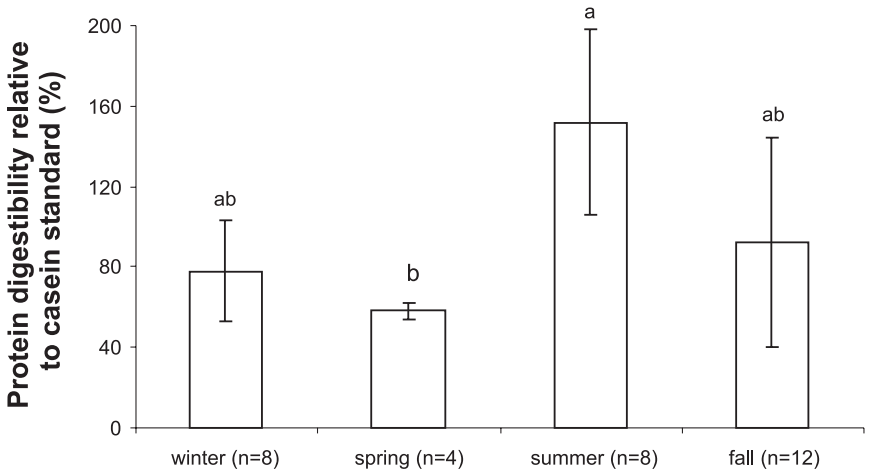


Table 4. Seasonal changes in essential and nonessential amino-acid compositions in walleye pollock expressed as a percentage of total amino acids.

Amino acid	Winter	Spring	Summer	Fall	$F_{[3,13]}$	p
Essential						
Histidine	2.25±0.078	2.24±0.058	2.18±0.048	2.43±0.164	0.669	0.586
Isoleucine	3.80±0.180	3.62±0.017	4.21±0.182	3.88±0.193	1.074	0.394
Leucine	7.78±0.305	8.24±0.257	8.19±0.235	8.09±0.289	0.354	0.787
Lysine	7.29±0.343	7.86±0.122	7.48±0.215	7.60±0.131	0.780	0.526
Methionine	2.16±0.128	2.15±0.124	2.21±0.083	2.33±0.133	0.423	0.740
Phenylalanine	3.51±0.164	3.75±0.197	3.47±0.190	3.56±0.133	0.293	0.830
Threonine	4.97±0.163	5.26±0.168	4.95±0.114	4.96±0.088	0.835	0.498
Tryptophan	1.07±0.064	1.18±0.035	1.01±0.048	1.10±0.142	0.201	0.894
Valine	4.43±0.188	4.38±0.039	4.56±0.183	4.50±0.111	0.185	0.905
Nonessential						
Alanine	7.08±0.212	7.46±0.022	7.00±0.189	7.28±0.172	0.74	0.542
Arginine	6.40±0.189	6.48±0.003	6.82±0.621	6.23±0.128	0.68	0.820
Aspartate	9.87±0.193	10.28±0.136	9.69±0.296	9.98±0.077	1.24	0.335
Cystine	1.01±0.039	0.98±0.002	0.91±0.043	0.96±0.096	0.23	0.871
Serine	5.34±0.172	5.59±0.242	5.46±0.082	5.45±0.067	0.48	0.700
Glutamate	14.60±0.401	14.55±0.357	14.41±0.244	14.84±0.094	0.68	0.578
Glycine	9.56±0.856	8.18±0.575	8.66±0.379	8.62±0.483	0.70	0.568
Proline	6.33±0.588	4.90±0.062	5.58±0.556	5.71±0.318	1.05	0.402
Tyrosine	2.54±0.145	2.91±0.439	3.22±0.462	2.49±0.174	1.53	0.255

pense for gonad production is also a major cause for the loss of lipid reserve prior to spawning. The decline in total crude lipid paralleled gonad development, with maximum lipid loss noted during prespawning months (January–March) when the gonad mass increased to their highest level. The maximum gonad mass was found in fish collected in Febru-

Table 5. Seasonal changes in saturated, monounsaturated, and polyunsaturated fatty-acid compositions of walleye pollock.

Fatty acid	Winter (n =31)	Spring (n =11)	Summer (n =58)	Fall (n =87)	df	F	p
Saturated and monounsaturated							
Capric (10:0)	0.93±0.070a	1.13±0.066a	1.19±0.073b	0.97±0.050a	3,183	3.3	0.022
Myristic (14:0)	7.45±0.358a	7.23±0.708a	9.55±0.298b	7.21±0.210a	3,183	15.98	<0.001
Palmitic (16:0)	24.56±0.911	23.35±0.593	23.41±0.272	24.10±0.290	3,183	1.23	0.302
Palmitoleic (16:1)*	9.89±0.72a	12.43±1.209b	11.33±0.329b	11.79±0.278b	3,183	8.55	0.001
Stearic (18:0)*	5.15±0.180b	4.57±0.216a	4.37±0.116a	5.06±0.155b	3,183	6.87	<0.001
Oleic (18:1)	22.38±0.639b	21.68±0.801b	19.56±0.361a	22.99±0.311b	3,183	16.19	<0.01
Polyunsaturated							
Linoleic (18:2n6)	1.29±0.155b	1.13±0.139b	0.93±0.044a	1.39±0.053b	3,183	8.97	<0.001
α-Linolenic (18:3n3)	0.57±0.096b	0.44±0.080b	0.28±0.041a	0.33±0.032a	3,183	5.046	0.002
Arachidonic (20:4n6)	0.30±0.052b	0.28±0.069b	0.07±0.018a	0.17±0.021a	3,183	10.446	<0.001
Eicosapentaenoic (20:5n3)	14.39±0.605b	14.53±0.657b	17.00±0.322a	14.59±.241b	3,183	12.779	<0.001
Docosahexaenoic (22:6n3)	13.10±0.527b	13.23±0.851b	12.32±0.372b	11.41±0.367a	3,183	3.058	0.03

Note: Values with different letters in the same row are significantly different, with the p values from a parametric (ANOVA) test. Values with no letters are not significantly different.

*Data for these variables were log-transformed to determine their significance.

ary and March when the gonadosomatic index reached 9.16% in females and 4.31% in males. These values are slightly lower than the gonadosomatic indices described by Maeda et al. 1981, which exceed 5% and 10% in ripe male and female pollock, respectively.

Maeda et al. (1981) reported that walleye pollock, like other gadids, do not feed during the spawning period; therefore energy changes during spawning consists of reallocation of previously acquired energy and do not involve significant acquisition of new energy (Smith et al. 1988). Adult pollock lost about 46% of the total available energy in ripe fish during spawning, whereas Atlantic cod (*Gadus morhua* L., 1758) used up 30% of the total energy available for spawning (Smith et al. 1988). In a study working with mature and immature Atlantic cod, Eliassen and Vahl (1982) reported that the total energy used for spawning, including gonad growth, spawning activities, and metabolism, accounted for about 30%–34% of the energy loss during the prespawning months. Of this, only 10% of energy was used for gonad growth. Unlike adult pollock, juvenile pollock allocated considerable energy into summer growth but did not develop energy stores for overwintering (Robards et al. 1999). Despite this fact, juvenile pollock maintain and improve their energy content over winter, suggesting that they continue to feed (Paul et al. 1998*b*).

Protein digestibility of walleye pollock was highest in the summer. Variability in protein digestibility can occur from variation in amino-acid composition of different protein sources. Among the essential amino acids found in pollock, leucine and lysine occurred in the highest amounts. Konosu et al. (1956) also reported high contents of leucine and lysine in the flesh of walleye pollock. However, higher contents of essential amino acids were reported in their study, making up about half of the total amino-acid content. Their results, however, were based on the fish flesh only, whereas our amino-acid values were determined from the whole fish carcass. Landgraft (1953) reported similar values of essential amino acids to ours in his experiment with Alaska pollock caught near Petersburg, Alaska, during the fall. He also found that the essential amino-acid content of walleye pollock compared favorably with that of beef liver and salmon eggs, both of which are considered to be good-quality protein sources for animal-feeding purposes (Landgraft 1953).

Walleye pollock make up a significant portion of the diets of many sea birds and marine mammals, particularly Steller sea lions. Understanding seasonal variation in nutritional values of this important prey can lead to a better understanding of the reproductive success of their predators. Seasonal differences in nutrient composition of pollock can affect Steller sea lions that seasonally change their feeding behaviors at various times of the year. The seasonal change in energy density of pollock appears to be disadvantageous to the sea lion when considering their seasonal feeding habits. The low level of energy in pollock during winter may be inadequate for young sea lions that need to build up the necessary energy stores to sustain themselves throughout the winter and spring. Most growth in wild Steller sea lions occurs in the months of November and March (Winship et al. 2001), when energy deposited into blubber reserves are directed for subsequent use during the reproductive seasons (Pitcher et al. 1998; Pitcher et al. 2000). The high energy density and high level of protein digestibility found in summer pollock, however, are likely not as beneficial to sea lions as territorial male sea lions are fasting during the summer breeding months. Kastelein et al. (1990) also found that the food consumption of a captive adult male Steller sea lion was less than its average monthly food consumption between April and September. In terms of protein quality, it is unlikely that the small differences in amino-acid content between seasons would affect the health of sea lions because pollock protein does not appear to lack any essential amino acids and contains good amounts of amino acids in all seasons. It is of particular interest that long-chain omega-3 fatty acids may be different between seasons and therefore more studies in this area of lipid quality is warranted.

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