

Ecology of small neritic fishes in the western Gulf of Alaska. II. Consumption of krill in relation to krill standing stock and the physical environment

Matthew T. Wilson^{1,*}, Christina M. Jump¹, Andre Buchheister²

¹Alaska Fisheries Science Center, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, 7600 Sand Point Way NE, Seattle, Washington 98115, USA

²Virginia Institute of Marine Science, PO Box 1346, Gloucester Point, Virginia 23062-1346, USA

ABSTRACT: Krill (Euphausiacea) is a patchily distributed taxon whose availability may limit neritic fishes in temperate oceans. In the western Gulf of Alaska, krill–fish aggregations were associated with high-flow areas over the shelf. We examined fish impacts on krill standing stocks in areas of different temperature, salinity, and net current velocity. Samples were collected during September 2000, 2001, and 2003 over a 48-site grid within a known walleye pollock nursery. Krill were a dietary staple of the dominant fishes: walleye pollock *Theragra chalcogramma*, capelin *Mallotus villosus*, and eulachon *Thaleichthys pacificus*, but their proportion in diets varied by predator species and predator length. Predators daily consumed $\leq 12\%$ of standing stocks; thus, krill appeared to be amply available. However, the krill consumed by eulachon and large (>120 mm) walleye pollock were, on average, large compared to krill in plankton samples; therefore, standing stock sizes might have been overestimated by including small krill. A compensatory response in consumption occurred during 2001 in proximity to the Shelikof sea valley due to increased per capita predation rates and local concentration of Age-1+ walleye pollock and eulachon. High abundance of krill in 2001 was associated with high ocean current flow. No compensatory response was observed where local standing stocks were dominated by small krill. Thus, apparent bottom-up influences of ocean currents on krill abundance in neritic areas can be partly compensated by localized top-down predation from nektonic fishes having prey size preferences that match available prey sizes.

KEY WORDS: Walleye pollock · Capelin · Eulachon · Diet · Geographic variability

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INTRODUCTION

Krill (Euphausiacea) is a patchily distributed taxon the availability of which may limit the productivity of nektonic fishes in temperate coastal oceans. Fish communities consume large quantities of krill (e.g. Yamamura et al. 1998, Robinson 2000). There is some indication that local availability limits fish consumption of krill. Trophodynamic modeling by Yamamura (2004) indicated that walleye pollock *Theragra chalcogramma* off Japan consumed more krill per annum than were produced locally, thus underscoring the importance of advective prey supplies. In the Barents Sea, the size of the krill population is apparently

largely controlled by predation from capelin *Mallotus villosus* (Dalpadado & Skjoldal 1996). These fishes may therefore be nutritionally motivated to forage where krill are abundant, or the rate of re-supply is high. Krill concentrate where ocean current–topography interactions and behavioral response facilitate accumulation of individuals (e.g. Mackas et al. 1997, Genin 2004, Ressler et al. 2005).

In the western Gulf of Alaska (GOA), krill was identified in a field study of the spatial ecology of small neritic fish as being well associated with fish geographic distributions (Wilson 2009, this volume). The study was conducted by the National Oceanic and Atmospheric Administration's (NOAA) Ecosystems and Fisheries-

*Email: matt.wilson@noaa.gov

Oceanography Coordinated Investigations Program (EcoFOCI). It was conducted during late summer (September 2000, 2001, 2003) when increasing Alaska Coastal Current (ACC) flow (Stabeno et al. 2004) and influx of Age-0 fish (e.g. Brodeur & Wilson 1996) coincide with declining zooplankton abundance (Coyle & Pinchuk 2003) to perhaps enhance geographic associations. The study focused on the dominant neritic fishes: walleye pollock, capelin, and eulachon *Thaleichthys pacificus*. Walleye pollock >120 mm and eulachon aggregated with krill over the shelf in relatively high-flow areas associated with sea valleys. Aggregations such as these were hypothesized by Cooney (1986) to contribute to the productivity of the coastal GOA ecosystem.

All of these fishes consume krill, but their combined impact on the resource has not been quantified. For walleye pollock, krill become more important as predator size increases, presumably due to predator gape-width limitations (Brodeur 1998). Mazur et al. (2007) showed that large krill are energy rich and that the growth potential of young-of-the-year (Age-0) walleye pollock was directly related to the proportion of krill in the diet. Ciannelli et al. (1998) report minimal potential for Age-0 walleye pollock to be food limited, but impacts on local prey resources by older walleye pollock and other fishes were not considered. Capelin also exhibit a size-related dietary transition to krill (Wilson et al. 2006a). The marine diet of eulachon, an anadromous species, has not previously been studied in the western GOA (Willson et al. 2006).

In the present paper, we first verify the importance of krill in the diets of the dominant neritic fishes (walleye pollock, capelin, eulachon). Next, we estimate fish consumption of krill for comparison to krill standing stock as a measure of site-specific depletion potential. We then examine consumption relative to standing stock among years within each of 5 meso-scale geographic areas, which were based on previously described differences in salinity, temperature, and net current velocity (Wilson 2009), to explore possible interannual and physical oceanographic effects on krill–fish trophic interactions. Finally, we compare krill size between the diet and plankton samples to verify that the krill in our plankton samples represented krill sizes consumed by the fish.

MATERIALS AND METHODS

Samples of fish and zooplankton were collected from a 48-site grid in the western GOA occupied during September 2000, 2001, and 2003. Most sites were sampled once during the day and again at night, usually

within 24 h. No samples were collected during twilight, and all sampling was confined to the upper 200 m of water. For further field-sampling details, see Wilson (2009).

Predator diets. Stomach contents were examined to determine walleye pollock *Theragra chalcogramma*, capelin *Mallotus villosus*, and eulachon *Thaleichthys pacificus* diets. Stomachs from Age-0 (≤ 120 mm standard length, SL) and Age-1+ (> 120 mm SL) walleye pollock were processed separately to maintain the size-based age distinction (Brodeur & Wilson 1996). Fish were selected from each sample to represent the different sizes available. No more than 20 Age-0 walleye pollock, the most abundantly collected group, and 10 of each other group were selected per sample. Individuals were blotted dry, measured to the nearest 1 mm SL, and weighed to the nearest 1 mg. Stomachs were excised between the esophagus and pylorus and preserved in a sodium borate-buffered 10% formalin solution.

The contents of each stomach were extracted, blotted dry, weighed to the nearest 0.01 mg, and sorted. Prey items were sorted into 12 broad taxonomic groups following Brodeur et al. (2000). Copepods were divided into small (≤ 2 mm prosome length, PL) and large (> 2 mm PL) individuals. Euphausiids were divided into furcillae (ca. ≤ 5 mm length; Siegel 2000), and juveniles and adults; hereafter, 'krill' refers only to juvenile and adult euphausiids). Within each group, well-digested prey fragments were sorted from intact ($> 75\%$ whole) individuals (most prey showed signs of digestion so feeding within the trawl net was probably negligible). Prey in each group were enumerated, blotted dry, and collectively weighed to the nearest 0.01 mg.

Predator consumption of krill. Daily consumption of krill by the target predator populations was compared to krill standing stock site-by-site and by hydrographic area. Krill standing stock (ind. km^{-2}) at each site was computed from depth-integrated population density (see Wilson 2009) and the depth range sampled. The standing stock was computed using samples collected at night to avoid possible daytime reduction in sampling efficiency (Wilson 2009). Consumption of krill by the 4 predator populations was estimated as:

$$DC_{ky} = \sum_{j=1}^4 (PA_{jky} \times PC_{jky}) \quad (1)$$

where PA_{jky} is fish population abundance (ind. km^{-2}) and PC_{jky} is the daily per capita consumption of krill (ind. $\text{fish}^{-1} \text{d}^{-1}$) by predator group j at collection site k during year y . Population abundance (PA_{jky}) was computed from nighttime depth-integrated population density (see Wilson 2009) and maximum trawl depth. Age-1+ pollock > 250 mm SL were excluded, because this size fraction was not represented in the diet data.

Per capita daily consumption of krill by each predator population was estimated as:

$$PC_{jky} = PW_{jky} \times DR_j \div 100 \times KP_{jky} \div KW_{jky} \quad (2)$$

where mean predator weight (PW_{jky} , g), diet portion of krill (KP_{jky} , g g⁻¹), and mean individual krill weight (KW_{jky} , g ind.⁻¹) were computed for each predator population j , collection site k and year y ; daily ration (DR_j , percent body weight [%BW]) was computed for each predator population j .

Mean predator weight (PW_{jky} , g) was based on abundance-weighted fish lengths collected at sea during the night. Length was converted to somatic weight (body weight minus stomach content weight) using length–weight relationships, which were based on the individual predator size measurements. All length–weight data were adjusted for preservation effects (Buchheister & Wilson 2005).

The krill diet portion (KP_{jky} , g g⁻¹) was computed as total krill weight divided by total stomach content weight using only fish collected at night. Due to considerable among-fish variability, ≥ 5 fish were deemed necessary to compute krill diet portions from observed data. For samples with fewer fish, krill diet portion was computed using total krill weight and total stomach content weight predicted from empirically derived relationships. Total krill weight was predicted using only data from nighttime sampling:

$$W_{ky} = \alpha + \text{year}_y + \beta_1 L_{ky} + \beta_2 A_{ky} + e_{ky} \quad (3)$$

where W_{ky} is krill weight (g^{0.25} fish⁻¹), L_{ky} is mean length (mm) of predators examined, and A_{ky} is krill abundance (ind. m⁻²)^{0.25} at collection site k during year y and e_{ky} is the random error. Total stomach content weight was predicted using all data:

$$W_{lyd} = \alpha + \text{diel}_d + \text{year}_y + \text{diel}_d \times \text{year}_y + \beta L_{lyd} + e_{lyd} \quad (4)$$

where W_{lyd} is stomach content weight (g^{0.25} fish⁻¹) and L_{lyd} is mean length (mm) of predators examined in size bin l collected during diel period d of year y and e_{lyd} is the random error. Size bins were structured in 10 mm intervals for Age-0 pollock and capelin (e.g. 77 to 84, 85 to 94 mm SL, and so on), and in 25 mm intervals for Age-1+ pollock and eulachon (e.g. 88 to 112, 113 to 137 mm SL, and so on). The number of fish examined was included as a weight. Models were reduced by sequential elimination of terms deemed non-significant ($p > 0.05$) (Milliken & Johnson 1996) by ANCOVA performed using SYSTAT (Ver. 11).

Krill body weight (KW_{jky} , g ind.⁻¹) was estimated from predator length, because most krill recovered from predator stomachs at each collection site were not intact. Krill–predator size relationships were examined using the same procedure associated with Eq. (4). A fourth-root transformation of mean krill

body weight was used so that the errors were normally distributed.

Daily ration (DR_j , % BW) was estimated using the MAXIMS program as implemented in SAS by Richter et al. (1999). The model assumes constant ingestion during the feeding period and an exponential rate of evacuation (Sainsbury 1986) such that, for each predator population:

$$dS/dt = J - E(S) \quad (5)$$

where S is mean stomach content weight at time t (h). Following Brodeur et al. (2000), individual stomach content weights (as percentages of somatic body weight, % BW) were arcsine-transformed and averaged by 3 h time bins. Means were back-transformed prior to model input. J is the rate of ingestion (%BW h⁻¹), and E is the instantaneous rate of evacuation (h⁻¹).

Site-specific estimates of consumption and standing stock were averaged by geographic sub-areas. Wilson (2009) divided the study area into 5 sub-areas (northeastern shelf: inner [NEin] and mid/outer [NEmid]; southwestern shelf: inner [SWin] and mid/outer [SWmid]; continental slope [Slope]; see Fig. 6) based on meso-scale geographic differences in water temperature, salinity, and net current velocity estimates. Area-specific consumption and standing stock estimates were computed by multiplying mean site-specific consumption and standing stock, respectively, by sea surface area (km²).

Krill size: plankton versus predator. Krill in the plankton samples were weighed and counted to provide an estimate of mean individual weight for site-specific comparison to intact krill from fish stomachs. For each plankton sample, krill were enumerated and collectively weighed to the nearest 0.01 mg. Large samples (>300 krill) were split and randomly sub-sampled prior to enumerating and weighing individuals (see Wilson 2009 for more sample processing details). For diet samples, the total number and weight of intact krill recovered from the stomachs of fish collected together at a site were used to compute mean individual weight. After applying a digestion correction, diet-based and plankton-based mean individual weights were paired by year, diel period, and collection site, and compared using paired t -tests.

The digestion-correction factor was computed as the difference in ln-transformed length-specific weight (ln-g) between digested and undigested krill. A total of 71 krill from 6 diet samples, and 58 krill from 6 plankton samples, which were paired by collection time and site to the diet samples, were measured and individually weighed. Following Shaw et al. (2008), body length was the distance from the curve of the carapace around the eye to the posterior margin of the last abdominal segment. Body weight was whole wet

weight measured to the nearest 0.01 mg after blotting off excess moisture. Each krill was scored on body appearance (exoskeletal wrinkling and extent of thorax deformation) to distinguish lightly digested krill from more heavily digested individuals. The mean difference between digested (diet) and undigested (plankton) krill in length-specific weight was determined by ANCOVA and regression analysis.

RESULTS

Stomach content weight and diet was determined for 4267 fish from 378 trawl hauls (Table 1). Walleye pollock (3015 fish) ranged in length from 39 to 250 mm SL, with an absence of individuals between 111 and 130 mm SL, which reflects the size separation between Age-0 (2585 fish) and older (Age-1+, 430 fish) fish (Brodeur & Wilson 1996). No Age-1+ sub-adult pollock *Theragra chalcogramma* were available in the daytime collections during 2003. Capelin *Mallotus villosus* (618 fish) ranged in length from 65 to 126 mm SL. Eulachon *Thaleichthys pacificus* (634 fish) ranged in length from 61 to 202 mm SL.

Predator diets

Stomach content weight varied considerably within and among predator groups, but krill generally comprised 50% or more of the recovered material (Fig. 1). The most commonly identified krill species were *Thysanoessa inermis* and *T. spinifera*. For Age-0 pollock and capelin, stomach content weight and the proportional weight of krill increased with fish size. The back-transformed mean stomach content weight for Age-0 pollock was 21.3 mg, with 3.2% of the stomachs empty; for capelin, the back-transformed mean was 7.2 mg, with a relatively high percentage (19%) of

Table 1. *Theragra chalcogramma*, *Mallotus villosus*, *Thaleichthys pacificus*. Number of fish stomachs examined for diet determination, tallied by year and diel period. All samples were collected at pre-determined stations in the western Gulf of Alaska during September

Year	Diel period	Walleye pollock		Capelin	Eulachon
		Age-0	Age-1+		
2000	Night	632	94	50	72
	Day	517	102	40	60
2001	Night	465	137	162	153
	Day	330	82	93	113
2003	Night	340	15	172	132
	Day	301	0	101	104
Total		2585	430	618	634

empty stomachs. For Age-1+ walleye pollock and eulachon, predator size-related increases in the proportional weight of krill were not apparent. With size, Age-1+ pollock increasingly fed on fishes. Stomach content weight of Age-1+ pollock averaged 181.1 mg, with only 2.3% of the stomachs empty. Eulachon had the highest percentage (31%) of empty stomachs, but krill dominated their diet more than any other predator group. Eulachon mean stomach content weight was 8.5 mg.

Predator consumption of krill

Considerable variation existed within and among the 4 predator groups with regard to predator weight, the proportion of krill in diets, the size of krill consumed, and daily ration. The variability incorporated into our estimation of predator consumption of krill differed among variables.

Predator weight (PW_{jky} , g). The somatic body weight of individual predators increased with body length ($R^2 \geq 0.99$), but the relationship for each predator species varied by year. For pollock and eulachon the year-body length interaction was significant ($p < 0.001$). For capelin, year was significant as a main effect ($p < 0.001$) due to a monotonic increase in length-specific weight from 2000 to 2003. Thus, year-specific length-weight equations were used to convert at-sea length to weight for each predator population.

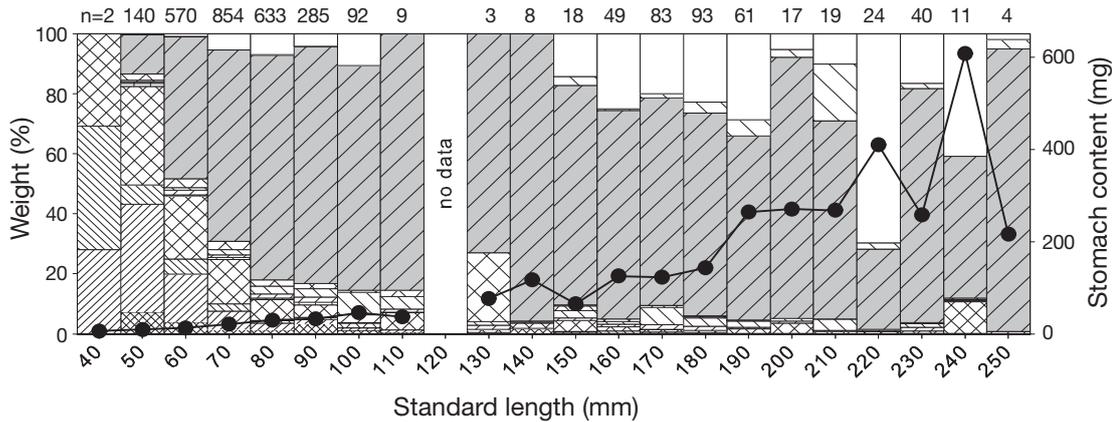
Proportion of krill in diets (KP_{jky} , g g⁻¹). Krill weight and stomach content weight were used to estimate KP_{jky} for 85 (of 257 total) samples that each consisted of <5 fish. Depending on predator group, krill weight in predator stomachs increased with krill abundance in the plankton and/or predator length (Fig. 2). Two of the 85 KP_{jky} estimates were set to 0, because predicted krill weight was negative. Stomach content weight increased with predator length (Fig. 3), and all but capelin exhibited significant ($p < 0.05$) interannual variability in the relationship. Five of the 85 KP_{jky} estimates were set to 1, because predicted krill weight exceeded predicted stomach content weight. None of the predicted KP_{jky} values resulted in extreme estimates of krill consumption by fishes.

Krill mean body weight (KW_{jky} , g ind.⁻¹). Mean body weight of intact krill from predator stomachs increased with predator length for Age-0 pollock and eulachon, but not for Age-1+ pollock and capelin (Fig. 4). The increase among Age-0 pollock was affected by year ($p = 0.001$). For eulachon, the year effect significantly interacted with the diel effect ($p = 0.006$). Consequently, year-specific relationships were used to estimate KW_{jky} for Age-0 walleye pollock, and year and diel-specific relationships were used to estimate KW_{jky} for eulachon. For Age-1+ pollock, krill mean size did not vary with

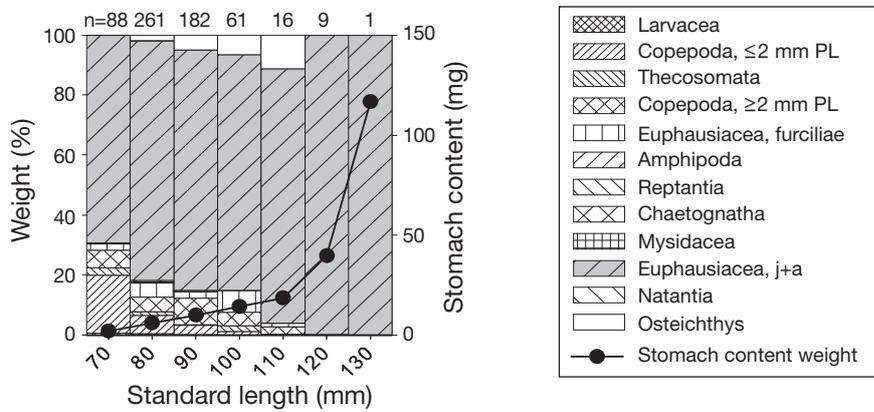
predator length, but it did vary with year ($p = 0.010$). Krill mean body weight was low in 2001 and high in 2003. For capelin, krill size did not vary significantly with year, diel, or predator length ($p > 0.05$). Thus, year-specific means were used to estimate KW_{jky} for Age-1+ pollock, while KW_{jky} for capelin was constant.

Daily ration (DR_j , %BW). Daily ration ranged from 0.50 to 1.67% BW, depending on predator group (Fig. 5). For Age-0 pollock, %BW increased from noon to late night, with a resulting daily ration estimate of 1.60% BW (± 1.00 standard error, SE). The model fit was significant ($p < 0.001$). There was no apparent overall

A Walleye pollock



B Capelin



C Eulachon

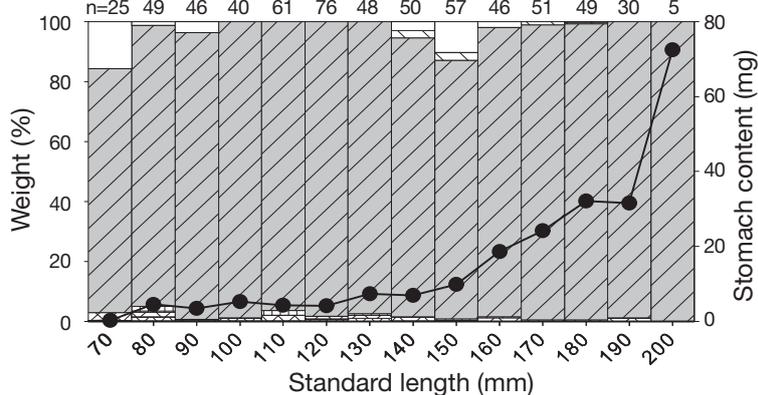


Fig. 1. *Theragra chalcogramma*, *Mallotus villosus*, *Thaleichthys pacificus*. Prey taxonomic composition and mean stomach content weight of Age-0 pollock, Age-1+ pollock, capelin, and eulachon by predator length. The number of stomachs examined is noted above each column. Panels for different taxa are positioned to align the predators by length. Shaded bars: krill (Euphausia juveniles [j] + adults [a]). PL: prosome length

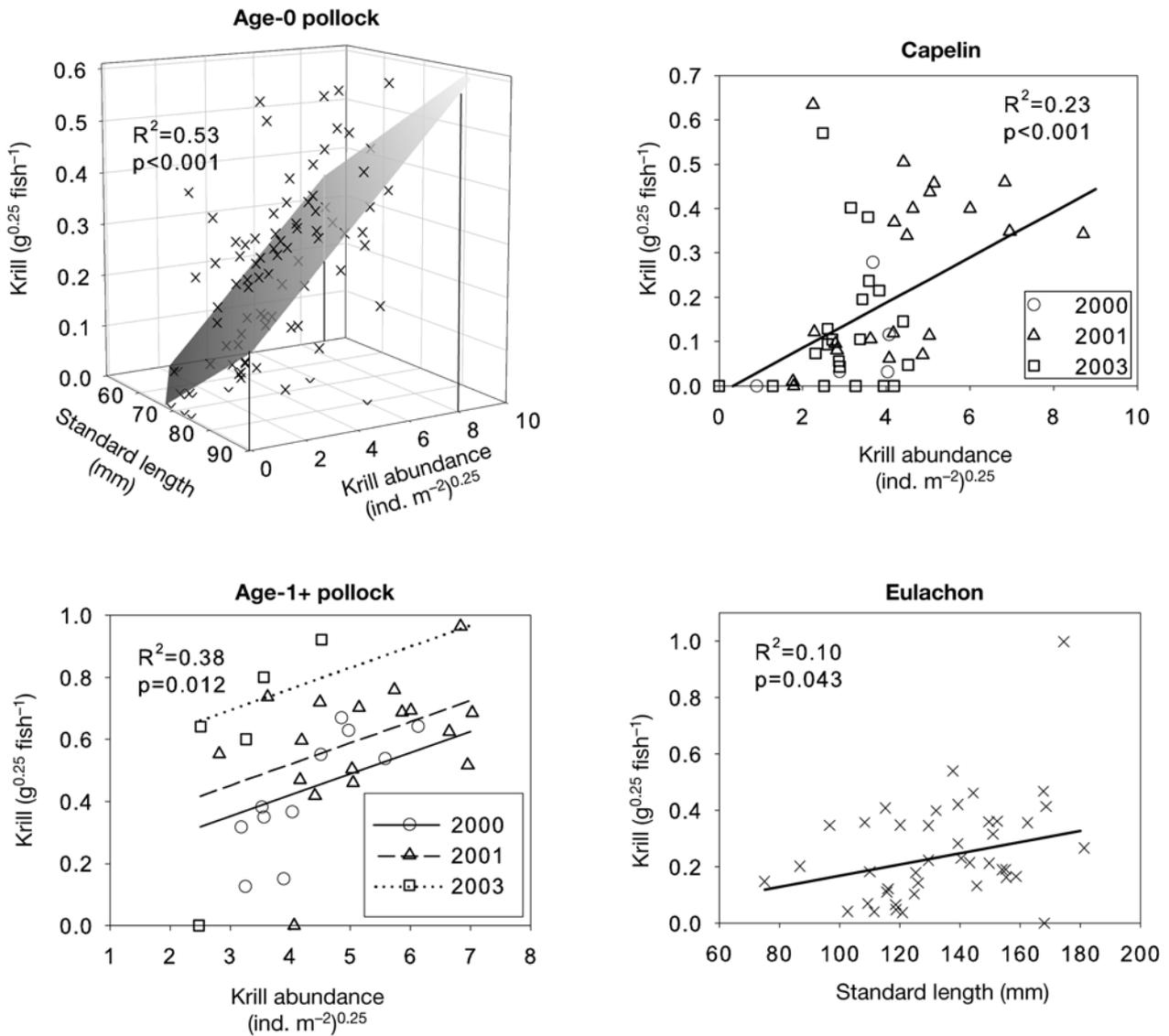


Fig. 2. *Theragra chalcogramma*, *Mallotus villosus*, *Thaleichthys pacificus*. Transformed weight of krill remains recovered from predator stomachs as a function of predator length, transformed krill abundance, and/or year (see Eq. 3). Lines and surfaces represent fitted least-squares regression equations

diel periodicity in taxonomic composition of the stomach contents; krill comprised $\geq 60\%$ of stomach content mass in any given 3 h time interval. In contrast, diel periodicity in taxonomic composition was apparent among Age-1+ pollock stomach contents. This reflected an increase in the percentage of fish remains from stomachs of individuals that corresponded with peaks in %BW at sunrise and sunset. Thus, 2 feeding periods were assumed. The estimated daily ration was $1.67\% \text{ BW}$ ($\pm 1.57 \text{ SE}$), but the model did not account for a significant amount of variation in %BW ($p = 0.096$).

For capelin, %BW was highest just after sunset when krill comprised 89% of stomach contents. A single

feeding period was assumed, and the resulting daily ration estimate was $0.68\% \text{ BW}$ ($\pm 0.58 \text{ SE}$). The model fit was statistically significant ($p = 0.041$).

A 2-period feeding schedule was apparent for eulachon. Eulachon daily ration was estimated at $0.50\% \text{ BW}$ ($\pm 0.13 \text{ SE}$), and the model fit was statistically significant ($p = 0.031$). There was little evidence of diel variation in taxonomic composition for eulachon and capelin stomach contents, although fish were only detected in the stomach contents of predators collected at night.

Site-specific daily consumption. The daily consumption of krill by juvenile pollock, capelin, and eulachon

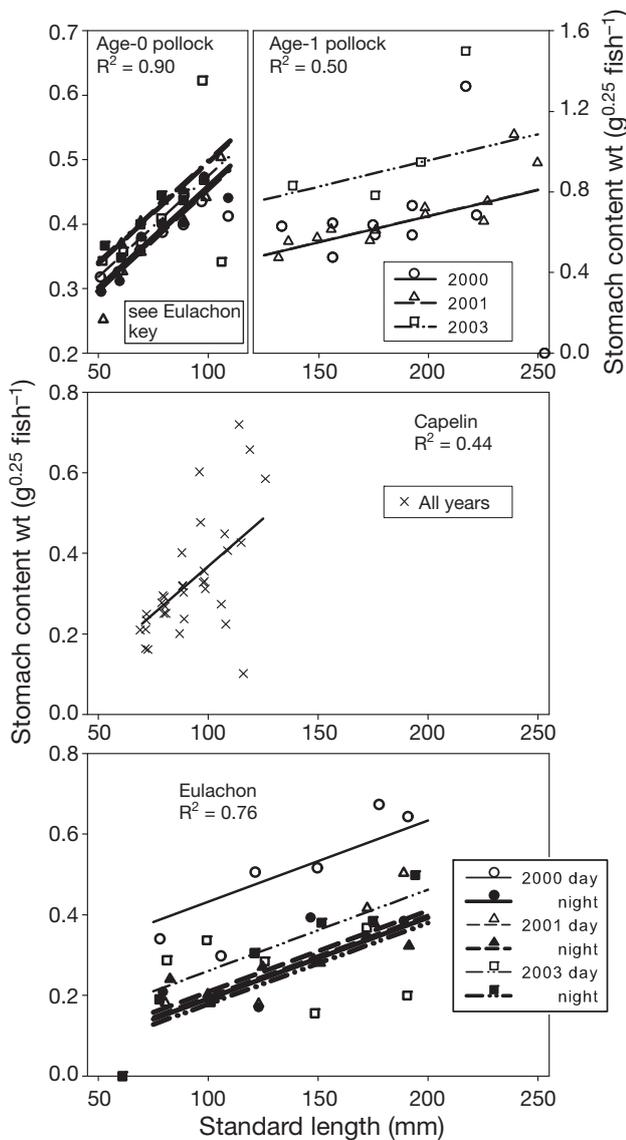


Fig. 3. *Theragra chalcogramma*, *Mallotus villosus*, *Thaleichthys pacificus*. Predator stomach content weight as a function of predator body length (see Eq. 4). Lines represent fitted least-squares linear regression equations. Symbol and line types distinguish levels of significant effects

was a small percentage of the krill standing stock at each collection site (Fig. 6). Daily consumption ranged from 0 to 20 krill d^{-1} and never exceeded 12% of the standing stock. During 2000, 2001, and 2003, the median percentages were 0.015% ($N = 43$), 0.026% ($N = 39$), and 0.018% ($N = 26$), respectively. Estimates from 5 sites were excluded because plankton samples were not collected, or because non-null consumption estimates were paired with null standing stock estimates (i.e. fish contained krill where we collected none).

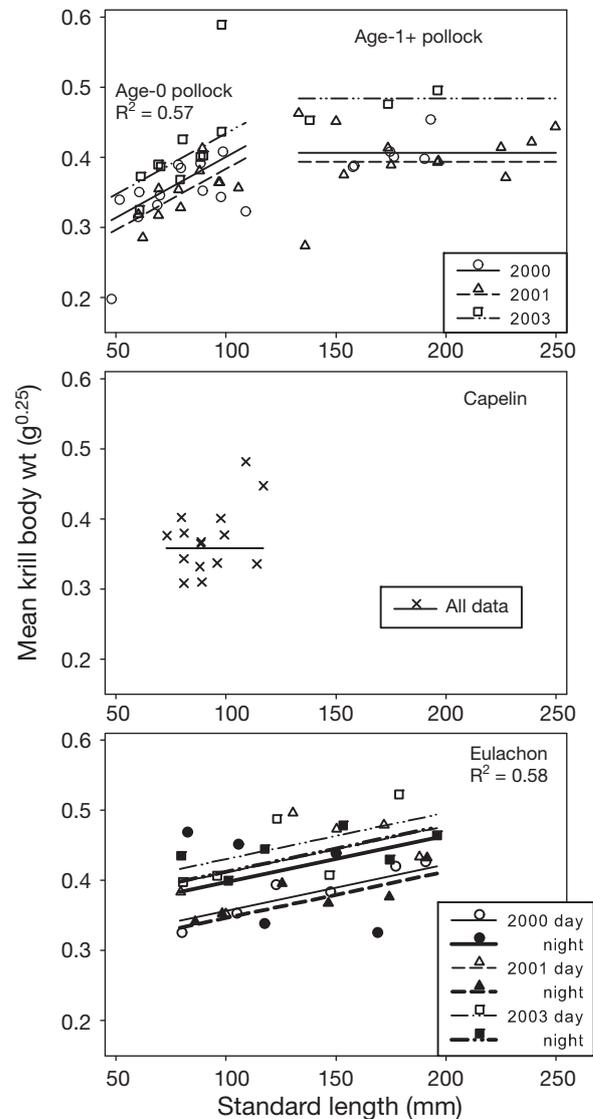


Fig. 4. *Theragra chalcogramma*, *Mallotus villosus*, *Thaleichthys pacificus*. Mean krill body weight plotted against predator mean length. Lines represent fitted least-squares linear regression models (see Eq. 4). Age-0 and Age-1+ wall-eye pollock are distinguished in the top panel by a gap at 120 mm SL

Area-specific daily consumption. Consumption of krill was lowest over the slope and highest in northeastern shelf areas (Table 2). Low consumption of krill over the slope reflects low predator abundance. High consumption of krill in northeastern shelf areas was due to high per capita consumption of krill by Age-1+ pollock. In these areas, Age-1+ pollock consumed an average of 7 to 59 krill d^{-1} . For each predator group, the highest per capita rate occurred in 2001, when krill were abundant, but relatively small (Table 2). The increased per capita consumption during 2001 trans-

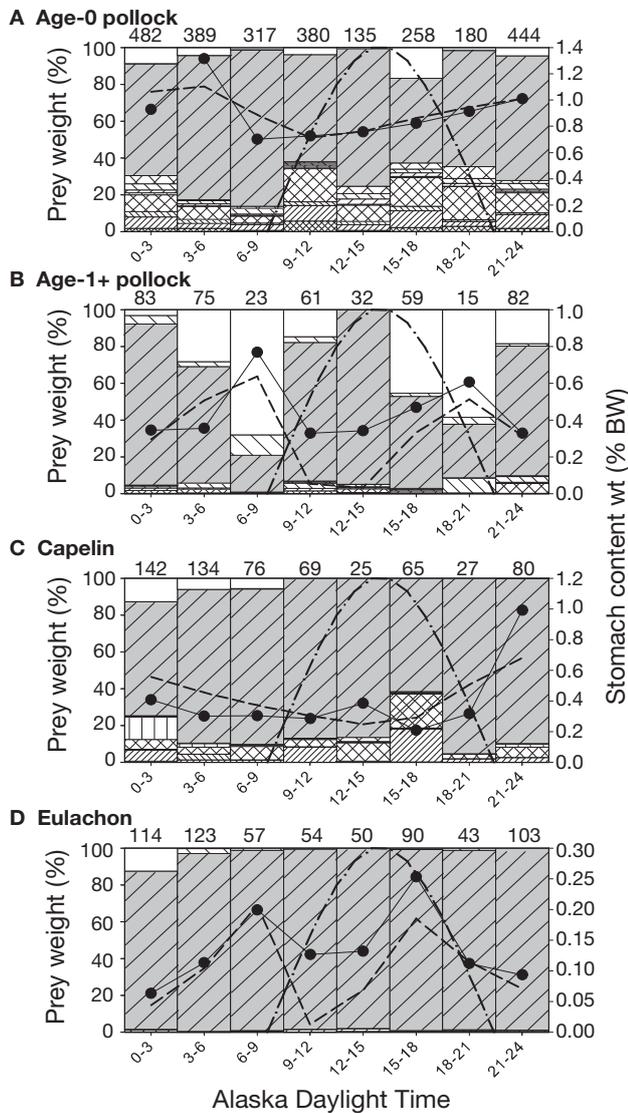


Fig. 5. *Theragra chalcogramma*, *Mallotus villosus*, *Thaleichthys pacificus*. Output from the MAXIMS (Richter et al. 1999) model (dashed line) fitted to percent body weight (%BW, dots) averaged by 3 h time intervals is superimposed on stacked-bar plots of the taxonomic composition (see Fig. 2 key) by prey weight (%) for (A) Age-0 pollock, (B) Age-1+ pollock, (C) capelin, and (D) eulachon. Hourly predictions of sun altitude [percent of maximum at 56° 18' N, 158° 24' W on 11 September (<http://aa.usno.navy.mil>)] are included (dot-dash line) to provide diel context. The number of fish is listed above each 3 h interval

lated into a greater impact on krill standing stock, but only in the NEin and NEmid areas. For example, relative consumption by the predator population increased in the NEin area from 0.24 % of the standing stock d^{-1} in 2000 to 0.57 % d^{-1} in 2001. Subsequently, in 2003, it declined to 0.20 % d^{-1} in 2003. No such compensatory response among years was apparent in the SWin and SWmid areas.

Krill size: plankton versus predator

The digestion-correction factor used to adjust mean individual weight of krill from fish stomachs prior to comparison with krill from the plankton was 0.162 ln-g. The length–weight model explained 95 % of the variation in krill weight. The undigested–digested effect was significant, due to a difference in line elevation ($p < 0.001$), but not slope ($p = 0.294$). No difference was detected between undigested and lightly digested krill weights ($p = 0.455$).

Mean krill body weight did not differ by sample type (stomachs vs. plankton) for Age-0 pollock and capelin, but it did differ for Age-1+ pollock and eulachon. The back-transformed, digestion-corrected weight of krill recovered intact from Age-1+ pollock stomachs weighed 0.029 g $ind.^{-1}$ compared to 0.020 g for individuals recovered from the plankton samples. This difference was significant (paired $t = -3.497$, $p = 0.002$). Similarly, krill recovered intact from eulachon stomachs averaged 0.031 g $ind.^{-1}$ compared to 0.022 g $ind.^{-1}$ krill collected from the plankton (paired $t = -2.561$, $p = 0.017$). Krill recovered from Age-0 walleye pollock (0.021 g $ind.^{-1}$) and capelin (0.014 g $ind.^{-1}$) stomachs were no different ($p > 0.106$) in terms of the mean weight of krill in the plankton samples with which they were paired (0.020 and 0.021 g $ind.^{-1}$, respectively). Thus, Age-0 walleye pollock and capelin consumed krill that, on average, were no different in size from the krill collected in the plankton net, but Age-1+ walleye pollock and eulachon consumed krill that were relatively large.

Mean individual weight of krill recovered from walleye pollock and eulachon stomachs increased with mean weight of krill in the plankton. The relationship was strongest for Age-1+ pollock where it approached unity [$W_{diet} = 0.05 + 0.91(W_{plankton})$, $r^2 = 0.52$, $p < 0.001$], weaker for Age-0 pollock ($r^2 = 0.26$, $p < 0.001$) and eulachon ($r^2 = 0.18$, $p = 0.027$), and not significant for capelin ($p = 0.95$). Thus, the size of krill consumed by Age-1+ walleye pollock increased with available sizes; in contrast, the smaller fishes appeared less able to exploit the large size fraction of the resource.

An unexpected finding was that the mean size of krill in the plankton samples exhibited a consistent geographic distribution pattern. Mean krill body weight tended to be highest near shore and over the Shelikof sea valley (Table 2, Fig. 7). The hydrographic-area effect on mean krill size was significant ($p = 0.008$). The significant year effect ($p = 0.002$) was attributed to the smallest means occurring in 2001. The year–area interaction term was not significant ($p = 0.829$). Thus, the consistent geographic pattern in distribution of krill mean size represents a qualitative component of the resource that was not reflected in either the distribution of abundance or biomass (mean weight \times abundance) (Fig. 7).

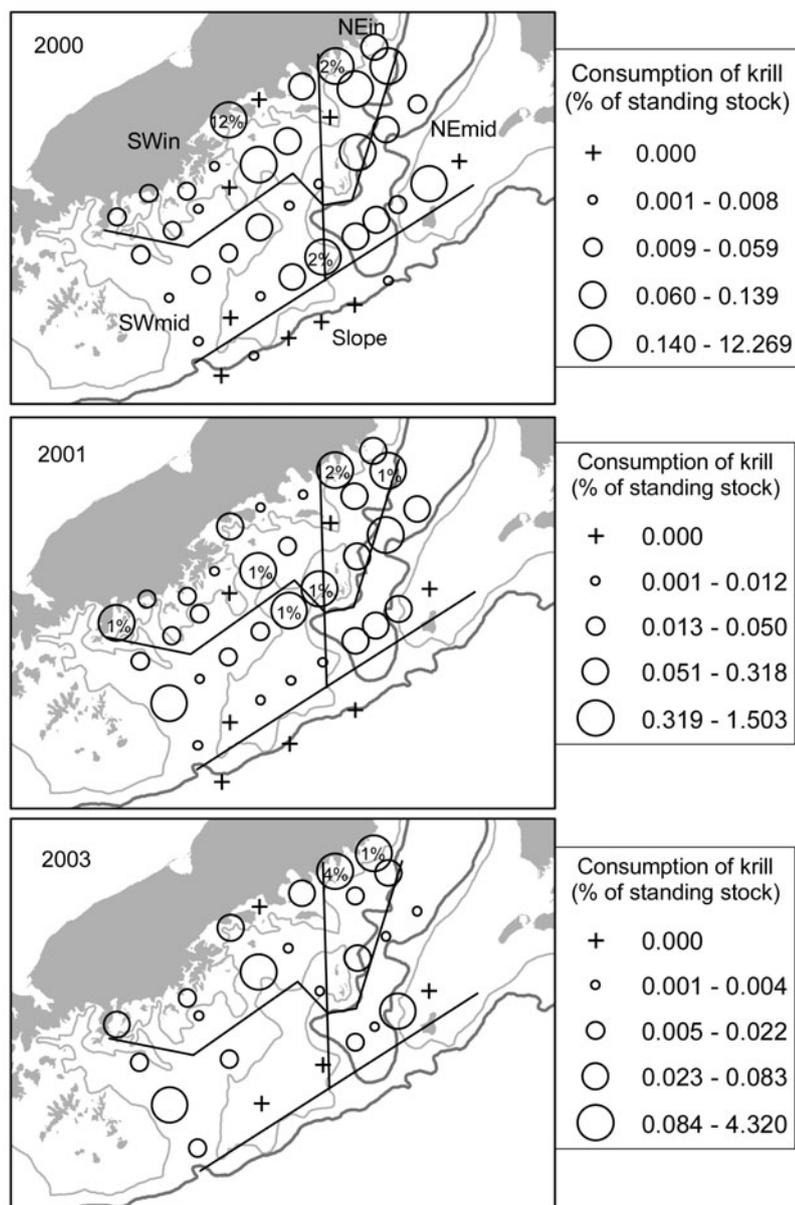


Fig. 6. Site-specific estimates of the relative daily consumption of krill by all predator taxa are shown as the percentages of local krill standing stock during September 2000, 2001, and 2003. Relative consumption is indicated at sites where it was $\geq 1\%$. Straight lines delineate the 5 hydrographic areas (Wilson 2009, this volume), which are labeled in the top panel. Thin/thick gray lines: 100/200 m isobaths, respectively

DISCUSSION

Predator diets

Walleye pollock *Theragra chalcogramma*, capelin *Mallotus villosus*, and eulachon *Thaleichthys pacificus* in the western GOA during September fed principally ($>50\%$) on krill. In this area and at this time of year, krill are known to be energy rich relative to most other

prey taxa, and large krill are especially energy rich (Mazur et al. 2007). Thus, there is a nutritional incentive for fish to recruit onto the krill resource, and to consume the largest krill possible. Observed diets were amply supported by krill standing stocks (Fig. 6); however, except for eulachon, fish diets were often considerably $<100\%$ krill (Fig. 1).

Predator consumption of krill

Age-0 pollock, capelin, and eulachon may have been constrained from access to the full spectrum of available krill sizes. Small Age-0 pollock may have been limited by mouth-gape size. Brodeur (1998) demonstrated the relevance of mouth-gape and prey size to Age-0 pollock dietary transitions. A similar size constraint may apply to eulachon, which also exhibited a positive fish-krill size relationship (Fig. 4). The apparent difference between Age-0 pollock and eulachon was that eulachon on average consumed large krill. In contrast, mean weight of krill consumed by capelin was small.

For Age-1+ pollock, there was no indication that access to local krill resources was limited by mouth-gape size. In fact, Age-1+ pollock appear to favor large prey. Selection of large krill was observed by Tanasichuk (1999) for another midwater gadid, hake *Merluccius productus*. Fish was another large prey item consumed by Age-1+ walleye pollock. In terms of mean individual body weight, fish were the largest prey consumed by Age-1+ pollock (Wilson et al. 2006b). Fish may not be available at all times of the day (Fig. 5), but their availability as an alternate prey could potentially alleviate the impact by Age-1+ pollock on krill populations. Thus, species-specific predator effects, predator-prey size relationships, and the availability of alternate prey appear to have been important in krill exploitation by, and perhaps allocation among, these fishes.

Relative consumption estimates were dependent on estimates of daily ration. For Age-0 pollock, literature estimates range from 1.0 to 8.5% BW d^{-1} (Wilson et al. 2006a), as compared to our estimate of 1.60% BW d^{-1} . For Age-1+ pollock, Dwyer et al. (1987) and Springer

Table 2. *Theragra chalcogramma*, *Mallotus villosus*, *Thaleichthys pacificus*. Predator abundance (in millions) and consumption (per capita and population [in millions] rates) of krill by hydrographic area (see Fig. 6, top panel) relative to krill standing stock (in millions) and mean body weight in the western Gulf of Alaska during September 2000, 2001, and 2003. 2003 slope was omitted because no zooplankton samples were collected at night

Year	Hydro. area	Area (km ²)	Predator abundance			Per capita consumption				Krill standing stock	Krill body weight (g ind. ⁻¹)			
			Age-0 pollock	Age-1+ pollock	Capelin	Eulachon	Age-0 pollock	Age-1+ pollock	Capelin			Eulachon		
2000	NEin	4871	193.469	137.733	46.349	20.273	1.13	7.11	0.29	0.68	1226	0.24	519517	0.0244
	NEmid	7799	435.895	53.603	100.262	22.466	0.94	23.59	0.10	2.74	1746	0.07	2644737	0.0148
	SWin	10520	658.204	0.177	292.455	0.004	0.83	8.42	0.15	1.68	592	0.10	616419	0.0208
	SWmid	12068	1759.213	0.102	34.117	3.701	0.15	1.18	0.21	0.93	269	0.02	1778192	0.0252
	Slope	6127	0.004	0	0.198	0	7E-05	0	0.57	0	0	0.00	1603100	0.0146
2001	NEin	4871	158.023	64.823	14.158	83.713	1.60	49.41	0.77	5.85	3957	0.57	689640	0.0269
	NEmid	7799	5.858	181.678	0.006	151.916	2.15	58.84	2.27	4.62	11405	0.14	7996945	0.0134
	SWin	10520	403.777	2.017	233.123	1.184	2.79	63.86	0.06	1.31	1271	0.08	1546807	0.0186
	SWmid	12068	294.263	9.015	99.920	15.597	0.93	21.62	0.81	0.70	559	0.01	10416154	0.0102
	Slope	6127	0	0	0	0	0	0	0	0	0	0.00	2611257	0.0113
2003	NEin	4871	417.345	2.308	131.017	38.086	0.91	12.92	0.55	1.53	539	0.20	268348	0.0367
	NEmid	7799	28.849	0	45.260	11.506	0.13	0	0.04	1.25	20	0.00	1104865	0.0316
	SWin	10520	100.485	0	151.093	1.516	0.34	0	0.05	0.45	42	0.01	367043	0.0387
	SWmid	12068	38.103	0.002	48.551	41.133	0.11	7.80	0.07	0.92	45	0.01	551274	0.0269

(1992) report daily ration estimates of 0.1 to 3.2% BW d⁻¹, as compared to our estimate of 1.67% BW d⁻¹. It is unusual for specific daily ration to increase with age. For capelin, our estimate of 0.68% BW d⁻¹ was low relative to other estimates, which range from 1.3 to 5% BW d⁻¹ (Wilson et al. 2006a). For eulachon, no other estimates of daily ration were found. Some of these discrepancies may reflect differences in predator size, prey energy density, and thermal conditions. In addition, the amplitude of the diel feeding cycle (Fig. 5) may have been damped by geographic and interannual integration of the data.

Much variation among individual predators was not included in the empirical relationships (e.g. Figs. 2 & 3) and daily rations used to estimate consumption. Data from individuals were averaged across samples within length bins, across fish within samples, or within time bins across samples. Variation among fish reflects species-specific and individual effects. Individuals differ in motivation to feed depending on hunger, which reflects recent feeding history, ontogenetic stage, and environmental conditions. Choice and acquisition of prey varies by prey size, shape, palatability, and availability. Fine-scale spatial and temporal effects on predator and prey probably were important, but are not well addressed by water column-integrated sampling at widely spaced sites. Thus, while variation among fish was not easily incorporated into statistical analyses, it probably is biologically relevant and warrants further investigation. To underscore the importance of small-scale variability, we point out that the higher estimates of localized consumption computed by Wilson et al. (2006a) were the result of assuming that the proportion of krill in predator diets did not vary among sites. In fact, no krill were recovered from predator stomachs where Wilson et al. (2006a) estimated that consumption was 30% of the standing stock. By incorporating more small-scale variability, which was possible due to the acquisition of more data, we feel that the present study provides a more realistic portrayal of site-specific consumption estimates.

Despite apparent ample standing stocks of krill, per capita consumption of krill responded to the increase in krill abundance from 2000 to 2001 and to the subsequent decline from 2001 to 2003 (Table 2). Strong recruitment of krill (mostly *Thysanoessa inermis*; Wilson 2009) to the area in 2001 explains the increase in krill abundance and decrease in mean krill size from 2000 to 2001. Subsequently, from 2001 to 2003, decreased krill abundance and increased mean individual weight likely reflects mortality and growth of individuals. Evidently, multiple year classes of krill co-occur in the western GOA. In the Barents Sea, multiple year classes of *T. inermis* co-occur during late summer (Dalpadado & Skjoldal 1996). Thus, fish responded to

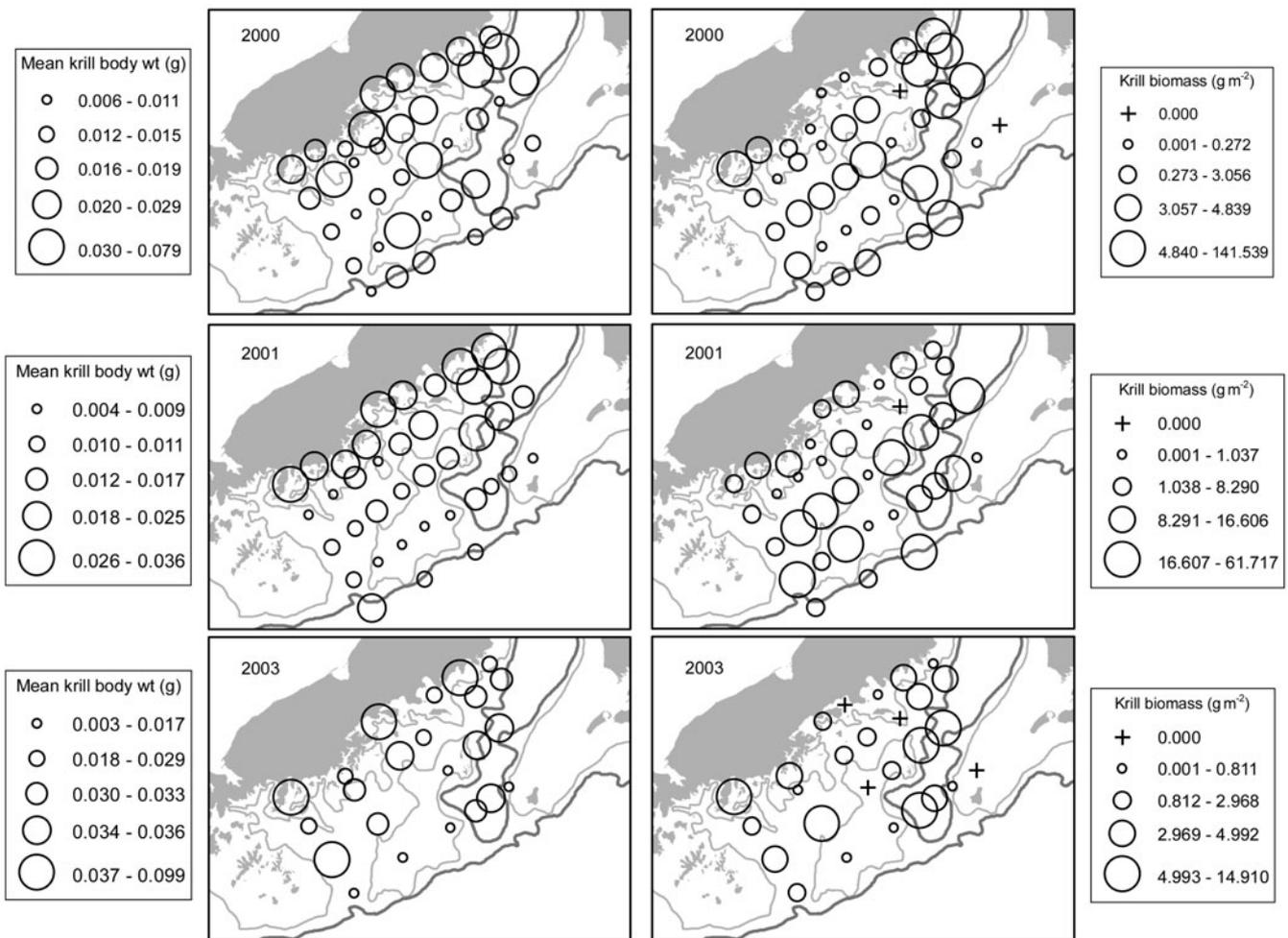


Fig. 7. Geographic distribution of the mean body weight (g) and biomass (g m⁻²) of krill in the western Gulf of Alaska from collections made at night during September 2000, 2001, and 2003. Thin/thick gray lines: 100/200 m isobaths, respectively

the strong krill recruitment in 2001 by increasing their consumption of krill, but area-specific impacts on local standing stocks varied with krill size and predator composition.

Early life-history stages of krill are more susceptible to near-surface transport than older stages, due to prolonged residence in the upper water column (Lu et al. 2003). In 2001, the high abundance and small mean size of krill near the Shumagin sea valley (Fig. 7) were therefore consistent with near-surface, downstream transport of young krill in the ACC and Alaskan Stream. Model-based estimates of mean net current velocity at 40 m depth for September were higher during 2001 than in 2000 and 2003 (Wilson 2009). Alternatively, Smith (1991) cited thermal mediation of growth rates to explain the size variability among *Thysanoessa inermis* and *T. raschi* in the Bering Sea (Smith 1991). In the present study, however, small krill sizes occurred during 2001, when temperatures were

intermediate to 2000 and 2003 (Wilson 2009). Smith (1991) attributed the geographic pattern in the distribution of krill abundance in the Bering Sea to predation. The effect of predation is complex because it can selectively target demographic subsets (e.g. size specific) of a prey species.

In northeastern areas, where topography was dominated by the Shelikof sea valley, fish responded to the 2001 increase in krill standing stock with a compensatory increase in consumption of krill. The impact of increased per capita consumption rates was most amplified by local concentrations of Age-1+ pollock and eulachon that feed on large krill apparently concentrated by flow-field and bathymetric effects (Wilson 2009). We suggest that the increase in krill abundance during 2001 triggered prey-switching behavior by predators, resulting in a compensatory functional response. The relatively small size of krill during 2001 might have reinforced this response if, despite possible

reductions in foraging efficiency, predators maintained ration sizes by consuming more krill. It is unknown if similar mechanisms explain apparent top-down control of krill populations by capelin (Dalpadado & Skjoldal 1996) and cod *Gadus morhua* (Dalpadado & Bogstad 2004) in the Barents Sea.

Krill size: plankton versus predator

Predator-specific differences in the size of krill consumed versus the size of those collected in our plankton samples suggest that our standing stock estimates were too high. The mean size of krill in the plankton samples were within the range of values reported elsewhere: Boldt (1997) in Prince William Sound (2.9 to 44.7 mg) and Dalpadado & Skjoldal (1996) in the Barents Sea (1.4 to 194.9 mg for *Thysanoessa inermis*). However, the comparatively large size of krill consumed by Age-1+ walleye pollock and eulachon indicates that fewer small krill were detected in fish stomachs than in the plankton samples. Small krill might be harder to detect among stomach contents than larger krill, but many small krill were recovered from other fish (Age-0 walleye pollock and capelin) stomachs making this explanation unlikely. If Age-1+ walleye pollock and eulachon consumed small krill in relatively low quantities, standing stock size might have been overestimated by including small krill. The percentage of the appropriate size fraction of the standing stock might actually have been greater than estimated. Thus, the observed compensatory response might have been underestimated.

Other factors relevant to estimating krill standing stock size include the availability of krill to our sampling gear and flux through the study area. Availability of krill to sampling gear is affected by their diel vertical migration and swimming (i.e. gear avoidance) capabilities (Sameoto et al. 1993, Wiebe et al. 2004). Presumably, these effects were minimized by using nighttime abundance estimates, but no absolute estimates were available for comparison. Flow-mediated flux of krill into and out of the study area undoubtedly affects standing stock size and population turnover, but this was beyond the scope of the present study.

In conclusion, krill were a dietary staple of walleye pollock, capelin, and eulachon that foraged over the western GOA shelf in late summer. Increases in the proportion of krill in Age-0 walleye pollock and capelin diets were indicative of size-related recruitment onto the prey resource. The size of krill consumed by Age-0 walleye pollock increased with predator size, but capelin were apparently confined to relatively small krill. Age-1+ walleye pollock and eulachon consumed more and larger krill. In combination, these predators

did not appear to greatly impact krill standing stocks; however, standing stock size estimates included many small krill that might not have been exploited by Age-1+ walleye pollock and eulachon. A compensatory response in consumption occurred in proximity to the Shelikof sea valley during 2001 when krill standing stock was high relative to that in 2000 and 2003. This response was due to increased per capita predation rates and local concentration of Age-1+ walleye pollock and eulachon. Strong recruitment of krill to the study area during 2001 was associated with high late-summer flow. No compensatory response was observed where small krill, apparently accumulated by near-surface transport, dominated local standing stocks. Thus, the apparent bottom-up influence of ocean current flow on the standing stock size of krill in neritic areas of the GOA can be at least partly compensated by localized top-down predation from nektonic fishes having prey size preferences that match available prey sizes.

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