PHYSICAL AND BIOLOGICAL FACTORS AFFECTING THE DIEL VERTICAL MIGRATION OF WALLEYE POLLOCK

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Abstract

The mechanisms underlying diel vertical migration (DVM) in marine fishes are unclear, although it is generally thought that this behavior is influenced by light, hydrography, food availability and predator avoidance. In the North Pacific Ocean, walleye pollock (*Theragra chalcogramma*) undergo DVM as juveniles, ascending to the surface at night and returning to the bottom at dawn. Adults are generally considered demersal. The objective of this research was to examine the effect of light, temperature and prey availability on the DVM of adult pollock. The work was undertaken to further our understanding of pollock biology, and the mechanisms underlying DVM in marine fishes in general. The study was conducted in the northern Gulf of Alaska in April, August and November 2003. Trawls < 80 m in April, and < 50 m in August, suggested that at least some portion of the pollock population was ascending to within 20 m of the surface in spring and summer. In November, acoustic data and targeted hauls > 100 m indicated that adults were not ascending to the surface at night, and that DVM behavior was occurring at depth. Euphausiids were the primary component of the diet in April and August. Decapods, primarily the shrimp *Pandalus borealis*, were the main component of the diet in November. Pollock passed through the thermocline during their ascent to the surface at night in August, and there was no relationship between the mean depth of pollock and the isolume (line of equal light intensity) necessary for visual foraging. In contrast, there was a significant relationship between the biomass of adult pollock above the 200 m isobath and the isolume necessary for visual foraging in November. Pollock did not pass through the thermocline at this time. It was concluded that in August adults ignore the isolume and thermocline, simply tracking the movements of euphausiid prey to feed upon them near the surface at night. In November, when euphausiids are no longer in patches, pollock shoals migrate up and down with the isolume necessary for visual foraging to feed on decapods.

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Acknowledgments

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Chapter 1 General Introduction

1.1. Significance and general background

Diel vertical migration (DVM) is a change in the position of an aquatic organism in the water column that occurs with a 24 h periodicity (Neilson and Perry, 1990). The mechanisms underlying DVM in marine fishes are unclear. The most recent review of the empirical data on DVM in marine fishes concluded that this behavior is a facultative process influenced by physical factors such as light and hydrography, as well biological factors, including food availability and predator avoidance (Neilson and Perry, 1990).

In the North Pacific Ocean, walleye pollock, *Theragra chalcogramma* (hereafter referred to simply as pollock), undergo clear DVM as juveniles. The general model for DVM in age–0 pollock in the Gulf of Alaska (GOA) is that they form either discrete ball–like aggregations, or dense layers, beginning approximately 5 m above bottom during the day; just prior to sunset they begin to move toward the surface, arriving at the 10 to 40 m depth strata within an hour; at night, they tend to disperse and form one or two layers extending 20 to 30 m in height; and shortly before dawn, they descend toward bottom, coalescing into the daytime aggregations described above (Brodeur and Wilson, 1996).

Pollock exhibit a decrease in DVM behavior with age. In the GOA, similar proportions of age–1 and age–2 pollock are found in midwater and bottom trawls, while there is a tendency for age–3+ pollock to occur in greater numbers in bottom trawls, suggesting that adults are primarily demersal (Duffy–Anderson et al., 2003). However, a completely demersal life history may not be an obligate process for adults, as they have been found in midwater layers at night off northern Japan (Miyashita et al., 2004).

Although several studies have inferred the role of light in the DVM of juvenile pollock by making day/night comparisons (e.g., Bailey, 1989; Schabetsberger et al., 2000), no field study has made *in situ* measurements of underwater light and related this to the vertical distribution and/or DVM of pollock. However, laboratory studies have quantified the amount of light that initiates downward movements in juvenile pollock

(Sogard and Olla, 1993), as well as the amount of light necessary for visual foraging (Ryer and Olla, 1999). Nothing is known about the role of light in the DVM of adult pollock.

Field studies have shown conflicting results on the effect of temperature on DVM in juvenile pollock. In the Bering Sea age–0 pollock congregate near the thermocline at night (Bailey, 1989), while in the GOA juvenile pollock regularly pass through a 6° C thermocline (Brodeur and Wilson, 1996). These conflicting results may be explained by laboratory work which found that juvenile pollock will only pass through a 6° C thermocline if there is food present (Olla and Davis, 1990). The role of temperature on the vertical movements in adult pollock is less clear, although some authors have speculated that they are unable to endure higher upper water column temperatures and/or cannot move through the thermocline, effectively making them obligate demersals (Duffy–Anderson et al., 2003).

The DVM of juvenile pollock in the Bering Sea appears to be a trade–off between prey availability and predator avoidance. When food is abundant juveniles will remain in warm surface waters to feed and avoid being cannibalized by adult pollock; on the other hand if prey are not abundant juveniles will descend to the bottom at dawn to digest at colder temperatures, where they risk being cannibalized by adults (Bailey, 1989). Schabetsberger et al. (2000) concluded that a strategy of "eat and avoid being eaten" most likely explained the DVM patterns of juvenile pollock at a front in the Bering Sea. However, there is a growing body of evidence that cannibalism is not nearly as important in the GOA (Smith et al., 1978; Yang, 1993; Yang and Nelson, 2000; Duffy–Anderson, 2003), suggesting that prey availability would be the more important biological factor in the DVM of adult pollock.

A fisheries acoustics survey around the Chiswell Island Steller sea lion (*Eumetopias jubatus*) rookery in the northern GOA in July/August 2002 regularly observed adult pollock in the upper 40 m of the water column at night. This observation suggested that at least some portion of the local pollock population was exhibiting DVM behavior. With this observation in mind, continuing seasonal surveys around the rookery in 2003 were used as a logistical platform to examine some of the physical and biological factors that might affect the DVM of adult pollock.

1.2. Statement of major goals and objectives

The major goals of this research were twofold. One was to advance our understanding of pollock biology by examining some of the physical and biological factors that contribute to the DVM of adult pollock. The second goal was to advance our understanding of DVM in general, by providing evidence of how these physical and biological factors might play a role in the DVM of otherwise demersal adults. These goals were achieved with the following 3 objectives:

Objective 1. Document the vertical distribution of adult pollock within 10 nmi of the Chiswell Island rookery at night. As noted in section 1.1, the research in this dissertation was funded through a contract to assess seasonal changes in the midwater fish prey available to Steller sea lions around the Chiswell Island rookery. Fulfillment of the contractual obligations provided the opportunity to document seasonal changes in the vertical distribution of adult pollock at night, thus providing a baseline for objectives 2 and 3. Objective 1 is addressed in Chapter 2.

Objective 2. Determine the role of prey availability and cannibalism on the DVM of adult pollock. The null hypothesis was that there would be no relationship between prey availability and/or cannibalism on the DVM of adult pollock; the alternative hypothesis was that one or both of these biological factors would be related to the DVM of adult pollock. Chapter 3 describes seasonal changes in the diet composition and prey selection of adult pollock, while the role of prey availability in the DVM of pollock is discussed in Chapters 4 and 5.

Objective 3. Determine the role of light and temperature on the DVM of adult pollock. The null hypothesis was that there would be no relationship between light and/or temperature on the DVM of adult pollock; the alternative hypothesis was that one or both of these physical factors would be related to the DVM of adult pollock. Objective 3 is addressed in Chapter 4.

Chapter 2 Seasonal changes in acoustic backscatter and pelagic fish biomass around the Chiswell Island Steller sea lion rookery in 2003[1]

2.1. Abstract

Fisheries acoustics surveys were conducted around the Chiswell Island rookery in the northern Gulf of Alaska (GOA) in April, August and November 2003 to assess seasonal changes in prey available to Steller sea lions (SSLs), *Eumetopias jubatus*, foraging around the rookery. Average nautical area scattering coefficient (s_A) between 5 to 200 m was compared seasonally. There was no significant difference in s_A between April (158.8 m^2/nmi^2) and August (147.6 m^2/nmi^2), but mean s_A was significantly greater in November (389.4 m^2/nmi^2) as compared with both April and August. In terms of acoustic backscatter at depth intervals relevant to female and juvenile SSLs, there was a seasonal increase in s_A in the upper 20 m of the water column, and the highest s_A in the 20 to 40 m depth interval occurred in August. Trawl catch composition suggested that walleye pollock, *Theragra chalcogramma* (~ 30 cm total length), constituted the dominant biomass in all 3 months. The vertical distribution of pollock changed seasonally: pollock were caught primarily in hauls < 80 m in April and August, but > 100 m in November.

2.2. Introduction

The western stock (west of 144° W) of Steller sea lions (SSLs), *Eumetopias jubatus*, decreased almost 80% between the late 1970s and late 1990s (Loughlin et al., 2003). One of the leading hypotheses to explain this decline was a change in the quantity and size of their prey (Merrick et al., 1987). Possible causes were changes in prey availability due to commercial fisheries (Braham et al., 1980); environmental changes resulting in a switch from feeding on high energy herring and osmerids to low energy

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gadids and flatfish (Alverson, 1992); and interspecific competition with groundfish for small forage fishes (Merrick, 1997).

Assessments of fish biomass available to foraging SSLs must be done seasonally to account for seasonal differences in SSL foraging patterns. In the central Gulf of Alaska (GOA) and Aleutian Islands, female SSLs with dependent young increase their foraging effort over the course of the year by spending more time at sea, diving deeper and having greater home ranges in winter as compared with summer (Merrick and Loughlin, 1997). In the northern GOA there is a sharp increase in the duration of foraging trips by nursing females in August (Maniscalco et al., 2006). Both of these observations are thought to be linked to seasonal changes in prey availability (Merrick and Loughlin, 1997; Maniscalco et al., 2006).

Seasonal assessments of fish biomass available to foraging SSLs must take into account the vertical distribution of available prey as well. Female SSLs with dependent young dive in the upper 50 m of the water column 97% and 90% of the time in summer and winter, respectively (Merrick and Loughlin, 1997). In the central GOA and Aleutian Islands young of the year SSLs do 89% of their winter dives in the upper 10 m of the water column, and all dives are done in the upper 50 m (Merrick and Loughlin, 1997). A similar study in the central GOA and Aleutian Islands found that the mean dive depth of young of the year and juvenile SSLs is 18.4 m (Loughlin et al., 2003).

Chiswell Island is a SSL rookery in the northern GOA that has been the focus of much recent study (e.g., Maniscalco et al., 2006). SSL diet in the Chiswell region during the mid 1970s consisted of 67% walleye pollock, *Theragra chalcogramma* (hereafter referred to as pollock), by frequency of occurrence, with a mean fork length (FL) of 29.8 cm (Pitcher, 1981). Recent scat analysis around the Chiswell rookery suggests that the primary prey is still pollock (Jason Waite, Alaska SeaLife Center, personal communication). Our objective in this study was to provide a seasonal assessment of the biomass and vertical distribution of midwater fishes available to SSLs foraging around the rookery in 2003.

2.3. Materials and methods

2.3.1. Field sampling

Echo integration midwater trawl surveys were done in April, August and November 2003 within an 18.5 km (10 nmi) radius of Chiswell Island (59° 36′ N, 149° 34′ W; Fig. 2.1). The April cruise was conducted aboard the 20 m R/V Pandalus, while the August and November cruises were conducted aboard the 23 m F/V Nightwatch. Acoustic data were collected at night, between evening and morning civil twilights, when the sun is 6° below the horizon (http://aa.usno.navy.mil/). Acoustic data were collected with a Hydroacoustic Technology, Inc. (HTI), model 244 split beam echosounder, equipped with a 38 kHz transducer. The transducer was towed beside the vessel at about 3 m/s in a dead–weight tow body about 4 m from the hull and 2 m below the surface. Sampling was restricted to calm conditions when noise due to surface bubbles and waves were not observed in the data. The system collected simultaneous 40 log *R* data for target strength (TS) and 20 log *R* data for echo–integration. The 20 log *R* data were integrated at 15 s time intervals and 1 m depth intervals, to a maximum depth of 200 m. Data within 3 m of the transducer were excluded to avoid near field effects. System calibrations were applied before writing the averaged voltages to computer files. Differential global positioning system (GPS) position and Greenwich Meridian Time (GMT) from the ship's navigation system were appended to each record before writing the data to disk.

The echosounder was calibrated by HTI at their calibration barge before the field season according to the methods described in Foote et al. (1987). Briefly, the beam pattern was measured by mounting the transducer on a rotator whose angular position was coupled to a special purpose instrumentation system. The echosounder was used to generate pulses which were measured by a U.S. Navy reference standard transducer (ST). The two transducers were aligned for maximum on–axis response, and the plotter was normalized for 0° and 0 dB. The beam pattern was started with the transducer rotated off axis by 90°. As the echosounder transmitter pulsed, the transducer was rotated back toward, and then past the ST. The echo level detected at the ST was converted to dB and plotted on the beam pattern plotter as a function of the off–axis angle. The system acoustic level was measured with the transducer and the ST aligned. Next, gain was determined with on–axis alignment of the transducer and the ST, with the latter used as the transmitting transducer. The known acoustic level was corrected for one–way transmission loss. Finally, the phase stiffness was plotted relative to angle off–axis. This was done for both the x– and y–axes of the transducer, corresponding to the quadrants of the ceramic elements within the transducer (Ransom et al., 1995). In addition to the factory calibration, field checks were done using a 38 mm tungsten carbide calibration sphere. The echosounder settings (Table 2.1) were optimized by HTI and were not altered during the cruises. The noise levels were determined by HTI. The noise threshold was set at 6 dB above the measured noise level for each depth interval and time–varied gain correction.

Parallel acoustics transects were spaced at 3 nmi intervals, perpendicular to the 200 m isobath, which is the median depth of pollock distribution (Smith, 1981).

Opportunistic midwater trawls were also done at night, when layers of high acoustic backscatter were observed while transecting. Midwater trawls were done with a Gourock, Inc., research scale net with vertical and horizontal openings of 12 and 22 m, respectively, in April and August. In contrast, November midwater trawls were done with an LFS, Inc., commercial fishing scale net with vertical and horizontal openings of 26 and 51 m, respectively. However, both nets were outfitted with the same 1.9 cm mesh cod end liner. Up to 200 random specimens of each species per tow were retained for shipboard measurements of FL, while additional fish were counted as they were released. Of the 200 retained fish, a sub–sample of 50 specimens were frozen for length–weight measurements in the laboratory.

2.3.2. Laboratory procedures

FL for all frozen specimens was measured to the nearest mm and weighed to the nearest 0.1 g. As total length (TL) measurements are required for the use of TS models, the FL measurements for pollock, capelin (*Mallotus villosus*) and eulachon (*Thaleichthys pacificus*) were converted to TL with the equations provided in Buchheister and Wilson (2005). Similarly, FL measurements for Pacific herring, *Clupea pallasii* (hereafter referred to simply as herring), were converted with the equations provided in Karpov and Kwiecien (1988). Shrinkage due to freezing was also corrected for pollock and eulachon length measurements (Buchheister and Wilson, 2005). No such correction exists for herring. Length–weight regressions were calculated for pollock, herring and eulachon. No capelin were collected for laboratory measurements and so the equation provided in Brown (2002) was used to generate a length–weight regression.

2.3.3. Echogram processing

Echo integration data were processed with Echoview software (SonarData Pty. Ltd., Hobart, Tasmania, Australia) and exported in two formats:

1. Nautical area scattering coefficient:

$$s_A = 4\pi(1852)^2 s_a \tag{2.1}$$

with the area backscattering coefficient between depth intervals z_1 and z_2 being:

$$s_a = \int_{z_1}^{z_2} \left(\sum \sigma / V\right) dz \tag{2.2}$$

where σ is the backscattering cross–section and V is the volume insonified. The exported s_A data were examined for outliers associated with acoustic noise in the water column and omitted from further analysis (Rivoirard et al., 2000). Note that s_A is expressed as m^2/nmi^2 by historical convention (MacLennan et al., 2002).

2. Abundance and biomass were estimated based on a modification to the methods outlined in Simmonds and MacLennan (2005). Echograms for each cruise were partitioned as a species mix based on the trawl catch for that cruise. Furthermore, this

partitioning was only done at depth intervals corresponding to trawl depths within a cruise. This partitioning was done as follows. The proportion of species i is given by:

$$w_i = \frac{\sum_{k=1}^{M} q_{ik} / q_k}{M} \tag{2.3}$$

where q_{ik} is the quantity of species i caught at station k, q_k is the total catch at station k, and M is the total number of trawls for the respective cruise. Note that only hauls containing at least 25 fish were used in the calculation of w_i. Next, echograms were partitioned with:

$$E_i = \frac{w_i \langle \sigma_i \rangle E_{\mathrm{m}}}{\sum_{i=1}^{I} w_i \langle \sigma_i \rangle} \tag{2.4}$$

where I is the total number of species, $\langle \sigma_i \rangle$ is the mean backscattering cross–section of species i, and E_{m} is the volume backscattering coefficient. TS–length equations of Gauthier and Horne (2004) were used to calculate $\langle \sigma_i \rangle$ for capelin, eulachon, herring and pollock (Table 2.2), with different size classes of pollock derived from length–frequency histograms (Anderson and Neumann, 1996). Lengths for other species were arithmetic means. Although there are no TS–length models for surf smelt (*Hypomesus pretiosus*) currently available, this species is a member of the Osmeridae family, along with capelin and eulachon. Surf smelt and capelin possess a swim bladder, while eulachon do not (Mecklenburg et al., 2002). Thus, we applied the TS–length equation for capelin to surf smelt. Backscatter not attributed to any of these five species was considered “other.” Finally, the abundance of species i was calculated with:

$$\rho_i = \frac{s_{\mathrm{A}}}{4\pi < \sigma_i >} \tag{2.5}$$

which has units of numbers/nmi^2. This abundance estimate was then converted to kg/nmi^2 using the length–weight regressions described above.

There were 4 exceptions to this procedure ($n = 3$ in August and $n = 1$ in November). Small portions of a few echograms (< 5% of a transect) could be identified as herring based on school structure. These regions were analyzed as follows. First the regions were excluded from the aforementioned species mix partitioning. Data within the regions were then partitioned based on the trawl catch from the single herring dominated haul (> 95% herring) in each cruise. Results were exported from Echoview and then added to the total species mix for that portion of the transect that had originally been excluded.

2.3.4. Preliminary data analysis

A retrospective analysis was done on the elementary distance sampling unit (EDSU), which is defined as the distance along a transect over which acoustic measurements are averaged to give one sample. If the EDSU is too large, information about the geographical distribution of the stock will be lost, whereas if it is too small, successive samples will be dominated by local variability (Simmonds and MacLennan, 2005). Thus, data were binned at 0.1, 0.5 and 1.0 nmi, and experimental variograms were generated for each bin size in each month with geoR (http://www.est.ufpr.br/geoR/) to determine the most appropriate EDSU for subsequent analysis.

Following Cressie (1993), a stationary model assumes that:

$$E\{Z(\mathbf{s}+\mathbf{h})-Z(\mathbf{s})\}=0 \tag{2.6}$$

and

$$\mathrm{var}\{Z(\mathbf{s}+\mathbf{h})-Z(\mathbf{s})\}=2\gamma(\mathbf{h}) \tag{2.7}$$

where the spatial index **s** varies along the surface *Z*, **h** is some distance vector and $2\gamma(\mathbf{h})$ is the variogram. The classic estimator of the variogram is:

$$2\hat{\gamma}(\mathbf{h})=\frac{1}{|N(\mathbf{h})|}\sum_{N(\mathbf{h})}[Z(\mathbf{s}_i)-(\mathbf{s}_j)]^2 \tag{2.8}$$

where the sum is over $N(\mathbf{h})=\{(i,j)\}:\mathbf{s}_i-\mathbf{s}_j=\mathbf{h}\}$, and $|N(\mathbf{h})|$ is the number of distinct elements of $N(\mathbf{h})$. The appropriate EDSU was chosen by visual inspection of variograms for a clear sill (asymptote).

Normality of s_A data for each month was checked with a Shapiro–Wilk test, and datasets that did not meet this criterion were log–transformed (Zar, 1999).

2.3.5. Seasonal differences in water column s_A

Adjacent acoustic measurements exhibit autocorrelation, which occurs when the error terms are not independent random variables (Neter et al., 1996). Treating autocorrelated data as independent samples would be a form of pseudoreplication (Hurlbert, 1984). To test the null hypotheses of no seasonal difference in s_A, we used PROC MIXED (SAS Institute, Cary, North Carolina, U.S.A.), which allows the use of spatially correlated error terms in the standard linear model $\mathbf{Y} = \mathbf{X}\boldsymbol{\beta} + \varepsilon$. When using PROC MIXED one must select some covariance structure. We used a spherical model:

$$\gamma(\mathbf{h}) = \left(\frac{3\|\mathbf{h}\|}{2a}\right) - \left(\frac{\|\mathbf{h}\|}{2a}\right)^3 \tag{2.9}$$

and exponential model:

$$\gamma(\mathbf{h}) = 1 - \exp(-\|\mathbf{h}\|/a) \tag{2.10}$$

where a is the variogram range (Cressie, 1993). Note that this differs from the standard formulation slightly, in that the covariance comes in on the left hand side. For example, with the exponential model:

$$\operatorname{cov}[\varepsilon(\mathbf{s}), \varepsilon(\mathbf{s}+\mathbf{h})] = \sigma^2 \times \exp(-\|\mathbf{h}\|/a) \tag{2.11}$$

and:

$$\operatorname{var}[\varepsilon(\mathbf{s})] = \sigma^2 + \tau^2 \tag{2.12}$$

where τ^2 is the nugget, which represents measurement error and/or microscale variation (Cressie, 1993). Starting values for the sill, range (distance where the sill is reached) and nugget were entered into PROC MIXED based on model fits in geoR.

The Akaike Information Criterion (AIC) was used to discriminate between model fit. The AIC is given by:

$$-2\log\{L(\theta|\,\text{data, model})\} + 2K \tag{2.13}$$

where $L(\theta|$ data, model) is the maximized log–likelihood of the unknown parameters θ, given the data and the model, and K is the number of parameters (Burnham and Anderson, 1998).

In one case (i.e., November) the raw s_A data were normally distributed, and log–transformation (so as to make statistical comparisons with the log–transformed April and August data) resulted in a severe departure from normality. A general probability statement allowed us to compare confidence intervals for the raw November data with back–transformed confidence intervals for the April and August data, with the caveat that the back–transformed data are not symmetrical around the mean (Zar, 1999). Assuming two independent sets of data A and B, $1 - \alpha$ confidence intervals for a parameter θ are calculated from the probability statements $P\{L(A) < \theta_A < U(A)\}$ and $P\{L(B) < \theta_B < U(B)\}$. Thus it follows that:

$$P\{L(B) - U(A) < \theta_B - \theta_A < U(B) - L(A)\} = (1 - \alpha)^2 \qquad (2.14)$$

In order to get a 95% confidence interval for $\theta_B - \theta_A$ one would generate $\sqrt{1-\alpha} = \sqrt{0.95} = 0.975$ confidence intervals for each data set A and B.

2.3.6. Vertical distribution of s_A within months

We originally planned to test the null hypothesis of no seasonal difference in s_A between 20 m depth bins within a month. However, breaking the s_A data down in this manner resulted in so many zeroes that the data could not be normalized with log or any other standard transformation (Zar, 1999). So this hypothesis could only be examined qualitatively.

2.3.7. Seasonal differences in 20 m depth bins of s_A

We also planned to test the null hypothesis of no seasonal difference in s_A at equivalent 20 m depth bins between months. As was noted above, breaking the s_A data down into 20 m depth bins resulted in so many zeroes that the data could not be normalized, so this hypothesis could only be examined qualitatively as well.

2.4. Results

2.4.1. Field sampling

Trawl stations were distributed throughout the study area in April, while they were concentrated in Aialik Bay and Dora Passage in August and November (Fig. 2.1). Catch data used to partition echograms are presented in Table 2.3. Hauls containing < 25 fish (n =1 in August and n = 2 in November) were not used in the calculation of w_i and so are not presented. Additionally, hauls containing > 95% herring (n = 1 for both August and November) that were used for partitioning the aforementioned identifiable herring schools are not shown. Trawl depths ranged between 22 and 87 m in April; between 18 and 48 m in August, with another haul between 101 and 124 m; and > 100 m in November. Pollock was the dominant trawl catch in all months. Small numbers of capelin, eulachon and herring were caught in April. The number of herring in August increased due to the catch in trawl 3. Surf smelt and eulachon were the second and third most abundant species in the November trawl catch, respectively.

2.4.2. Laboratory procedures

Length–weight regressions for pollock, herring and eulachon are presented in Table 2.4. The length–weight regression provided in Brown (2002) was used for capelin and surf smelt.

The length–frequency histogram for April pollock shows clear peaks at 14.5 and 36.0 cm (Fig. 2.2), which corresponds to age–1 juveniles and age–3 adults, respectively (Hughes and Hirschhorn, 1979; Shima et al., 2002; Duffy–Anderson et al., 2003; Dorn et al., 2004). August peaks occur at 9.0, 19.0 and 32.5 cm, which correspond to age–0 juveniles, age–1 juveniles and age–3 adults, respectively. November peaks occur at 12.5, 23.0 and 42.0 cm and correspond to age–0 juveniles, age–1 juveniles and age–4 adults, respectively. For brevity, the age–3 fish in April and August, will be referred to simply as adults for the remainder of this paper, even though the left–hand tail of this distribution clearly contains some age–2 juveniles. Similarly, the age–4 fish in November will be referred to as adults, even though the left–hand tail contains age–3 adults, etc.

2.4.3. Echogram processing

Values used to partition echograms into species mix and herring schools are presented in Tables 2.5 and 2.6 respectively. Note that August data are split according to trawl depths as noted above.

2.4.4. Preliminary data analysis

Variograms of water column s_A data binned at an EDSU of 0.1 nmi were dominated by local variability, while those at 0.5 nmi were not. An example of this is shown in Fig. 2.3, where the variogram for the 0.1 nmi data peaks and then drops down again; in contrast the 0.5 nmi binning results in a clear sill. Thus we used an EDSU of 0.5 nmi for all subsequent analysis.

Mean s_A was 2.5 and 2.6 times higher in November as compared with April and August, respectively (Table 2.7). Higher CVs in April and August corresponded to patchier distributions of s_A in both months (Fig. 2.4).

Severe departures from normality were detected for the April and August water column s_A data, which was corrected by log–transformation (Table 2.8). Conversely, the November water column s_A data were normally distributed, and log–transformation resulted in a severe departure from normality. Thus, the subsequent ANOVA was only run on the April vs. August data.

2.4.5. *Seasonal differences in water column s_A*

AIC values were lower with the exponential model in all 3 months (Table 2.9), indicating a better fit. Thus, exponential models were used in all subsequent statistical analyses.

There was no significant difference between log–transformed water column s_A in April as compared with August ($F = 0.30$, d.f = 1, $P = 0.59$). The 97.5% confidence intervals for back–transformed April and August data, as well as the raw November data, are presented in Table 2.10. Note that the back–transformed data (April and August) are biased for the median. The approximate confidence interval for November – April (145.14, 388.48) did not include zero, so we can say with 95% confidence that November water column s_A was significantly greater than April water column s_A. Similarly, the approximate confidence interval for November – August (166.54, 362.42) did not include zero, so we can say with 95% confidence that November water column s_A was significantly greater than August water column s_A as well.

2.4.6. *Vertical distribution of s_A within months*

Mean s_A in April ranged from 15.42 m^2/nmi^2 in the 5 to 20 m bin, to 32.60 m^2/nmi^2 in the 180 to 200 m bin (Fig. 2.5). Mean s_A in August ranged from 5.12 m^2/nmi^2 in the 60 to 80 m bin, to 31.74 m^2/nmi^2 in the 180 to 200 m bin. Mean s_A in November ranged from 20.75 m^2/nmi^2 in the 20 to 40 m bin, to 82.81 m^2/nmi^2 in the 80 to 100 m depth bin.

2.4.7. *Seasonal differences in 20 m depth bins of s_A*

Mean s_A was greatest at all depths in November with the exception of the 20 to 40 m depth bin (Fig. 2.5), when August s_A was larger (26.43 m^2/nmi^2) than both November (20.75 m^2/nmi^2) and April (17.27 m^2/nmi^2).

We also note the seasonal increase in mean s_A in the 5 to 20 m depth bin, from 15.42 m^2/nmi^2 in April, to 29.74 m^2/nmi^2 in August, to 43.56 m^2/nmi^2 in November.

2.4.8. Partitioning s_A to biomass

Partitioning the s_A data, at depth intervals where trawl catch data was available, shows that adult pollock was the dominant biomass in all months (Table 2.11).

April adult pollock mean biomass was greatest in the 40 to 60 m depth bin (1866.2 kg/nmi^2). The mean biomass of herring (9.18 kg/nmi^2) and age–1 pollock (8.20 kg/nmi^2) in this depth bin were both three orders of magnitude lower.

August adult pollock mean biomass was greatest in the 20 to 40 depth bin (1931.40 kg/nmi^2). Herring (315.39 kg/nmi^2) had the second largest mean biomass in this depth bin. Adult pollock also had the largest mean biomass in the 100 to 120 m depth bin, but here capelin and eulachon ranked second and third at 28.46 and 20.25 kg/nmi^2, respectively.

November adult pollock mean biomass was greatest in the 180 to 200 m depth bin (5569.84 kg/nmi^2). Age–1 pollock (201.71 kg/nmi^2) and eulachon (126.34 kg/nmi^2) ranked second and third in this depth bin, respectively.

Seasonal comparisons can only be made for two depth bins. In the 20 to 40 m depth bin, mean biomass of adult pollock was greater in August (1931.4 kg/nmi^2) as compared with April (1689.45 kg/nmi^2). Similarly, mean biomass of herring was greater in August (315.39 kg/nmi^2) as compared with April (8.31 kg/nmi^2). In contrast, mean biomass of age–1 pollock was greater in April (7.42 kg/nmi^2) as compared with August (2.04 kg/nmi^2). Small amounts of capelin and eulachon were found in this depth bin in April, but not in August.

Seasonal comparison of the 100 to 120 m depth bin shows that mean biomass of adult pollock was greater in November (3453.72 kg/nmi^2) as compared with August (1171.74 kg/nmi^2). Similarly, mean biomass of eulachon was greater in November (78.34 kg/nmi^2) as compared with August (20.25 kg/nmi^2). Conversely, capelin was greater in

August (28.46 kg/nmi^2) as compared with November (2.17 kg/nmi^2). Herring, surf smelt, age–0 and age–1 pollock were found in this depth bin in November, but not in August.

2.5. Discussion

2.5.1. Error budget

Acoustically derived biomass estimates contain both sampling error, caused by the measurements being stochastic samples of the true mean density, and systematic error, which affects all the observations equally. Examples of the latter include equipment sensitivity, transducer motion, the surface bubble layer, etc. (Simmonds and MacLennan, 2005).

The largest source of sampling error results from survey design (Simmonds and MacLennan, 2005). Other sources of sampling error are variation in the mean TS over the surveyed region; species discrimination through echogram partitioning; diurnal variability affecting fish distribution and TS; sampling echogram marks by fishing to provide species proportions; and sudden changes in fish distribution and behavior due to storms events, etc. (Simmonds and MacLennan, 2005). Given the small size of the study area, it was assumed that we were dealing with a single pollock population, and so it follows that variation in mean TS would be negligible. With the exception of 4 herring schools, all echograms were categorized as a species mix, so any error resulting from species discrimination through partitioning was also considered negligible. Transects were run between evening and morning civil twilights, during the period when vertical migrators are near the surface, so it was assumed that there was no diurnal variability in fish distribution or TS during data collection. Finally, there were no major storm events during any of the cruises so it is unlikely there were major changes in fish distribution over the course of each cruise. This leaves partitioning echogram marks based on species proportions in trawl catch as the largest source of sampling error in this study.

A minimum of 5 to 7 trawl stations are needed per 100 nmi^2 in order to minimize statistical parameters such as CV in abundance estimates (Godø et al., 1998). Although we met these minimum criteria in all 3 cruises, not all trawl catch data could be used for the partitioning of echograms. Our method of partitioning echograms for a 10 nmi radius study area based on as little as one tow (i.e., August 100 to 120 m depth bin) undoubtedly introduced the largest source of error in this study. However, we minimized the vertical aspect of this error by not extrapolating species composition and biomass outside trawl depths.

2.5.2. Vertical distribution of pollock

Given the dominance of pollock in our trawl catch, and the importance of prey availability < 50 m to female and juvenile SSLs, a few words on the vertical distribution of pollock are necessary. During the period 1973 to 1975 the biomass of adult pollock in the Chiswell region was greatest between 91 to 180 m (Hughes and Hirschhorn, 1979). However, this study used bottom gear, did not sample at depths < 91 m, and it is unclear whether the data were collected during the day or night, so it is difficult to make comparisons with our findings.

Two recent studies further west in the GOA used both midwater and bottom gear to assess the vertical distribution of pollock. The mean depth of adult pollock at night was within 30 m of bottom, corresponding to depths between 110 to 140 m (Wilson et al., 2003). Duffy–Anderson et al. (2003) found similar proportions of age–1 and age–2 pollock in midwater and bottom trawls. In general, there was a tendency for age–3+ pollock to occur in greater numbers in bottom trawls, suggesting that adults are primarily demersal in the GOA. However, it is unclear whether these data were collected during the day or at night, so comparisons with our findings should be done with caution.

Vertical distribution of pollock has also been assessed off northern Japan. Miyashita et al. (2004) report that pollock > 30 cm are distributed between the bottom and midwater layer at night in June. In another study off northern Japan it was found that the mean depth of pollock layers during the night was 150 to 250 m in April, and 400 to 500 m in October (Kooka et al., 1998).

The depth distribution of pollock we caught around Chiswell Island in November (i.e., > 100 m) is consistent with these other studies. However, the preponderance of adult pollock in our trawl catch at depths < 80 m in April, and < 50 m in August, may be explained in several ways. One is that the expected escapement of smaller fish through the rope wings of midwater gear would result in under–representation of age–0 pollock (Karp and Walters, 1994). Another possible explanation is that adult pollock in the region feed primarily on vertically migrating euphausiids (Smith et al., 1978; Yang, 1993; Yang and Nelson, 2000; Adams et al., 2007), and so adults would be expected to be near the surface at night. A third possible explanation has to do with interannual variability in year class strength. In the Bering Sea, the midwater biomass of age–4 adults was greater than the demersal biomass of age–4 adults in 1982 and 1988, while in 1979 and 1985 the reverse was true. The 1982 phenomenon was thought to be due to an extremely strong year class in 1978 (Karp and Walters, 1994). Analogously, there were relatively strong year classes of pollock in the GOA in 1999 and 2000 (Dorn et al., 2004), which would have corresponded to age–4 and age–3 fish, respectively, during our study. While it is beyond the scope of this study to address the issue of year class strength on vertical distribution of pollock, we raise this point to illustrate that the observed biomass of adult pollock < 50 m in April and August 2003 may not be representative of other years.

2.5.3. Midwater fish prey available to Chiswell SSLs

Our objective in this study was to provide a seasonal assessment of the biomass and vertical distribution of midwater fishes available to SSLs foraging around the Chiswell Island rookery in 2003. Midwater trawling is not the best method for assessing pelagic prey such as herring, capelin, and salmonids (*Oncorhynchus* spp.); furthermore, midwater trawling will not sample pollock near bottom or other demersal prey such as Pacific cod, *Gadus macrocephalus*, and arrowtooth flounder, *Atheresthes stomias*

(Gunderson, 1993). Nevertheless, our results provide a number of potential insights into the availability of pelagic pollock to SSLs foraging around the Chiswell rookery.

Adult pollock were the dominant biomass in the upper 50 m of the water column in April, where female SSLs with dependent pups do 90% of their dives (Merrick and Laughlin, 1997). Given that the mean dive depth for juvenile SSLs is 18.4 m (Loughlin et al., 2003), it is likely that this biomass of adult pollock would have been available to this cohort as well.

The biomass of adult pollock increased in August, indicating a greater availability of this primary prey species to female and juvenile SSLs foraging in the upper 50 m of the water column. There was also an increase in herring in this depth interval at this time, suggesting potential diversity in prey availability. An abrupt increase in foraging trip durations by Chiswell females occurs in late July (Maniscalco et al., 2006). Laboratory study of shallow dives by female SSLs found that increased prey encounter rates resulted in increased dive durations and foraging times (Cornick and Horning, 2003). Given the increase in pollock and herring biomass between April and August, it is reasonable to assume that foraging females would experience an increased encounter rate with prey, which in turn would lead to more time spent foraging.

Although the largest s_A occurred between 40 and 100 m in November, we were unable to convert this to biomass due to a lack of trawl catch data at these depth intervals. Because these targets were not detected with the ship's commercial fishing echosounder, which had settings optimized to detect commercial size adult pollock, we assume this biomass consisted of small age–0 pollock, or fishes with no swim bladder. Furthermore, the fact that commercial size targets were deeper than 100 m suggests that adult pollock were restricted to depths in which female SSLs only do 10% of their winter dives, and would have been completely beyond the range of juvenile SSLs (Merrick and Loughlin, 1997). If it is assumed that adult pollock are the primary prey of female SSLs, then the deeper depth distribution of these classes of pollock may provide an alternate explanation for the observation that females SSLs spend more time at sea and dive deeper in winter as compared with summer (Merrick and Loughlin, 1997).

Overall midwater fish prey available to SSLs foraging around the Chiswell Island rookery may be lower than it is in the western GOA. For example, the highest s_A value we observed in our entire study was 1541.3 m^2/nmi^2. In contrast, the highest s_A value for adult pollock in Barnabas Trough, south of Kodiak Island, was 12,000 m^2/nmi2 (Wilson et al., 2003; Fig. 4). This is particularly important for Chiswell SSLs, as s_A data precludes the errors associated with midwater trawling and the partitioning of echograms discussed above. In other words, even allowing for escapement of juvenile pollock and other species, the overall biomass of prey available to Chiswell SSLs may be an order of magnitude lower than it is in the western GOA.

2.6. Acknowledgements

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Table 2.1. 38 kHz settings for HTI model 244 split–beam echosounder used within a 10 nmi radius around Chiswell Island in 2003. Note that 33 dBW = 1995.3 W. Calculation: $W = 10^{(33/10)}$.

Absorption coefficient	10.2 dB/km
Beam angle	7°
Ping rate	0.8 pps
Equivalent beam angle	–29.05 dB re 1 steradian
Pulse length	5 ms
Source level	217.78 dB re 1 µPa
Transmit power	33 dBW
TVG Gain	–2.4 dB

Table 2.2. Target strength–length equations from Gauthier and Horne (2004) used to partition echograms within a 10 nmi radius around Chiswell Island in 2003. L: total length of fish in cm.

Capelin	$24.9 \log L - 75$
Eulachon	$27.3 \log L - 94$
Pacific herring	$13.3 \log L - 55.9$
Walleye pollock	$19.2 \log L - 66$

Table 2.3. Trawl catch data used to partition echograms within a 10 nmi radius around Chiswell Island in 2003. Min HR: minimum headrope depth during tow. Max FR: maximum footrope depth during tow. Note that Min HR and Max HR were recorded at the start and end of acoustic data collection and do not include deployment and retrieval of the net. The number of each species is presented, with totals in bold font.

April	Min HR (m)	Max FR (m)	Capelin	Eulachon	Herring	Pollock	Surf smelt	Other
Trawl 1	29.3	46.8	–	–	–	63	–	–
Trawl 2	25.6	38.4	–	–	–	79	–	–
Trawl 3	22.0	78.6	2	3	–	378	–	1[1]
Trawl 4	22.0	62.2	2	–	–	23	–	–
Trawl 5	25.6	86.6	1	–	6	92	–	–
Trawl 6	38.4	58.5	–	6	–	183	–	–
Trawl 7	25.6	76.8	–	–	–	1107	–	–
Total			**5**	**9**	**6**	**1925**	**-**	**1**
August								
Trawl 1	100.6	124.4	16	1	–	11	–	2[2]
Trawl 3	18.3	43.9	–	–	127	315	–	2[3]
Trawl 4	23.8	47.5	–	–	4	85	–	–
Total			**16**	**1**	**134**	**411**	**-**	**4**
November								
Trawl 1	100.6	170.1	1	157	12	794	–	1[4]
Trawl 4	190.2	236.0	–	9	3	288	84	8[5]
Trawl 5	175.6	217.6	–	22	2	33	125	12[6]
Trawl 7	153.6	188.4	6	14	7	39	7	0
Total			**7**	**202**	**24**	**1154**	**216**	**21**

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[1] Arrowtooth flounder (*Atheresthes stomias*)
[2] Unidentified juvenile salmonids
[3] Prowfish (*Zaprora silenus*)
[4] Spiny dogfish (*Squalus acanthias*)
[5] Unidentified eelpouts
[6] Includes 11 unidentified eelpouts and 1 unidentified myctophid

Table 2.4. Summary of length–weight regressions used to convert abundance estimates to biomass within a 10 nmi radius around Chiswell Island in 2003. *n*: number of fish. *L*: length of fish in cm. Min: minimum. Max: maximum.

	n	Min (cm)	Max (cm)	Regression	r^2
Eulachon	40	16.4	23.3	$0.0046L^{3.0697}$	0.84
Herring	211	7.0	27.0	$0.008L^{3.0555}$	0.94
Pollock	379	9.7	52.6	$0.0095L^{2.9095}$	0.97

Table 2.5. Data used to partition echograms within a 10 nmi radius around Chiswell Island in 2003. TS: target strength. TL: average total length. Note that in the case of pollock TL represents the median length for the respective size class, derived from length–frequency histograms in Fig. 2.

	TS (dB)	TL (cm)	Weight (g)	% mix
April				
Capelin	–49.92	10.2	6.2	1.36
Eulachon	–57.92	21.0	52.4	0.57
Herring	–37.35	24.8	145.8	0.87
Age–1 pollock	–44.30	13.5	18.5	6.12
Adult pollock	–36.47	34.5	283.1	91.05
Other	NA	NA	NA	0.04
August (18–48 m)				
Herring	–37.66	23.5	123.7	18.11
Age–0 pollock	–48.66	8.0	4.0	2.57
Age–1 pollock	–41.34	19.3	51.9	0.34
Adult pollock	–37.10	32.0	227.5	78.76
Other	NA	NA	NA	0.22
August (101–124 m)				
Capelin	–51.20	9.0	3.8	53.33
Eulachon	–58.68	19.7	43.3	3.33
Adult pollock	–37.10	32.0	227.5	36.67
Other	NA	NA	NA	6.67
November				
Capelin	–49.98	10.4	6.8	2.08
Eulachon	–58.81	19.5	41.7	12.27
Herring	–42.26	10.6	10.9	3.16
Age–0 pollock	–44.94	12.5	14.8	0.74
Age–1 pollock	–39.85	23.0	87.0	9.39
Adult pollock	–34.93	41.5	484.7	46.54
Surf smelt	–49.07	11.0	8.6	23.86
Other	NA	NA	NA	1.95

Table 2.6. Data used to partition *n* = 3 (August) and *n* = 1 (November) herring schools within a 10 nmi radius around Chiswell Island in 2003. TS: target strength. TL: average total length. Note that in the case of pollock TL represents the median length for the respective size class, derived from length–frequency histograms in Fig. 2.

	TS (dB)	TL (cm)	Weight (g)	% mix
August				
Capelin	–51.20	9.0	3.8	0.21
Herring	–37.66	23.5	123.7	94.64
Age–0 pollock	–48.66	8.0	4.0	0.21
Age–1 pollock	–41.34	19.3	51.9	0.43
Adult pollock	–37.10	32.0	227.5	2.15
Other	NA	NA	NA	2.36
November				
Eulachon	–58.81	19.5	41.7	0.90
Herring	–42.26	10.6	10.9	99.10

Table 2.7. Basic statistics for nautical area scattering coefficient (s_A) within a 10 nmi radius around Chiswell Island in 2003, based on an EDSU of 0.5 nmi. CV: coefficient of variation.

	n	$\bar{x}$	Minimum	Maximum	CV
April	190	158.83	0.92	1541.29	1.28
August	188	147.63	6.91	913.77	1.00
November	188	389.42	17.22	946.67	0.46

Table 2.8. Shapiro–Wilk *W* statistics for nautical area scattering coefficient (s_A) within a 10 nmi radius around Chiswell Island in 2003, based on an EDSU of 0.5 nmi.

		Raw data		Log transformed data	
	n	*W*	*P*–value	*W*	*P*–value
April	190	0.65	< 0.0001	0.98	0.1122
August	188	0.69	< 0.0001	0.99	0.5357
November	188	0.99	0.0586	0.87	< 0.0001

Table 2.9. AIC values for nautical area scattering coefficient (s_A) within a 10 nmi radius around Chiswell Island in 2003, based on spherical and exponential covariance models in PROC MIXED.

	Spherical	Exponential
April	136.1	123.6
August	114.9	101.4
November	2461.5	2428.5

Table 2.10. Predicted mean and 97.5% confidence intervals for nautical area scattering coefficient (s_A) within a 10 nmi radius around Chiswell Island in 2003. The mean and median are provided for comparison.

				Confidence limits	
	$\bar{x}$	Median	$\hat{Y}$	Lower	Upper
April	158.83	93.42	92.58	49.48	172.14
August	147.63	102.50	106.77	75.54	150.74
November	389.42	384.18	377.62	317.28	437.96

Table 2.11. Mean biomass (kg/nmi^2) by 20 m depth bin within a 10 nmi radius around Chiswell Island in 2003. Age–0P: age–0 pollock. Age–1P: age–1 pollock. AdultP: adult pollock. Coefficient of variation (CV) is the same for all species within a depth bin and so is only presented once per row. Note that only depth bins with available trawl catch data are presented.

Depth bin (m)	Capelin	Eulachon	Herring	Age–0P	Age–1P	AdultP	Surf smelt	CV
April								
20 – 40	0.55	1.96	8.31	–	7.42	1689.45	–	2.93
40 – 60	0.61	2.16	9.18	–	8.20	1866.20	–	3.41
60 – 80	0.52	1.84	7.81	–	6.97	1586.83	–	2.24
August								
20 – 40	–	–	315.39	1.11	2.04	1931.40	–	2.23
100 – 120	28.46	20.25	–	–	–	1171.74	–	1.82
November								
100 – 120	2.17	78.34	5.27	1.68	125.06	3453.72	31.42	1.34
120 – 140	1.59	57.55	3.87	1.23	91.89	2537.32	23.08	1.63
140 – 160	2.10	76.01	5.12	1.63	121.35	3350.96	30.48	1.45
160 – 180	2.96	106.89	7.20	2.29	170.66	4712.45	42.87	1.70
180 – 200	3.49	126.34	8.51	2.70	201.71	5569.84	50.67	1.29

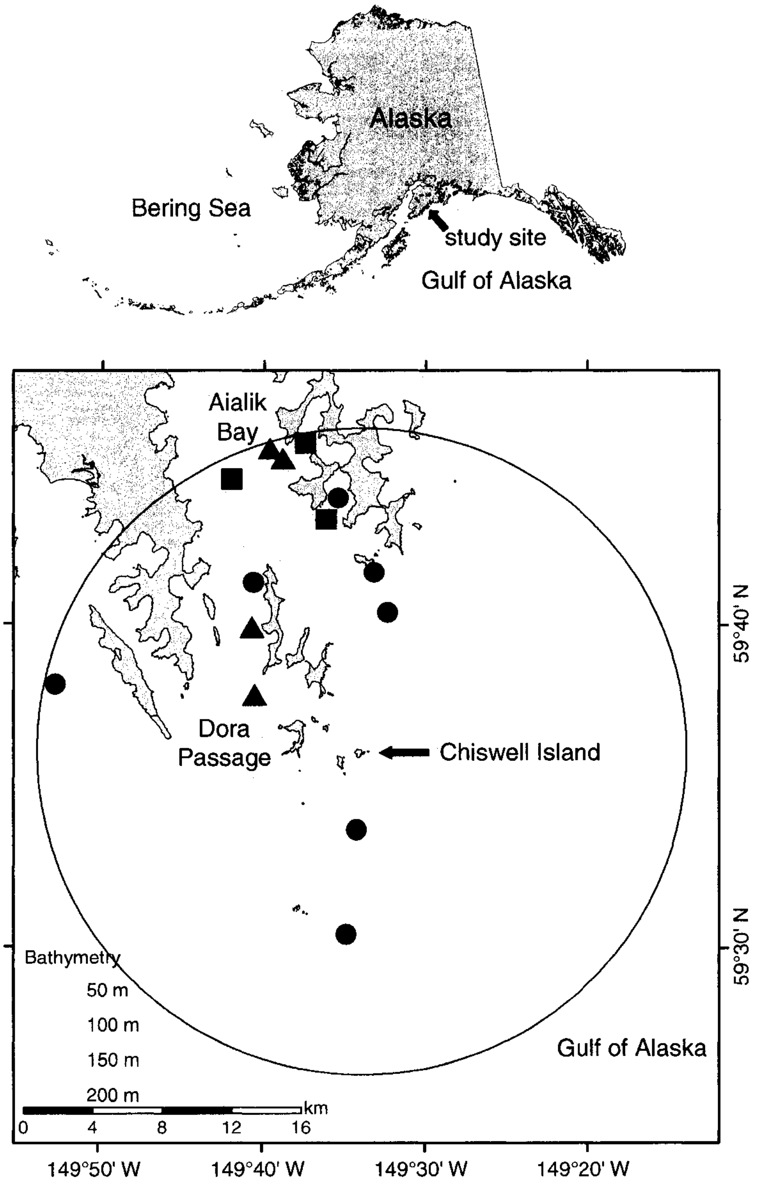

Figure 2.1. General map of Alaska (above), with a close up of the study area (below). Large circle depicts the 18.5 km (10 nmi) study radius, centered around the Chiswell Island rookery. Trawl stations are shown for April (●), August (■) and November (▲) 2003.

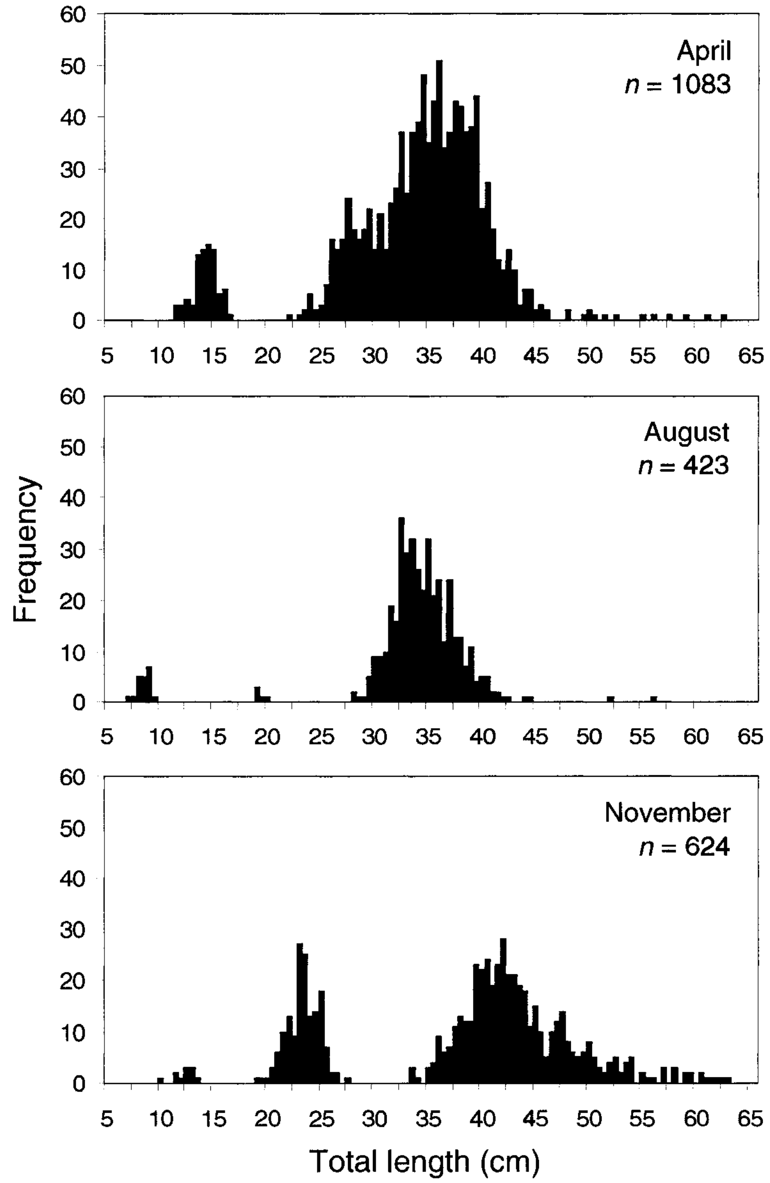

Figure 2.2. Length–frequency histograms for walleye pollock sampled by midwater trawl within a 10 nmi radius around Chiswell Island in 2003.

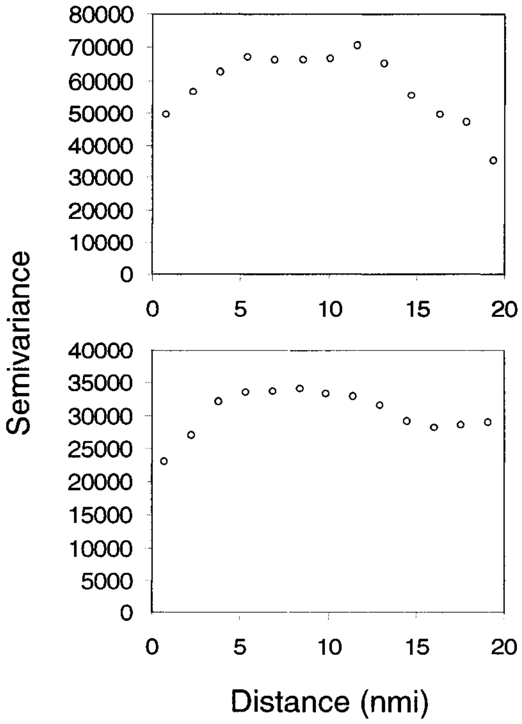

Figure 2.3. Variograms for nautical area scattering coefficient (s_A) binned at 0.1 nmi (upper) and 0.5 nmi (lower).

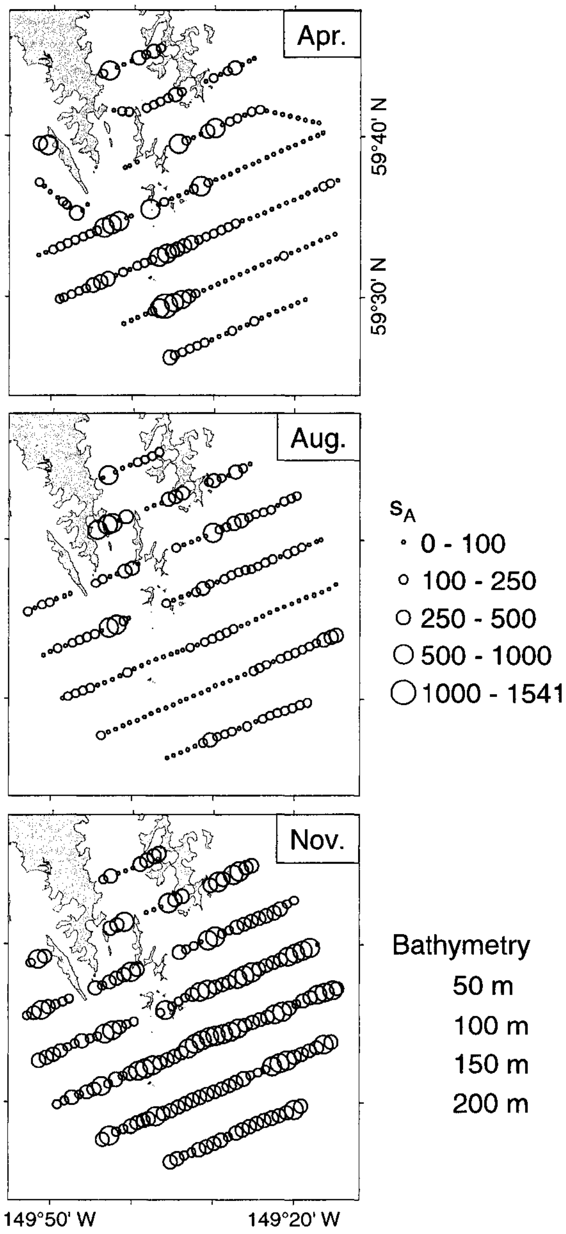

Figure 2.4. Post plots of nautical area scattering coefficient (s_A) within a 10 nmi radius around Chiswell Island in 2003.

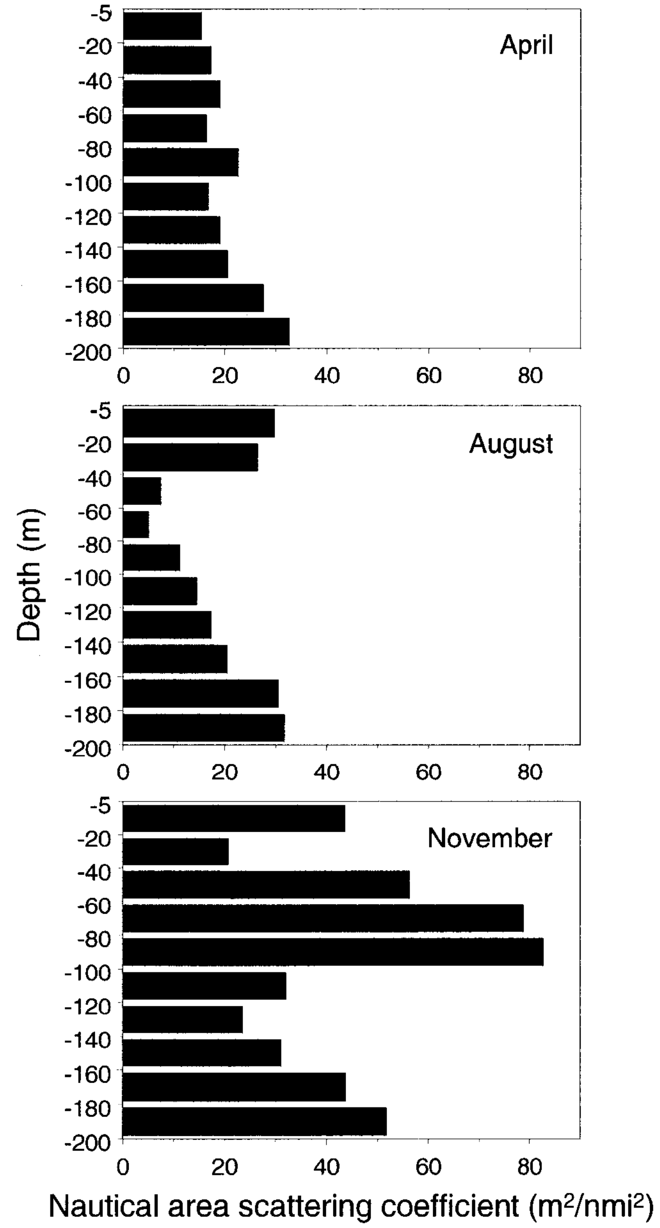

Figure 2.5. Mean nautical area scattering coefficient (s_A) by depth within a 10 nmi radius around Chiswell Island in 2003. Note that the upper 5 m of data were excluded (transducer was towed at a depth of 2 m, and the first 3 m of data were excluded to avoid near field effects).

Chapter 3 Seasonal changes in the diet composition and prey selection of walleye pollock (*Theragra chalcogramma*) in the northern Gulf of Alaska[1]

3.1. Abstract

Walleye pollock, *Theragra chalcogramma*, are one of the dominant fishes in the Gulf of Alaska (GOA) ecosystem, yet relatively little information is available on the diet and prey selectivity of pollock in the northern GOA. Stomachs of midwater trawled adult pollock were collected in April, August and November 2003 in the northern GOA. Euphausiids were the dominant prey in April, averaging 59% by number and 70% by weight. Euphausiids persisted as the dominant prey in August, averaging 84% by number and 95% by weight. Decapods were the dominant prey item in November. This was primarily due to the shrimp *Pandalus borealis*, which averaged 68% by number and 53% by weight. Stomach contents were also compared with available prey fields using chi–square based resource selection statistics. This analysis revealed significant differences between the environmental and dietary distributions of prey types. Additional analysis found significant selection for euphausiids over all other categories of available zooplankton in both spring and summer. Amongst euphausiids, there was significant selection for *Thysanoessa inermis* in spring and *T. spinifera* in summer.

3.2. Introduction

In the Gulf of Alaska (GOA) walleye pollock, *Theragra chalcogramma* (hereafter referred to as pollock), make up the 2nd largest groundfish biomass (Yang and Nelson, 2000). They are important prey for apex predators such as Steller sea lions (*Eumetopias jubatus*), harbor seals (*Phoca vitulina*), common murres (*Uria aalge*) and tufted puffins (*Fratercula cirrhata*); pollock are also important prey for the dominant groundfish in the GOA, arrowtooth flounder (*Atheresthes stomias*), and commercially important species

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such as Pacific cod (*Gadus macrocephalus*), Pacific halibut (*Hippoglossus stenolepis*), sablefish (*Anoplopoma fimbria*) and other pollock (Smith, 1981; Springer, 1992).

As a predator with a biomass averaging 1 million tons in the GOA, pollock may remove a considerable amount of prey from the ecosystem (Bailey et al., 2005). Much research has been done on the diet of pollock, both on juvenile (see review in Brodeur and Wilson, 1996) and adult stages (e.g., Dwyer et al., 1987; Shuntov et al., 2000; Yamamura et al., 2002). Not surprisingly, there is geographical variation in the diet of adults. For example, adults cannibalize juveniles in the Bering Sea (Dwyer et al., 1987), whereas in the Gulf of Alaska (GOA) euphausiids contribute the most to the diet of adults (Smith et al., 1978; Yang, 1993; Yang and Nelson, 2000). There is also seasonal variation in the diet of adult pollock. In the southeastern Bering Sea, the largest component of the diet in spring and summer is euphausiids, while in fall and winter it is juvenile pollock (Dwyer et al., 1987). However, no seasonal information exists on the diet of adult pollock in the GOA. Additionally, the aforementioned studies all sampled pollock with bottom gear, and relatively little information is available on the diet of pelagic adults. Two studies that did sample with midwater gear found very different diets: in the western GOA the diet of adults consisted primarily of (non–pollock) fishes (Duffy–Anderson et al., 2003), whereas off northern Japan the diet of adults consisted primarily of amphipods and euphausiids (Kooka et al., 1998). No information is available on the diet of pelagic adults in the northern GOA.

Prey selection is defined as a difference between the environmental and dietary distributions of prey types (Eggers, 1977). Although several studies have examined prey selection by juvenile pollock (Brodeur, 1998; Purcell and Sturdevant, 2001; Sturdevant et al., 2001; Wilson et al., 2006), only one study has examined prey selection by adults. Off northern Japan adult pollock exhibit positive selection primarily for amphipods (Kooka et al., 1998). Nothing is known about prey selectivity by adult pollock in the northeastern Pacific Ocean.

As fisheries science moves toward an ecosystem based approach it is clear that diet information collected in one area cannot be extrapolated to other regions. Nor can the results of dietary data collected in summer be considered representative of diet in other seasons (Hanson and Chouinard, 2002). In this paper we provide seasonal information on the diet of pelagic adult pollock in the northern GOA, which complements previous work on the summer diet of demersal adults in the region. We also provide evidence that the observed diet was due to prey selectivity, rather than random feeding, which complements previous work on juvenile pollock in the GOA.

3.3. Materials and methods

3.3.1. Study area

The study site (Fig. 3.1) was centered around Chiswell Island (59° 36' N, 149° 34' W), a Steller sea lion rookery in the northern GOA, where two of us (CFA, KOC) did an acoustic assessment of potential fish prey available to foraging sea lions as part of another study. Midwater trawls provided biological samples that allowed us to investigate seasonal changes in the diet of pollock in the present paper. The study area was adjacent to Global Ocean Ecosystems Dynamics (GLOBEC) stations 1 through 4. GOA shelf waters are characterized by two major currents: the Alaska stream, which flows westward at or near the shelf break, about 200 km offshore; and the Alaska Coastal Current, a buoyancy–driven current flowing westward within 40 km of the coast (Weingartner et al., 2002). Given the flow characteristics of the latter current, we assumed that data on zooplankton abundances taken from GLOBEC stations 1 through 4 could be used as a rough estimate of available prey fields in our study area.

3.3.2. Field sampling

Pollock were collected at night, between evening and morning civil twilights, in April, August and November 2003. The April cruise was conducted aboard the 20 m R/V Pandalus, while the August and November cruises were conducted aboard the 23 m F/V

Nightwatch. Midwater trawls were done with a Gourock, Inc., research scale net with vertical and horizontal openings of 12 and 22 m, respectively, in April and August. In contrast, November midwater trawls were done with an LFS, Inc., commercial fishing scale net with vertical and horizontal openings of 26 and 51 m, respectively. However, both nets were outfitted with the same 1.9 cm mesh cod end liner. Opportunistic midwater trawls were aimed at layers of high acoustic backscatter observed in a Hydroacoustic Technology, Inc., 38 kHz transducer, a standard frequency for the detection of pollock (e.g., Traynor, 1996). Up to 200 specimens of each species per tow were retained for shipboard measurements of fork length (FL). Stomachs were removed from at least five pollock per haul. Fish that showed signs of regurgitation (food in the mouth or throat) were not used. Each stomach was placed in an individual cloth sample bag with a tag containing the FL and haul number of the sample and preserved in 10% formalin.

Zooplankton were collected at night at GLOBEC stations 1 through 4 in April and August 2003. A 1 m^2 multiple opening/closing and environmental sampling system (MOCNESS), equipped with an externally mounted flowmeter and 500 μm mesh black nets, was towed at 4.5 km/h behind the 41 m R/V Alpha Helix. Five oblique samples were collected in 20 m increments from 100 m depth to the surface. Samples were preserved in 10% formalin (Coyle and Pinchuk, 2005).

3.3.3. Laboratory procedures

Stomach contents were identified to the lowest taxonomic category possible, enumerated and weighed. All unidentifiable material was categorized as digested material and omitted from data analysis.

Stomach fullness was assessed with the total fullness index:

$$\mathrm{TFI} = \frac{1}{n} \times \sum_{j=1}^{n} \frac{\text{stomach contents}_j}{\mathrm{FL}_j} \times 10^4 \qquad (3.1)$$

where n is the total number of j stomachs examined per cruise, stomach contents is in g, and FL is in cm (Nielsen and Andersen, 2001). TFI values ≤ 0.05 are considered indicative of minimal feeding (Mello and Rose, 2005)

MOCNESS samples from the same tow are autocorrelated and cannot be considered independent when running statistical analyses. Thus an integrated estimate of abundance for each station was computed as follows. The total number of each taxon was divided by the total volume sampled and expressed as number/m^3. These data were then integrated through the 20 m depth interval for each net to estimate number/m^2. All five of these values were then summed to give the number/m^2 during the entire 100 m MOCNESS tow. The number/m^3 for each station was determined by dividing the number/m^2 by the total depth interval (100 m) sampled by the tow. A recent multiyear monitoring study in the coastal GOA showed that the cross–shelf distribution of water properties and zooplankton could be characterized by dividing the shelf into four separate zones, with GLOBEC stations 1 through 4 comprising a nearshore zone (Coyle and Pinchuk, 2005). Thus, results for all four stations were averaged, and the coefficient of variation was calculated as the standard deviation divided by the mean.

3.3.4. Trophic diversity curves

Trophic diversity curves (Pielou, 1966; Hurtubia, 1973) were used to determine whether a sufficient number of stomachs were examined to describe the diet of pollock for each cruise. Trophic diversity was calculated with the Brillouin index:

$$H_k = \frac{1}{u_{+k}} \log_{10} \frac{u_{+k}!}{\prod_{i=1}^{I} u_{ik}!} \tag{3.2}$$

where u_{+k} is the total number of prey in k pooled stomachs, u_{ik} is the number of prey category i in k pooled stomachs, and I is the total number of prey categories. For each cruise, 100 random orders of stomachs were calculated, and the mean H_k was plotted against the cumulative number of stomachs. Curves were considered asymptotic if at least two values prior to the total trophic diversity (H_z) were within the range H_z ± 0.05 H_z (Koen Alonso et al., 2002).

3.3.5. Diet composition

Standard diet indices were calculated according to Bowen (1996). Frequency of occurrence (%FO) is the percentage of stomachs containing prey category *i*. High %FO values indicate whether fish in the sample can be characterized as a single feeding unit. Composition by number (%N) is the number of prey category *i* expressed as a percentage of the total number of prey in the *j*th stomach. Composition by weight (%W) is the weight of prey category *i* expressed as a percentage of the total weight of prey in the *j*th stomach. Results for %N and %W were summarized for each cruise by calculating the mean and 95% confidence intervals. Percentage data are not normally distributed and were arcsine–transformed to calculate proper confidence intervals. Note that when such confidence intervals are back–transformed to the original units they are centered around the median rather than the mean (Zar, 1999).

3.3.6. Resource selection statistics

We used the resource selection statistics of Manly et al. (2002) to test for differences between the dietary and environmental distributions of prey types. These statistics are based on chi–square tests, which require count data. Thus, all resource selection statistics were only done on prey numbers, and not on prey weight. In the Design II protocol of Manly et al. (2002) the resource units used by the *j*th fish are known, allowing statistical inference based on the use of individuals as replicates. There are three null hypotheses that can be tested:

H_{01}: individual fish used prey categories in the same proportions, regardless of whether selection occurred. The test statistic is:

$$\chi^2_{L1} = 2\sum_{j=1}^{n}\sum_{i=1}^{I} u_{ij} \log_e\left(\frac{u_{ij}}{E(u_{ij})}\right) \tag{3.3}$$

where u_{ij} is the number of prey category *i* consumed by fish *j*, and $E(u_{ij})$ is the expected number of prey category *i* consumed by the *j*th fish. For this equation $E(u_{ij}) = u_{i+}u_{+j} / u_{++}$, where u_{i+} is the total number of prey category *i* in all stomachs, u_{+j} is the total number of prey consumed by fish *j*, and u_{++} is the total number of all prey found in all stomachs. The test statistic is compared to the chi–square distribution with $(I - 1)(n - 1)$ d.f.

H_{02}: prey selection occurred in proportion to availability. The test statistic is:

$$\chi^2_{L2} = 2\sum_{j=1}^{n}\sum_{i=1}^{I} u_{ij} \log_e\left(\frac{u_{ij}}{E(u_{ij})}\right) \tag{3.4}$$

In this case $E(u_{ij}) = \pi_i u_{+j}$, where π_i is the proportion of prey category *i* in the environment. There are $n(I - 1)$ d.f.

H_{03}: on average, fish used prey in proportion to availability, regardless of whether they were selecting categories in the same proportions. This null is tested with:

$$\chi^2_{L2} - \chi^2_{L1} \tag{3.5}$$

with $I - 1$ d.f.

For all resource selection statistics α levels were set to 0.05.

3.3.7. Selection ratios

When resource selection statistics revealed that pollock were feeding selectively, we used selection ratios to test the null hypothesis of random feeding on discrete prey categories. Continuing with the Design II protocol of Manly et al. (2002), the estimator of the average selection ratio for the population is given by:

$$\hat{w}_i = \frac{u_{i+} / u_{++}}{\pi_i} \tag{3.6}$$

The variance of (6) is calculated by:

$$\operatorname{var}(\hat{w}_i) = \frac{\sum_{j=1}^{n}\left(\frac{u_{ij}}{\pi_i} - \hat{w}_i u_{+j}\right)^2}{n-1} \times \frac{n}{(u_{++})^2} \tag{3.7}$$

The standard error follows as:

$$\operatorname{se}(\hat{w}_i) = \sqrt{\operatorname{var}(\hat{w}_i)} \tag{3.8}$$

Simultaneous Bonferroni confidence intervals for (3.7) can be constructed with overall confidence level of 100(1 – α)%, so that the probability of all the intervals containing the true value is approximately 1 – α. These intervals are given by:

$$\hat{w}_i \pm z_{\alpha/2I}\operatorname{se}(\hat{w}_i) \tag{3.9}$$

Unlike standard confidence intervals that are centered around zero, these confidence intervals are centered around 1 (Manly et al., 2002, p. 70). In other words, when these intervals include the value 1 there is no selection for or against the prey category. Intervals greater than 1 indicate significant selection for the prey category, while intervals less than 1 indicate significant selection against the prey category.

The difference $(\hat{w}_h - \hat{w}_i)$ between two selection ratios can be estimated by:

$$\operatorname{var}(\hat{w}_h - \hat{w}_i) = \frac{n/(n-1)}{(u_{++})^2} \times \sum_{j=1}^{n}\left(\frac{u_{hj}}{\pi_i} - \frac{u_{ij}}{\pi_i} - \hat{w}_h u_{+j} + \hat{w}_i u_{+j}\right)^2 \tag{3.10}$$

Finally, Bonferroni intervals for (3.10) can be constructed by:

$$(\hat{w}_h - \hat{w}_i) \pm z_{\alpha/2I'}\operatorname{se}(\hat{w}_h - \hat{w}_i) \tag{3.11}$$

where $I' = I(I-1)/2$ is the number of differences that can be calculated between different selection ratios. In this case, intervals that include zero indicate no significant difference between selection ratios.

3.4. Results

3.4.1. Field sampling

Sampled pollock ranged in size from 29.5 to 60.5 cm in April; 28.1 to 54.4 cm in August; and 37.1 to 61.0 cm in November (Table 3.1). In the GOA these size classes can be considered adults (Hughes and Hirschhorn, 1979; Duffy–Anderson et al., 2003).

All April stomachs were sampled from pollock caught in the upper 87 m of the water column (Table 3.1). Four of 40 April stomachs examined were empty and were excluded from all subsequent statistical analyses. Mean fullness was 0.40, eight times higher than minimal feeding.

One August haul occurred at depths greater than 100 m (Table 3.1). Although these data were used in the diet composition analysis, they were excluded from resource selection statistics, as zooplankton samples were only taken in the upper 100 m of the water column. Thus, data from this haul are presented separately in Table 3.1. Two of 9 stomachs from this deeper haul were empty. In the 3 tows < 100 m, 7 of 43 stomachs were empty. All empty stomachs were excluded from the diet composition analysis. Mean fullness for the deeper haul was 0.37, while mean fullness for the tows < 100 m was 0.57. Both values were well above minimal feeding.

All November stomachs were sampled from pollock caught > 100 m (Table 3.1). All 21 stomachs examined contained prey. Mean fullness was 1.02, the highest value observed in all 3 cruises.

Table 3.2 shows that copepods were the most abundant taxon in our study area in April (122.12/m^3) and August (58.04/m^3). Amongst euphausiids, *T. spinifera* had the highest abundance in April (0.95/m^3), while *T. inermis* was more abundant in August (0.86/m^3).

3.4.2. Trophic diversity curves

The trophic diversity curves reached an asymptote around $n = 22$ stomachs in April, $n = 18$ stomachs in August, and $n = 16$ stomachs in November (Fig. 3.2). Thus, samples sizes were considered large enough to evaluate the diet.

3.4.3. Diet composition

Euphausiids were found in 83% of April stomachs (Table 3.3). Decapods and larvaceans ranked 2nd in terms of occurrence at 39%. Euphausiids were also the primary component of the diet in terms of numbers and weight, averaging 59% and 70%, respectively. All but one of the euphausiids identified to species in April stomachs were *Thysanoessa inermis* and *T. spinifera*, with the latter contributing more to the diet at 33% by number and 32% by weight.

Euphausiids were found in 98% of August stomachs (Table 3.3). Copepods ranked 2nd in terms of occurrence at 35%. Euphausiids were also the primary component of the diet in terms of numbers and weight, averaging 84% and 95%, respectively. Once again *T. spinifera* was the dominant euphausiid, averaging 58% by number and 51% by weight. *Euphausia pacifica* entered the diet in August, ranking 2nd amongst euphausiids at 19% by number and 13% by weight.

Decapods were found in all November stomachs (Table 3.3). Amphipods ranked 2nd in terms of occurrence at 33%. Decapods were also the primary component of the diet in terms of numbers and weight, averaging 77% and 96%, respectively. This was largely due to the shrimp *Pandalus borealis*, which averaged 68% and 53% by number and weight, respectively.

The high frequency of occurrence values for the primary prey items in each month indicate that the sampled pollock could be treated as a single feeding unit within each month (Bowen, 1996).

3.4.4. Resource selection statistics

All three null hypotheses were rejected for the April data with respect to taxonomic order (Table 3.4), suggesting that individual fish were not using prey categories in the same proportions, and that prey selection was not in proportion to availability. For the August data, H_{01} was not rejected, indicating that individual fish were selecting prey categories in the same proportions. However, both H_{02} and H_{03} were rejected, suggesting that, on average, fish were not using prey in proportion to availability, regardless of whether individual fish were selecting prey categories in the same proportions.

Amongst euphausiids, H_{01} was not rejected for either the April or August data (Table 3.4), indicating that individual fish were selecting prey in the same proportions in the respective months. However, both H_{02} and H_{03} were rejected for both sets of data, suggesting that, on average, fish were not using prey in proportion to availability in the respective months, regardless of whether individual fish were selecting prey categories in the same proportions.

3.4. Selection ratios

In April there was statistically significant selection for euphausiids and decapods, random feeding on amphipods, larvaceans and pteropods, and significant selection against copepods (Table 3.5). Furthermore, the selection ratio for euphausiids was significantly greater than the selection ratio for all other categories, except larvaceans (Table 3.6). The latter was due to the large amount of variation associated with these two selection ratios, resulting in overlap between the two intervals (Table 3.5). In August there was statistically significant selection for euphausiids, random feeding on amphipods and decapods, and significant selection against copepods (Table 3.5). Larvaceans and pteropods did not appear in the diet at this time. The selection ratio for euphausiids was significantly greater than the selection ratio for all other categories (Table 3.6).

Amongst euphausiids, the selection ratios for April show that there was statistically significant selection for *T. inermis*, random feeding on *T. spinifera* and significant selection against *T. raschii* (Table 3.5). *E. pacifica* did not appear in the diet at this time. The selection ratio for *T. inermis* was significantly greater than the selection ratio for all other categories (Table 3.6). In August there was significant selection for *T. spinifera*, random feeding on *E. pacifica* and other *Thysanoessa* spp., and significant selection against *T. inermis* (Table 3.5). The selection ratio for *T. spinifera* was significantly greater than the ratio for *E. pacifica* and *T. inermis*, but not from other *Thysanoessa* spp. (Table 3.6). The latter resulted from a single occurrence of *T. longipes* in one stomach. The Bonferroni intervals for differences between selection ratios (Eq. 3.11) are particularly sensitive to this situation (Manly et al., 2002).

3.5. Discussion

3.5.1. Field sampling

Various authors have discussed the effect of fishing gear on abundance estimates of gadids (e.g., Godø et al., 1998). Although logistical constraints required us to switch to a commercial scale net for the November cruise, we used the same cod end liner throughout the study to minimize variation in capture efficiency. It should also be noted that the November hauls were not deeper because of the switch to a commercial scale net, but simply because that was where layers of high acoustic backscatter were observed in the 38 kHz.

In the analysis of stomachs contents some prey categories may be underestimated due to rapid digestion times, while others may be overestimated due to slow digestion times (Bowen, 1996). Our stomach fullness values were well above the minimal feeding value, and were within the range of TFI values reported for other gadids (Nielsen and Anderson, 2001; Mello and Rose, 2005). Thus, we considered digestive effects to be minimized.

The seasonal increase in stomach fullness that we observed may at first appear inconsistent with generally accepted models of a decrease in feeding between fall and winter (e.g., Paul et al., 1998). However, we note that off southern Japan, stomach fullness of 30 to 40 cm pollock increases between August and November, and then decreases sharply after November (Yamamura et al., 2002). Thus, it is likely that our November sampling occurred just prior to the expected winter decrease in feeding.

3.5.2. Trophic diversity curves

Trophic diversity in April was almost double what it was in August and November. Other dietary studies of marine fishes have reported relatively consistent trophic diversity throughout the seasons, except in winter (Braccini et al., 2005; Figueiredo et al., 2005). The reduced trophic diversity we observed in August was coincident with a seasonal decrease in the abundance of copepods, decapods and larvaceans, suggesting that this was simply due to reduced availability of these prey categories. Alternatively, there was an increase in euphausiid abundance between April and August, suggesting that some critical density threshold was reached allowing pollock to abandon other prey types in favor of euphausiids. Significant selection ratios for euphausiids in both April and August support this latter explanation.

3.5.3. Diet composition

The primary component of the diet of adult pollock in our study area in April was euphausiids, both in terms of percent numbers and percent wet weight. Euphausiids are also the largest component of the spring diet of 25 to 35 cm pollock in southeast Alaska (Clausen, 1983) and all size classes of adults in the southeastern Bering Sea (Dwyer et al., 1987). However, in the northeastern Bering Sea euphausiids are only the primary prey item for pollock < 40 cm, while larger individuals feed on larvaceans and decapods (Dwyer et al., 1987). Off northern Japan there is interannual variation in the spring diet, with amphipods being the dominant prey item in some years and euphausiids in others (Kooka et al., 1998). Euphausiids are the dominant food item for 30 to 40 cm pollock off southern Japan, while individuals > 40 cm prey on juvenile pollock (Yamamura et al., 2002). Spring feeding on euphausiids appears to be a consistent trend for pollock < 40 cm. In contrast, pollock > 40 cm show geographic variation in the diet. Our study suggests that the northern GOA is one of the areas where all sizes of adult pollock feed primarily on euphausiids in spring.

Euphausiids persisted as the primary prey item of adult pollock in our study area in August. This is consistent with data collected in the northern GOA during the NMFS triennial groundfish surveys in the 1990s (Yang, 1993; Yang and Nelson, 2000). Euphausiids are also the primary component of the diet in the GOA east of our study area (Smith et al., 1978). However, in the western GOA, fishes other than pollock make up 80% of the diet of adult pollock (Duffy–Anderson et al., 2003). In the southeastern Bering Sea euphausiids make up the largest component of the diet of pollock > 40 cm. This is similar to the northeastern Bering Sea, except that individuals > 50 cm cannibalize juveniles in summer (Dwyer et al., 1987). Similarly, in the western Bering Sea euphausiids are the primary food item for pollock < 50 cm, while larger adults prey on juvenile pollock and other fishes (Shuntov et al., 2000). Off northern Japan amphipods are the most frequent prey item (Kooka et al., 1998). Finally, off southern Japan mesopelagic fishes are the dominant prey item for pollock > 30 cm in summer (Yamamura et al., 2002). There is a trend towards piscivory in the summer diet of adult pollock in the western GOA. Previous reports have noted that this does not appear to be the case in the northern GOA (Smith et al., 1978; Yang, 1993; Yang and Nelson, 2000). Our findings provide further evidence that euphausiids are the dominant prey item for adult pollock in summer in the northern GOA.

Amongst euphausiids, *T. spinifera* was the primary species consumed in April and August, both in terms of percent number and weight. This is in contrast with southeast Alaska and the western Bering Sea, where *T. raschii* is the primary euphausiid consumed in spring and summer, respectively (Clausen, 1983, Shuntov et al., 2000). In August, *E.*

pacifica ranked 2nd in terms of both percent number and percent wet weight in our study area. Off southern Japan, *E. pacifica* is the dominant euphausiid consumed by all age classes of pollock (Yamamura et al., 2002). These differences may be explained by the distribution and biology of the respective euphausiids. *T. spinifera* is neritic, being most abundant near shore (Brinton et al., 2000), and so would be readily available on the northern GOA shelf. In contrast, *T. raschii* occurs along the inside passages of southeast Alaska (Brinton et al., 2000), and in the Bering Sea it is particularly abundant in shallower waters (< 100 m) inshore (Coyle and Pinchuk, 2002). Therefore it is not surprising that *T. raschii* would be the dominant euphausiid in southeast Alaska and in the shallow western Bering Sea. *E. pacifica* is an oceanic species found primarily in the major currents of the North Pacific, including the Oyashio (Brinton et al., 2000). Thus it might be expected that this species would be the primary euphausiid in the diet off southern Japan. In the northern GOA *E. pacifica* is most abundant on the outer shelf, but often occur in substantial densities nearshore in late summer, apparently being advected by seasonal onshore transport of sub–halocline water over the shelf (Coyle and Pinchuk, 2005; Weingartner et al., 2005).

Decapods, primarily the shrimp *P. borealis*, were the primary component of the diet of adult pollock in our study area in November, suggesting that a dietary shift occurred sometime between late August and early November. This was coincident with a shift in habitat: all pollock hauls were deeper than 100 m in November, whereas in April and August all but seven stomachs used in the diet composition analysis were from pollock caught in the upper 100 m of the water column. Shrimp are also the primary component of the diet of pollock in southeast Alaska in autumn (Clausen, 1983). However, in the eastern Bering Sea, juvenile pollock are the primary prey item for adults in autumn (Dwyer et al., 1987). In the western Bering Sea euphausiids are the primary component of the diet of adult pollock, except for individuals > 50 cm, which consume primarily fish (Shuntov et al., 2000). Off northern Japan amphipods are the dominant prey item in the fall (Kooka et al., 1998). Off southern Japan mesopelagic fishes are the primary prey item for pollock > 30 cm in fall (Yamamura et al., 2002). The preponderance of piscivory in other geographic areas suggests that shrimp consumption in fall may be a local trend in southeast Alaska and the northern GOA. Indeed, the only region in the GOA where levels of pandalid shrimp consumption remained high throughout the 1990s was our study area (Yang and Nelson, 2000).

Only one instance of piscivory was observed in our study. Previous reports have already noted that fish are not nearly as important in the diet of adult pollock in the northern GOA as compared with the Bering Sea (Smith et al., 1978; Yang, 1993; Yang and Nelson, 2000).

3.5.4. Resource selection statistics

The extreme chi–square values of our resource selection analysis left little doubt that pelagic, adult pollock in our study area were exhibiting prey selection. The chi–square tests provided in Manly et al. (2002) have also recently been used to detect significant differences between environmental and dietary distributions of prey types in marine butterflyfishes (Berumen et al., 2005).

3.5.5. Selection ratios

Adult pollock in our study area showed significant selection for euphausiids and decapods in April, and only euphausiids in August. The confidence intervals developed by Manly et al. (2002) have also been used to detect significant selection in a variety of other marine fishes (Lukoschek and McCormick, 2001; Berumen et al., 2005; Martinetto et al., 2005). Our findings are somewhat consistent with a study off northern Japan, where adult pollock showed positive selection for amphipods in one year, and euphausiids in another (Kooka et al., 1998). Amongst euphausiids, pollock in our study area showed significant selection for *T. inermis* in April and *T. spinifera* in August. Off northern Japan adult pollock showed positive selection for *T. longipes* in the year when there was overall selection for euphausiids (Kooka et al., 1998).

Studies of prey selection by juvenile pollock in the western GOA suggest an ontogenetic shift in selectivity towards euphausiids as predator size and gape width increases (Brodeur, 1998; Wilson et al., 2006). Our findings suggest that selection for euphausiids may persist throughout adult stages in the northern GOA.

Resource selection statistics are designed to detect and measure the degree to which a resource is selected for or against (Manly et al., 2002). If these techniques reveal disproportionate use or avoidance of a resource category then this provides a basis for further study of the mechanisms underlying such selectivity. A variety of factors contribute to prey selection in fishes including encounter rate, prey density, handling time, profitability, mechanical/morphological constraints, competition, predation risk, sensory modalities, hunger and learning (Hughes, 1997).

Laboratory studies have shown that juvenile pollock are capable of both visual and non–visual foraging (Ryer et al., 2002), and that a number of factors affect this behavior, including temperature (Sogard and Olla, 1996), light (Ryer and Olla, 1999), turbidity (De Robertis et al., 2003), predation risk (Ryer and Olla, 1998), social cues (Baird et al., 1991) and prey density (Ryer et al., 2002). Our resource selection analysis allows us to make inferences on the latter two factors with respect to prey selectivity by adult pollock.

When food is spatially clumped juvenile pollock forage in social groups, as this allows individuals to observe each other and rapidly aggregate at locations where food patches have been discovered (Ryer and Olla, 1992). In contrast, when food is spatially dispersed juvenile pollock forage independently, ignoring the behavior of conspecifics (Ryer and Olla, 1995). Our resource selection analysis suggests that this applies to adult pollock as well. While euphausiids often occur in horizontal patches, copepods do not, unless they are passively aggregated by eddies or frontal circulation (Coyle and Pinchuk, 2005). We found significant selection for euphausiids among the local pollock population as a whole, which corresponds to large scale group foraging. On the other hand, while copepods were selected against by the local population as a whole, the high counts of this taxon in relatively few stomachs corresponds to independent foraging by individual pollock, perhaps in the upper 20 m of the water column, where copepod abundance is highest (Coyle and Pinchuk, 2005).

Prey density affects non–visual foraging by juvenile pollock (Ryer et al., 2002). This may explain the apparent discrepancy between the mean abundances of *T. inermis* and *T. spinifera* and the selection ratios for these species. *T. inermis* form dense spawning aggregations in the spring, while *T. spinifera* spawn throughout the production season (Pinchuk, unpublished data). Thus, even though the mean abundance of *T. spinifera* was higher in April, *T. inermis* was more likely to have been encountered in dense spawning aggregations, rendering them more susceptible to large scale predation by pollock once they were detected. Conversely, *T. spinifera* would have occurred in spawning aggregations in August, making them more susceptible to large scale predation once they were detected, even though the mean abundance of *T. inermis* was higher at this time.

In spite of relatively small samples sizes that were limited to a single year, our findings add to the literature that geographic and seasonal variation in the diet of marine fishes must be incorporated into ecosystem based fisheries management strategies (Hanson and Chouinard, 2002). In addition to previous work on prey selectivity by juvenile pollock (Brodeur, 1998; Purcell and Sturdevant, 2001; Sturdevant et al., 2001; Wilson et al., 2006), our resource selection analysis adds to a growing body of evidence that prey selectivity is common in marine fishes (Juanes et al., 2001; Lukoschek and McCormick, 2001; Schabetsberger et al., 2003; Berumen et al., 2005; Martinetto et al., 2005), and that such complex feeding behaviors need to be incorporated into ecosystem based management models as well (Pinnegar et al., 2003).

3.6. Acknowledgements

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3.7. References

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Table 3.1. Trawl catch data for adult walleye pollock, *Theragra chalcogramma*. Trawls: number of tows from which pollock stomach samples were taken. Min HR: minimum headrope depth during trawls. Max FR: maximum footrope depth during trawls. Min FL: fork length of smallest sampled pollock. Max FL: fork length of largest sampled pollock. Stomachs: number of stomachs examined. %Empty: percentage of examined stomachs that were empty. TFI: Total fullness index. Data for the deeper August haul are presented separately. Note that Min HR and Max HR were recorded when the net was at the desired fishing depth and does not include deployment/retrieval.

	Trawls	Min HR (m)	Max FR (m)	Min FL (cm)	Max FL (cm)	Stomachs	%Empty	TFI
April	7	18.3	86.6	29.5	60.5	40	10.0	0.40
August	1	100.6	124.4	37.3	54.5	9	22.2	0.37
	3	18.2	49.4	28.1	39.5	43	16.3	0.57
November	2	100.6	236.0	37.1	61.0	21	0.0	1.02

Table 3.2. Abundance (number/m^3) of zooplankton categories at GLOBEC stations 1 through 4. Prey are grouped by taxonomic order above, while data for Euphausiacea are detailed below. CV: coefficient of variation.

	April		August	
	$\bar{x}$	CV	$\bar{x}$	CV
Order				
Amphipoda	0.05	1.29	0.56	0.71
Copepoda	122.12	0.45	58.04	0.50
Decapoda	0.49	1.63	0.14	1.11
Euphausiacea	1.57	0.89	1.93	0.61
Larvacea	2.95	1.06	0.15	1.51
Pteropoda	1.12	0.62	3.48	0.83
Euphausiacea				
Euphausia pacifica	0.02	1.22	0.44	0.40
Thysanoessa inermis	0.42	1.17	0.86	1.49
Thysanoessa longipes	0.02	0.62	<0.01	1.43
Thysanoessa raschii	0.17	1.74	<0.01	1.41
Thysanoessa spinifera	0.95	1.30	0.62	0.31

Table 3.3. Diet of adult walleye pollock, *Theragra chalcogramma*. n: number of stomachs examined. %FO: percent frequency of occurrence. %N: mean percent composition by number. %W: mean percent composition by weight (g). +: category contained fragments that could not be enumerated.

	April (n = 36)			August (n = 43)			November (n = 21)		
Prey category	%FO	%N	%W	%FO	%N	%W	%FO	%N	%W
Amphipoda									
Byblis spp.	–	–	–	2.33	0.07	0.04	–	–	–
Parathemisto libellula	–	–	–	4.65	1.13	1.11	4.76	0.75	0.03
Parathemisto pacifica	5.56	1.67	0.82	16.28	2.58	0.46	9.52	7.02	0.03
Parathemisto spp.	–	–	–	2.33	0.69	0.04	–	–	–
Primno macropa	–	–	–	2.33	0.06	0.03	–	–	–
Cyphocaris challengeri	–	–	–	–	–	–	9.52	2.63	0.01
Unidentified Amphipoda	–	–	–	–	–	–	9.52	+	0.01
Total Amphipoda	5.56	1.67	0.82	25.58	4.53	1.68	33.33	10.40	0.08
Cephalopoda									
Berryteuthis magister	–	–	–	–	–	–	4.76	1.75	3.37
Copepoda									
Calanus marshallae	27.78	4.91	3.42	27.91	7.97	2.61	4.76	1.75	<0.01
Candacia columbiae	–	–	–	–	–	–	4.76	1.32	<0.01
Eucalanus bungii	2.78	0.02	0.01	2.33	0.14	<0.01	–	–	–
Metridia okhotensis	2.78	0.03	<0.01	–	–	–	–	–	–
Metridia pacifica	–	–	–	4.65	0.66	0.01	–	–	–
Neocalanus cristatus	2.78	0.01	0.02	2.33	0.21	0.06	–	–	–
Neocalanus plumchrus/flemingeri	25.00	12.39	1.94	4.65	1.96	0.12	4.76	1.32	<0.01
Pareuchaeta elongata	–	–	–	–	–	–	4.76	0.88	0.01
Unidentified Copepoda	8.33	+	2.58	–	–	–	–	–	–

Table 3.3 continued.

Total Copepoda	36.11	17.35
Decapoda		
Cancridae megalopae	–	–
Chionoecetes megalopae	8.33	0.78
Crangon communis	–	–
Pasiphaea pacifica	2.78	1.52
Pandalus spp.	–	–
Pandalus borealis	2.78	0.07
Pandalidae zoeae	30.56	5.12
Pinnotheridae megalopae	–	–
Unidentified Caridea	–	–
Total Decapoda	38.89	7.49
Euphausiacea		
Euphausia pacifica	–	–
Thysanoessa inermis	55.56	25.86
Thysanoessa longipes	–	–
Thysanoessa raschii	2.78	0.05
Thysanoessa spinifera	69.44	32.71
Unidentified Euphausiacea	72.22	+
Total Euphausiacea	83.33	58.62
Larvacea		
Oikopleura spp.	38.89	13.93
Pteropoda		
Clione limacina	–	–
Limacina helicina	5.56	0.94

7.96	34.88	10.94	2.80	19.05	5.27	0.01
–	4.65	0.68	0.21	–	–	–
0.14	–	–	–	–	–	–
–	–	–	–	4.76	3.51	0.29
2.77	–	–	–	9.52	6.14	1.67
–	–	–	–	14.29	+	8.05
2.16	–	–	–	80.95	67.67	52.93
1.40	–	–	–	–	–	–
–	2.32	0.06	0.01	–	–	–
–	–	–	–	90.48	+	32.65
6.47	4.65	0.74	0.22	100.00	77.32	95.59
–	53.49	19.32	13.04	–	–	–
20.98	27.91	6.01	4.89	4.76	2.63	0.14
–	2.33	0.63	0.81	–	–	–
0.01	–	–	–	–	–	–
31.93	83.72	57.83	50.47	–	–	–
17.48	67.44	+	26.10	9.52	+	0.72
70.40	97.67	83.79	95.31	14.29	2.63	0.86
13.36	–	–	–	–	–	–
–	–	–	–	4.76	1.32	0.01
0.13	–	–	–	–	–	–

Table 3.3 continued.

Unidentified Pteropoda	2.78	+	0.86	–	–	–	–	–	–
Total Pteropoda	8.33	0.94	0.99	–	–	–	4.76	1.32	0.01
Stomiiformes									
Unidentified stomiiform fish	–	–	–	–	–	–	4.76	1.32	0.05

Table 3.4. Resource selection statistics for hypotheses regarding prey selection by adult walleye pollock, *Theragra chalcogramma*. H_{01}: individual fish used prey categories in the same proportions, regardless of whether selection occurred. H_{02}: prey selection occurred in proportion to availability. H_{03}: on average, fish used prey in proportion to availability, regardless of whether they were selecting categories in the same proportions.

	April				August		
Hypothesis	χ^2 statistic	d.f.	*P*-value	Hypothesis	χ^2 statistic	d.f.	*P*-value
Order							
H_{01}	2584.10	175	$<1.0 \times 10^{-15}$	H_{01}	149.62	175	0.92
H_{02}	16718.84	180	$<1.0 \times 10^{-15}$	H_{02}	2885.68	180	$<1.0 \times 10^{-15}$
H_{03}	14314.74	5	$<1.0 \times 10^{-15}$	H_{03}	2736.06	5	$<1.0 \times 10^{-15}$
Euphausiacea							
H_{01}	123.68	105	0.10	H_{01}	124.62	105	0.09
H_{02}	461.53	108	$<1.0 \times 10^{-15}$	H_{02}	620.01	108	$<1.0 \times 10^{-15}$
H_{03}	337.85	3	$<1.0 \times 10^{-15}$	H_{03}	495.39	3	$<1.0 \times 10^{-15}$

Table 3.5. Selection ratios $\hat{w}_i$, standard errors and simultaneous 95% confidence intervals for adult walleye pollock, *Theragra chalcogramma*. Limits were calculated using the Bonferroni inequality with a confidence level of 99.16% for $I = 6$ prey categories (order) and 98.75% for $I = 4$ prey categories (Euphausiacea). Note that confidence intervals for $\hat{w}_i$ are centered around 1, not zero (Manly et al., 2002): intervals that include 1 indicate no selection for or against the prey category; intervals greater than 1 indicate significant selection for the prey category; and intervals less than 1 indicate significant selection against the prey category.

	April				August			
			Confidence limits				Confidence limits	
Prey category	$\hat{w}_i$	se($\hat{w}_i$)	lower	upper	$\hat{w}_i$	se($\hat{w}_i$)	lower	upper
Order								
Amphipoda	5.45	4.29	0.00[a]	16.75	3.77	1.79	0.00[a]	8.50
Copepoda	0.35	0.11	0.05	0.65	0.06	0.02	<0.01	0.13
Decapoda	6.40	1.89	1.58	11.21	1.98	1.32	0.00[a]	5.47
Euphausiacea	33.23	8.16	11.74	54.72	30.28	1.02	27.58	32.97
Larvacea	8.29	3.88	0.00[a]	18.50	0.00	0.00	–	–
Pteropoda	4.71	3.68	0.00[a]	14.40	0.00	0.00	–	–
Euphausiacea								
Euphausia pacifica	0.00	0.00	–	–	0.77	0.14	0.43	1.11
Thysanoessa inermis	2.12	0.16	1.73	2.51	0.06	0.03	0.00[a]	0.12
Thysanoessa spinifera	0.85	0.09	0.64	1.07	2.47	0.11	2.19	2.75
Other[b]	0.01	0.01	0.00[a]	0.05	0.80	0.85	0.00[a]	2.93

[a] Impossible negative confidence limits were replaced with zero

[b] Includes *Thysanoessa longipes* and *Thysanoessa raschii*

Table 3.6. Significant differences (+) between estimated selection ratios $\hat{w}_i$ for adult walleye pollock, *Theragra chalcogramma*. Note that Larvacea and Pteropoda did not appear in the August diet. Amp: Amphipoda. Cop: Copepoda. Dec: Decapoda. Eup: Euphausiacea. Lar: Larvacea.

	April					August		
Order	Amp	Cop	Dec	Eup	Lar	Amp	Cop	Dec
Copepoda	–					–		
Decapoda	–	+				–	–	
Euphausiacea	+	+	+			+	+	+
Larvacea	–	–	–	–				
Pteropoda	–	–	–	+	–			

	April			August		
Euphausiacea	*E. pacifica*	*T. inermis*	*T. spinifera*	*E. pacifica*	*T. inermis*	*T. spinifera*
T. inermis	+			+		
T. spinifera	+	+		+	+	
Other	–	+	+	–	–	–

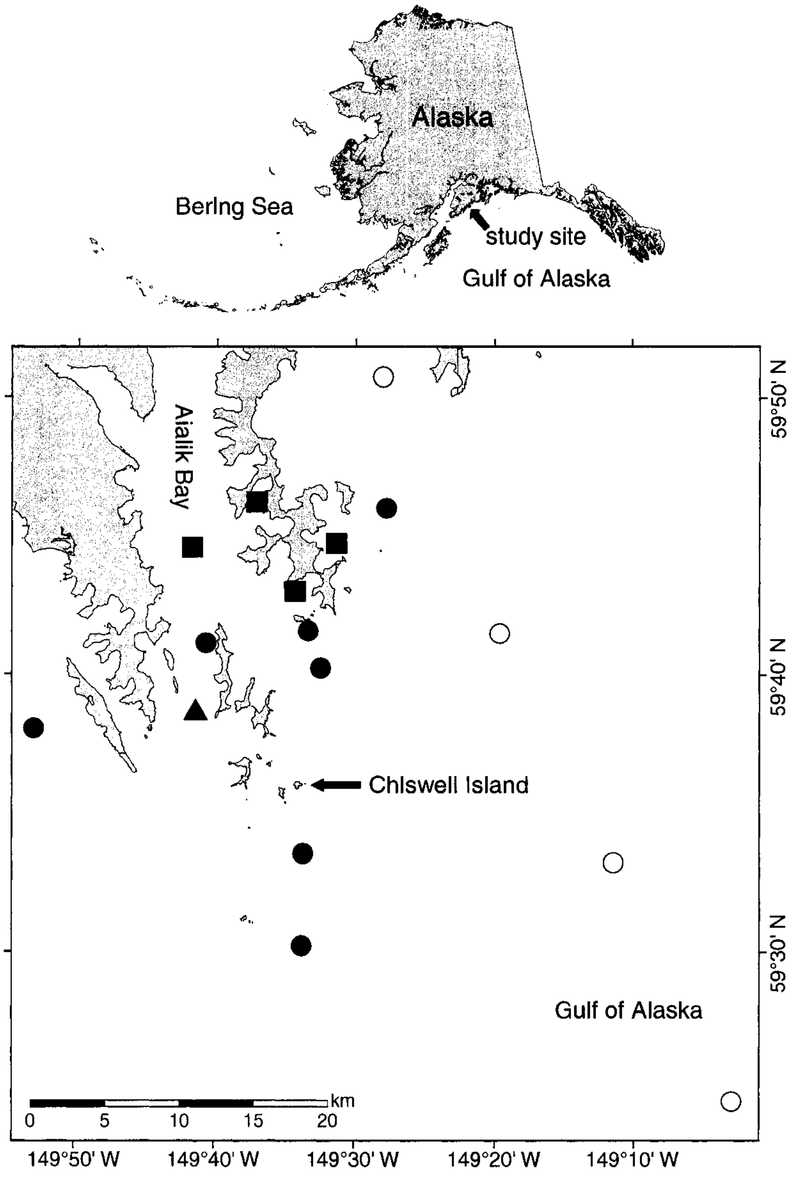

Figure 3.1. General map of Alaska (above), with a close up of the study area (below), centered around Chiswell Island. Trawl stations where pollock stomachs were sampled are shown for April (●), August (■) and November (▲). Empty circles (○) show GLOBEC stations where zooplankton were sampled. Bathymetry contour is 100 m.

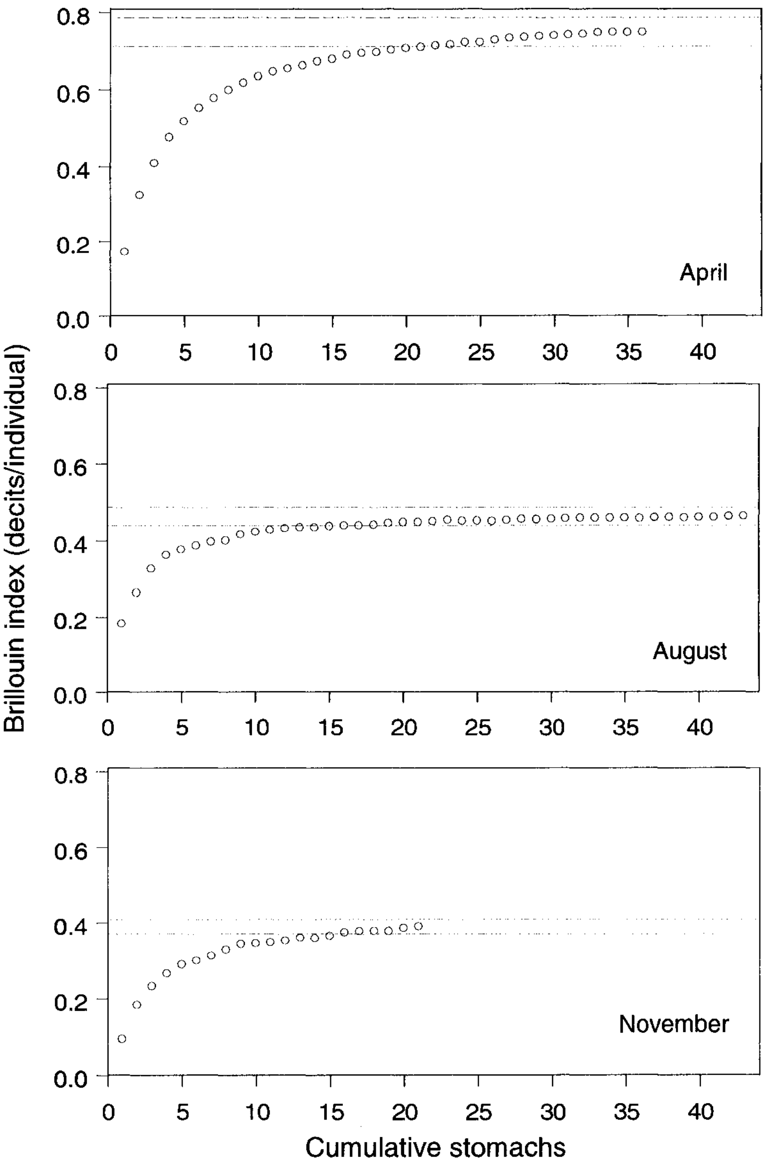

Figure 3.2. Cumulative trophic diversity (H_z) in the diet of walleye pollock, *Theragra chalcogramma*. Dashed lines indicate the range of asymptotic diversity $H_z \pm 0.05\ H_z$.

Appendix 3.1. 95% confidence limits for the diet of adult walleye pollock, *Theragra chalcogramma*. *n*: number of stomachs examined. %N: mean percent composition by number. %W: mean percent composition by weight (g). +: category contained fragments that could not be enumerated. Note that back–transformed confidence limits are biased for the median may not be symmetrical around the means presented in Table 3.

	April ($n = 36$)				August ($n = 43$)				November ($n = 21$)			
Prey category	%N		%W		%N		%W		%N		%W	
	lower	upper	lower	upper	lower	upper	lower	upper	lower	upper	lower	upper
Amphipoda												
Byblis spp.	–	–	–	–	<0.01	0.02	<0.01	<0.01	–	–	–	–
Parathemisto libellula	–	–	–	–	0.01	0.36	0.01	0.33	0.05	0.40	<0.01	0.01
Parathemisto pacifica	0.04	0.65	<0.01	0.28	0.01	1.28	<0.01	0.16	0.46	8.62	<0.01	0.01
Parathemisto spp.	–	–	–	–	0.02	0.18	<0.01	<0.01	–	–	–	–
Primno macropa	–	–	–	–	<0.01	0.01	<0.01	<0.01	–	–	–	–
Cyphocaris challengeri	–	–	–	–	–	–	–	–	0.07	1.81	<0.01	<0.01
Unidentified Amphipoda	–	–	–	–	–	–	–	–	+	+	<0.01	<0.01
Total Amphipoda	0.03	0.65	<0.01	0.28	0.16	2.81	<0.01	0.75	<0.01	13.92	<0.01	11.51
Cephalopoda												
Berryteuthis magister	–	–	–	–	–	–	–	–	0.13	1.01	0.27	2.14
Copepoda												
Calanus marshallae	0.02	4.73	0.01	2.81	0.48	5.64	0.01	1.51	0.13	1.01	<0.01	<0.01
Candacia columbiae	–	–	–	–	–	–	–	–	0.09	0.73	<0.01	<0.01
Eucalanus bungii	<0.01	<0.01	<0.01	<0.01	<0.01	0.03	<0.01	<0.01	–	–	–	–
Metridia okhotensis	<0.01	<0.01	<0.01	<0.01	–	–	–	–	–	–	–	–
Metridia pacifica	–	–	–	–	0.01	0.19	<0.01	<0.01	–	–	–	–
Neocalanus cristatus	<0.01	<0.01	<0.01	<0.01	<0.01	0.05	<0.01	0.01	–	–	–	–
N. plumchrus/flemingeri	0.31	10.72	<0.01	1.04	0.02	0.67	<0.01	0.01	0.09	0.73	<0.01	<0.01
Pareuchaeta elongata	–	–	–	–	–	–	–	–	0.06	0.47	<0.01	<0.01
Unidentified Copepoda	+	+	<0.01	1.11	–	–	–	–	–	–	–	–

Appendix 3.1 continued.

Total Copepoda	1.26	19.69	0.08	7.87
Decapoda				
Cancridae megalopae	–	–	–	–
Chionoecetes megalopae	<0.01	0.30	<0.01	0.05
Crangon communis	–	–	–	–
Pasiphaea pacifica	0.06	0.52	0.19	1.63
Pandalus spp.	–	–	–	–
Pandalus borealis	<0.01	0.02	0.10	0.83
Pandalidae zoeae	0.12	3.60	0.01	0.76
Pinnotheridae megalopae	–	–	–	–
Unidentified Caridea	–	–	–	–
Total Decapoda	0.23	7.37	0.05	5.59
Euphausiacea				
Euphausia pacifica	–	–	–	–
Thysanoessa inermis	7.06	30.33	5.57	21.45
Thysanoessa longipes	–	–	–	–
Thysanoessa raschii	<0.01	0.01	<0.01	<0.01
Thysanoessa spinifera	12.90	43.62	12.51	38.23
Unidentified Euphausiacea	+	+	5.94	20.73
Total Euphausiacea	40.22	80.33	57.95	91.20
Larvacea				
Oikopleura spp.	0.15	12.71	0.65	14.13
Pteropoda				
Clione limacina	–	–	–	–

0.90	9.84	<0.01	2.00	<0.01	4.59	<0.01	3.78
0.01	0.20	<0.01	0.05	–	–	–	–
–	–	–	–	–	–	–	–
–	–	–	–	0.31	2.41	0.02	0.13
–	–	–	–	0.53	7.75	0.05	0.98
–	–	–	–	+	+	0.18	8.79
–	–	–	–	49.98	91.35	29.37	68.02
–	–	–	–	–	–	–	–
<0.01	0.01	<0.01	<0.01	–	–	–	–
–	–	–	–	+	+	16.46	46.34
<0.01	0.25	<0.01	0.05	67.39	97.26	95.86	100.00
5.14	22.21	2.33	13.95	–	–	–	–
0.34	4.13	0.10	2.95	0.21	1.63	<0.01	0.07
0.02	0.16	0.02	0.20	–	–	–	–
–	–	–	–	–	–	–	–
46.22	73.78	34.96	64.05	–	–	–	–
+	+	9.17	31.40	+	+	0.03	0.38
83.04	96.41	96.15	99.89	0.21	1.63	0.01	0.53
–	–	–	–	–	–	–	–
–	–	–	–	0.09	0.73	<0.01	<0.01

Appendix 3.1 continued.

Limacina helicina	0.01	0.35	<0.01	0.04
Unidentified Pteropoda	–	–	0.03	0.25

Appendix 3.1 continued.

Total Pteropoda	0.01	0.35	0.01	0.34
Stomiiformes				
Unidentified stomiiform fish	–	–	–	–

–	–	–	–	–	–	–	–
–	–	–	–	–	–	–	–
–	–	–	–	0.09	0.73	<0.01	<0.01
–	–	–	–	0.09	0.73	<0.01	0.02

Chapter 4 Seasonal effects of light and temperature on the diel vertical migration of walleye pollock (*Theragra chalcogramma*) in the northern Gulf of Alaska[1]

4.1. Abstract

Walleye pollock (*Theragra chalcogramma*) perform diel vertical migration (DVM) as juveniles, but there is an increasing tendency to be associated with the bottom with age. We studied the DVM of a local population of adult pollock at two stations in the northern Gulf of Alaska (GOA) in August and November 2003. In particular we tested the hypothesis that adults followed an isolume (line of equal light intensity) by comparing underwater measurements of light with acoustic records of pollock shoals. We also assessed whether pollock passed through the thermocline during their DVM. There was no significant relationship between the depth of pollock and the isolume necessary for visual foraging in August. Trawl catch data demonstrated that pollock passed through the thermocline during their DVM. In November, however, there was a significant relationship between the amount of pollock biomass above/below the 200 m isobath and the isolume necessary for visual foraging. It is hypothesized that in August adults ignore the isolume and thermocline, simply tracking the movements of their prey (euphausiids) to feed upon them near the surface at night. In November, when euphausiids are no longer in patches, relatively denser pollock shoals migrate up and down with the isolume necessary for visual foraging to feed on decapods.

4.2. Introduction

The phenomenon of diel vertical migration (DVM) in marine fishes has been studied for over half a century. Understanding DVM can advance our knowledge of the interactions among fish, their predators and prey, and the abiotic environment (Neilson and Perry, 1990). Not accounting for DVM can be a source of bias in the estimation of

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[1] Adams, C.F., Foy, R.J., Coyle, K.O. Prepared for submission to Fisheries Research

stock abundance and indices of recruitment (Walsh, 1988). Early studies on DVM hypothesized that Atlantic herring, *Clupea harengus*, follow a line of equal light intensity (isolume) over the 24 h cycle, ascending to the surface at dusk, and descending around dawn (Woodhead, 1966). Subsequent work, however, concluded that fish do not have preferred levels of illumination, but initiate migration in response to changes in brightness (Blaxter, 1975). A brief review of some recent studies will illustrate that this issue remains unresolved.

Among studies that actually recorded underwater measurements of light, the work by Giannoulaki et al. (1999) is notable for their large sample size (~ 150 quantum sensor casts) and statistical analyses that account for the autocorrelation present in times series data. These authors examined the DVM of *Sardina pilchardus* in the Aegean Sea in relation to surface light, bottom depth and changes in ambient light intensity at the depth occupied by the sardines. They found that sardines regulate their position in the water column according to the ambient light intensity when they are not restricted by the sea bed. They also observed that, during the early hours of the day when there is a sudden increase in light over the dark background of the sea, sardines abruptly descended; but later in the day, when light is diffuse and the background light intensity is high, the fish did not change their depth significantly. Thus, they conclude that background luminance is the most important factor for DVM.

In contrast, studies of the pearlside *Maurolicus muelleri* in the fjords and oceanic waters off Norway support the isolume hypothesis. The upper boundary of layers consisting of this species varies according to an isolume of 0.20 to 0.33×10^{-7} $\mu E/s/m^2$ during winter. Furthermore, there is a significant positive correlation between the rate of change of surface light and the migrational velocity of pearlside layers (Baliño and Aksnes, 1993). During summer, pearlside layers continually adjust their position around an isolume of 10^{-3} to 10^{-4} μmol photons/s/m^2 during the day, then migrate upward at dusk to feed at an isolume of 10^{-1} to 10^{-2} μmol photons/s/m^2 (Rasmussen and Giske, 1994). There have also been observations of a rapid increase in the depth occupied by pearlsides at a front characterized by an abrupt increase in fluorescence (chlorophyll a), which caused a “shadow effect” (Kaartvedt et al., 1996). These authors also observed that the demersal gadid, *Trisopterus esmarkii*, was found off the benthos just inside the front, and as shallow as 50 to 100 m further inside the front, where the fish were feeding on the euphausiid *Thysanoessa inermis*.

Amongst gadids there is a relatively consistent pattern of DVM. Pre–recruit Norway pout, *Trisopterus esmarkii*, ascend to the surface at dusk, and descend to the bottom at dawn (Gordon, 1977), while adults only rise about 20 m off the bottom at night (Albert, 1994). Similarly, juvenile Atlantic cod, *Gadus morhua*, ascend to the surface at night (Neilson and Perry, 1990), while adults only rise 25 to 50 m off bottom (Beamish, 1966). In the North Pacific Ocean, walleye pollock, *Theragra chalcogramma* (hereafter referred to simply as pollock), undergo DVM as juveniles, forming dense shoals near the bottom during the day and dispersing up into the water column at night (Smith, 1981). There is a reduction in this behavior with age, as adult pollock are increasingly associated with the bottom (e.g., Duffy–Anderson et al., 2003). However, recent work in the northern Gulf of Alaska (GOA) has found shoals of adult pollock in the upper 40 m of the water column at night feeding on euphausiids (Adams et al., 2007). These findings are in agreement with a report from northern Japan, where adult pollock are sometimes found feeding near the surface at night (Miyashita et al., 2004). Both of these studies suggest that at least some adults undergo DVM.

Although laboratory studies on DVM in juvenile pollock have measured underwater light (e.g., Sogard and Olla, 1996), field studies have generally inferred the role of light through day/night comparisons (Bailey, 1989; Brodeur and Wilson, 1996; Schabetsberger et al., 2000). The only field study to actually measure underwater light found that the best predictor of the mean depth of larval pollock was temperature (Haldorson et al., 1993), which is typically the case for larval fishes (Neilson and Perry, 1990). No study has examined the role of light on the DVM of adult pollock.

The objective of this research was to assess the effect of light and temperature on the DVM of adult pollock. The effect of light was studied by comparing the mean depth (or biomass) of adult pollock with the isolume necessary for visual foraging in juvenile pollock (Ryer and Olla, 1999). Although the minimum amount of light necessary for adults to forage is unknown, the value for juveniles can be used instead, as visual acuity increases with growth in fish (Fernald, 1989). Temperature was examined qualitatively, by noting whether or not pollock passed through the thermocline during their DVM.

4.3. Materials and methods

4.3.1. Study area

The study site (Fig. 4.1) was centered around Chiswell Island (59° 36' N, 149° 34' W), a Steller sea lion (*Eumetopias jubatus*) rookery in the northern GOA, located offshore of the Kenai Peninsula. Bottom topography includes submarine canyons and ridges. Oceanography is characterized by the Alaska Coastal Current, a buoyancy–driven current flowing westward within 40 km of the coast (Weingartner et al., 2002).

4.3.2. Field sampling

Data were collected in August and November 2003 aboard the 23 m F/V Nightwatch. August midwater trawls were done with a Gourock, Inc., research scale net with vertical and horizontal openings of 12 and 22 m, respectively. In contrast, November midwater trawls were done with an LFS, Inc., commercial fishing scale net with vertical and horizontal openings of 26 and 51 m, respectively. However, both nets were outfitted with the same 1.9 cm mesh cod end liner.

Details of acoustic data collection are provided in Adams et al., chapter 2. Briefly, a Hydroacoustic Technology, Inc. (HTI) 38 kHz transducer was used to record the depth of acoustic backscatter believed to be from pollock. The minimum depth of acoustic data collection was 3 m, the maximum depth was 200 m, with depth strata of 1 m. Data were integrated at 15 s intervals. Time, as well as longitude and latitude positions, were recorded with a shipboard global positioning system (GPS) linked to the HTI.

Radiometric data were collected with a Biospherical Instruments, Inc., PRR 2600 profiling reflectance radiometer system, which measures photosynthetically active radiation (PAR), downwelling irradiance and upwelling radiance. PAR is defined as radiation in the 400 to 700 nm waveband, and has units of photons/s/m^2 (Mobley, 1994). Note that this unit is also expressed in the literature as mol photons/s/m^2 or Einsteins/s/m^2, where 1 Einstein = 1 mol photons (6.023×10^{23} photons). The PRR 2600 also measures downwelling irradiance and upwelling radiance at 8 wavelengths: 412, 443, 490, 510, 555, 665 and 683 nm. Radiant flux is the rate of flow of radiant energy, and is denoted by the Watt (Jerlov, 1976). Radiance is the radiant flux per unit steradian, and has units of W/m^2/sr; irradiance is the radiant flux received from all directions and has units of W/m^2 (Jerlov, 1976). Maximum depth of radiometer casts was restricted to the cable length, which was 100 m.

Temperature at depth was recorded with a Sea–Bird Electronics, Inc., model 25–143 CTD, rated to 700 m.

DVM data collection was done as follows. A station was selected based on echosign at 38 kHz suggesting the presence of pollock. This inference was made by comparing the echosign with our own library of echograms collected during previous pollock hauls. We also consulted with the Captain of the F/V Nightwatch, a commercial pollock fisherman. Radiometer casts were done every 10 min from 1 hr before sunset to PM civil twilight, and then again from AM civil twilight to 1 hr after sunrise. Note that civil twilight is defined as the time when the center of the sun is 6° below the horizon (http://aa.usno.navy.mil/). Between radiometric casts the ship's engines were used to put us back on the starting coordinates if the vessel had drifted during the cast. Acoustic data were collected continuously at each station. At the end of a station a midwater trawl was done, aimed at the targets we had been observing during data collection. Up to 200 specimens of each species per tow were retained for shipboard measurements of fork length (FL), while additional fish were counted as they were released. Of the 200 retained fish, a sub–sample of 50 specimens were frozen for length–weight measurements in the laboratory. Finally, a CTD cast was done at the starting coordinates.

4.3.3. Laboratory procedures

FL for all frozen specimens was measured to the nearest mm and weighed to the nearest 0.1 g. As total length (TL) measurements are required for the use of target strength (TS) models, the FL measurements for pollock, capelin (*Mallotus villosus*) and eulachon (*Thaleichthys pacificus*) were converted to TL with the equations provided in Buchheister and Wilson (2005). Similarly, FL measurements for Pacific herring, *Clupea pallasii* (hereafter referred to simply as herring), were converted with the equations provided in Karpov and Kwiecien (1988). Shrinkage due to freezing was also corrected for pollock and eulachon (Buchheister and Wilson, 2005). No such correction exists for herring. Length–weight regressions were calculated for pollock, herring and eulachon. No capelin were collected for laboratory measurements and so the equation provided in Brown (2002) was used to generate a length–weight regression.

4.3.4. Echogram processing

Echo integration data were processed with Echoview software (SonarData Pty. Ltd., Hobart, Tasmania, Australia). Abundance and biomass were estimated according to the methods outlined in Simmonds and MacLennan (2005). Briefly, echograms for a station were partitioned according to the trawl catch for the station using the equation:

$$E_i = \frac{w_i < \sigma_i > E_{\mathrm{m}}}{\sum_{i=1}^{I} w_i < \sigma_i >} \tag{4.1}$$

where w_i is the proportion of species i in the haul, $\langle \sigma_i \rangle$ is the mean backscattering cross–section of species i, I is the total number of species, and E_{m} is the volume backscattering coefficient. TS–length equations of Gauthier and Horne (2004) were used to calculate $\langle \sigma_i \rangle$ for capelin, eulachon, herring and pollock (Table 4.1), with different size classes of pollock derived from length–frequency histograms (Anderson and Neumann, 1996; see chapter 2 for histograms). Although there are no TS–length models for surf smelt (*Hypomesus pretiosus*) currently available, this species is a member of the Osmeridae family, along with capelin and eulachon. Surf smelt and capelin possess a swim bladder, while eulachon do not (Mecklenburg et al., 2002). Thus, we applied the TS–length equation for capelin to surf smelt. Backscatter not attributed to any of these five species was considered "other." Finally, the abundance of species *i* was calculated with:

$$\rho_i = \frac{s_A}{4\pi < \sigma_i >} \tag{4.2}$$

which has units of numbers/nmi^2. This abundance estimate was then converted to kg/nmi^2 using the length–weight regressions described above.

4.3.5. Radiometric data processing

Radiometric data were processed with Profiler software (Biospherical Instruments, Inc., San Diego, California, U.S.A.). Briefly, all files were dark corrected for baseline readings when there is no light (http://www.biospherical.com/BSI%20WWW/Support/FAQs/dark.htm) and then profile plots were inspected for offsets that resulted in negative light readings, or slopes that did not approach zero. In several cases the latter occurred and data for the particular wavelength were omitted from that cast for subsequent analysis.

PAR at depth *z* was calculated as:

$$Ed_z = Ed_0\, e^{-kz} \tag{4.3}$$

where *k* is the attenuation coefficient derived from an exponential fit of the data (Smith and Baker, 1984). Similar calculations were done for each wavelength of downwelling irradiance and upwelling radiance. When fitting these regressions a clear transition zone was observed in the upper 30 m of the water column (Fig. 4.2). In order to accurately calculate light levels below 100 m (the extent of the radiometer cable), only data from below the transition zone were used to derive *k*.

4.3.6. Hydrographic data processing

Temperature (*T*) data were processed with SBE Data Processing software (Sea–Bird Electronics, Inc., Bellevue, Washington, U.S.A.) at 1 m depth bins. The thermocline was calculated for each CTD cast as the depth where dT/dz was maximum.

4.3.7. Data analysis: general

A subset of irradiance data (Tables 4.2 and 4.3) were compared with the respective PAR data to determine if the latter could be used to calculate an isolume as follows. First, the amount of PAR at 30 m was calculated for every radiometer cast where data were available. A depth of 30 m was chosen because it avoided the aforementioned transition zone (e.g., Fig. 4.2). PAR values for a particular station were plotted as a function of time and the slope was determined. This procedure was then repeated for each wavelength of irradiance where there was at least $n = 5$ data points. We then tested whether the slope of PAR and the slope of a given wavelength of irradiance for a particular station were different with a *t* test (Zar, 1999). No significant difference was found between any wavelength of irradiance and the respective PAR data for that station.

There was an even smaller sample size for the radiance data, and a subset (Table 4.2) were compared with the respective PAR data in the same manner as the irradiance data. Once again, no significant difference was found between any wavelength of radiance and the respective PAR data for that station. Thus, we used PAR instead of downwelling irradiance and upwelling radiance for all subsequent data analysis in order to maximize sample size.

The threshold illumination for juvenile pollock to forage visually is 5×10^{-7} $\mu E/s/m^2$ (Ryer and Olla, 1999). Thus, the depth of minimum PAR (minPAR) necessary for visual foraging was calculated for all radiometer casts.

The weighted mean depth (WMD) of biomass was calculated as:

$$\text{WMD} = \frac{\sum_{i=1}^{I} n_i z_i}{\sum_{i=1}^{I} n_i} \tag{4.4}$$

where n_i is biomass at depth stratum i, and z_i is depth stratum i (Giannoulaki et al., 1999; Schabetsberger et al., 2000).

All minPAR and WMD data were checked for normality with a Shapiro–Wilk test prior to subsequent statistical analysis (Zar, 1999). As all data were normally distributed no transformations were required.

All other statistical analyses were done in PROC AUTOREG (SAS Institute, Cary, North Carolina, U.S.A.), which augments the standard linear model $Y = X\beta + \varepsilon$ with an autoregressive model for the random error at time t:

$$\varepsilon_t = \rho\varepsilon_{t-1} + u_t \tag{4.5}$$

where ρ is the autocorrelation parameter estimated along with the regression coefficient β, subject to the constraint that $|\rho| < 1$; and u is an independent normal random variable with mean 0 and variance equal to 1 (Neter et al., 1996).

PROC AUTOREG also provides a Durbin–Watson statistic, which tests whether the error terms are independent. The statistic is given as:

$$D = \frac{\sum_{t=2}^{n} (e_t - e_{t-1})^2}{\sum_{t=1}^{n} e_t^2} \tag{4.6}$$

where e is the residuals from the regression function. A table of lower and upper bounds d_L and d_U for D is then consulted and the decision rule is:

If $D > d_U$, conclude H_0: $\rho = 0$

If $D < d_L$, conclude H_a: $\rho > 0$

If $d_L \leq D \leq d_U$, the test is inconclusive.

A test for negative correlation is also possible using $4 - D$, and if this quantity falls below d_L conclude $\rho < 0$ (Neter et al., 1996). PROC AUTOREG outputs P–values for both positive and negative serial correlation. In the Results we list the P–value for positive correlation, as the P–value for negative correlation is $1 - P$. For example, if the P–value for positive correlation is 0.70 then the P–value for negative correlation is 0.30.

4.3.8. Data analysis: August

Three DVM stations were done in August, but only Three Hole Bay had trawl catch verifying that the observed acoustic sign was indeed pollock (Table 4.4). Data were collected at Three Hole Bay on August 26 (dusk) and August 27 (dawn). Logistical constraints prevented us from doing a trawl after the dawn station. Thus, for data analysis, we assumed that the targets observed during the August 27 dawn station were the same as those collected at the same station approximately 8 hrs earlier as part of the August 26 dusk station.

We tested the null hypothesis H_{01} of no relationship between minPAR and pollock WMD for the August 26 dusk data; the same hypothesis was then tested for the August 27 dawn data. For each station there were sufficient data points to plot a regression of WMD as a function of minPAR. This allowed a direct test of whether the level of illumination necessary for visual foraging could be used to predict the mean depth of pollock. Accepting H_{01} would indicate no relationship between the line of equal light intensity and pollock WMD. Alternatively, rejecting H_{01} would indicate a significant relationship between minPAR and WMD, thereby suggesting that pollock were following the isolume necessary for visual foraging. The hypothesis was tested as follows. For the calculation of WMD pollock biomass was binned at 2 m × 10 min intervals to correspond with the timing of radiometer casts. Biomass data below 150 m were excluded in the calculation of WMD to avoid any potential bias resulting from inconsistent bottom depth. Finally, we tested H_{01} for each station by fitting a regression of WMD (Y variable) as a function of minPAR (X variable) in PROC AUTOREG.

The effect of temperature was assessed qualitatively by noting whether or not pollock WMD passed through the thermocline in the dusk and/or dawn station.

4.3.9. Data analysis: November

Three DVM stations were done in November, two of which had trawl catch verifying that acoustic targets were indeed pollock (Table 4.4). Data were collected at Dora Passage on November 7 (dusk) and Three Hole Bay on November 11 (dawn).

We had to modify our hypothesis for the November data somewhat because pollock were deeper, moving above and below the 200 m isobath. The maximum depth of our acoustic data collection was 200 m, which would have introduced a bias in the calculation of WMD. For example, each calculation of WMD would be weighted toward 200 m as an increasing biomass of pollock continued to rise above the 200 m isobath during dusk data collection. Thus, we calculated the total biomass between 150 to 200 m, assuming that this number would increase over time as pollock migrated upward in the evening. Conversely, we assumed this number would decrease over time as pollock migrated downward in the morning.

We tested the null hypothesis H_{02} of no relationship between minPAR and pollock biomass for the November 7 dusk data; the same hypothesis was then tested for the November 11 dawn data. For each station there were sufficient data points to plot a regression of biomass as a function of minPAR. This allowed a direct test of whether the level of illumination necessary for visual foraging could be used to predict the amount of pollock biomass between 150 to 200 m. Accepting H_{02} would indicate no relationship between the line of equal light intensity and pollock biomass above the 200 m isobath. Alternatively, rejecting H_{02} would indicate a significant relationship between minPAR and pollock biomass, thereby suggesting that pollock were following the isolume necessary for visual foraging. The hypothesis was tested as follows. Pollock biomass data between 150 to 200 m were summed for 10 min intervals to correspond with the timing of radiometer casts. Note that for the November 7 dusk data biomass was summed between 130 to 200, as the top of a clear pollock shoal could be observed at that depth in the latter part of the station. Finally, we tested H_{02} for each station by fitting a regression of biomass (Y variable) as a function of minPAR (X variable) in PROC AUTOREG.

The effect of temperature was assessed qualitatively by noting whether or not pollock WMD passed through the thermocline in the dusk and/or dawn station.

4.4. Results

4.4.1. August

August 26 dusk. Trawl catch from this station was primarily pollock (Table 4.5). Sixty–six percent of the total trawl catch consisted of pollock (Table 4.6) ranging in size from 28.5 to 41.6 cm, which can be considered adults in the GOA (Hughes and Hirschhorn, 1979; Duffy–Anderson et al., 2003). The thermocline occurred at 39 m (Fig. 4.3). Minimum headrope depth during this trawl was 18.3 m, while maximum footrope depth was 43.9 m (Table 4.5). Thus, 81% of the trawl data were obtained above the thermocline. Pollock were assumed to have passed through the thermocline during their ascent.

A regression of WMD as a function of minPAR was not significant ($t(1) = 0.79$, $P = 0.47$) and did not exhibit serial correlation ($D = 1.78$, $P = 0.35$). The null hypothesis H_{01} was accepted, indicating no relationship between the minPAR isolume and the dusk ascent of pollock.

August 27 dawn. Trawl catch data from August 26 dusk were used to partition the echograms for this station (Tables 4.5 and 4.6).

A regression of WMD as a function of minPAR was not significant ($t(1) = 0.72$, $P = 0.50$) and did not exhibit serial correlation ($D = 1.07$, $P = 0.17$). The null hypothesis H_{01} was accepted, indicating no relationship between the minPAR isolume and the dawn descent of pollock.

4.4.2. November

November 7 dusk. Trawl catch from this station was dominated by pollock (Table 4.5). Forty–two percent of the total trawl catch consisted of pollock (Table 4.6) ranging in size from 32.4 to 59.2 cm, which can be considered adults in the GOA (Hughes and Hirschhorn, 1979; Duffy–Anderson et al., 2003). The thermocline occurred at 117 m (Fig. 4.4). Minimum headrope depth during this trawl was 101 m, while maximum footrope depth was 170 m (Table 4.5). Thus, 76% of the trawl data were obtained below the thermocline. Furthermore, acoustic data analysis was done between 130 to 200 m. Pollock were assumed not to have passed through the thermocline during their ascent above the 200 m isobath.

A regression of biomass as a function of minPAR was significant ($t(1) = 4.32$, $P = 0.005$) and did not exhibit serial correlation ($D = 2.38$, $P = 0.54$). The null hypothesis H_{02} was rejected, suggesting that pollock were following the isolume necessary for visual foraging during their dusk ascent above the 200 m isobath.

November 11 dawn. Trawl catch data from this station contained 74% pollock (Tables 4.5 and 4.6) ranging in size from 34.0 to 61.4 cm, which can be considered adults in the GOA (Hughes and Hirschhorn, 1979; Duffy–Anderson et al., 2003). Although the thermocline was calculated as 4 m, a plot of the data shows a gradual decrease in temperature until about 180 m, where it remained around 6° C (Fig. 4.5). Minimum headrope depth during this trawl was 190 m, while maximum footrope depth was 236 m (Table 4.5). Thus, all of the trawl data were obtained from a part of the water column with constant temperature. Pollock were assumed not to have passed through the thermocline during their descent below the 200 m isobath.

A regression of biomass as a function of minPAR was significant ($t(1) = 6.02$, $P < 0.002$) and did not exhibit serial correlation ($D = 3.09$, $P = 0.91$). The null hypothesis H_{02} was rejected, suggesting that pollock were following the isolume necessary for visual foraging during their dawn descent below the 200 m isobath.

4.5. Discussion

4.5.1. Error budget

Various authors have discussed the effect of fishing gear on abundance estimates of pollock in the GOA (e.g., Godø et al., 1998). Although logistical constraints required us to switch to a commercial scale net for the November cruise, we used the same cod end liner throughout the study to minimize variation in capture efficiency.

Acoustically derived biomass estimates contain both sampling error, caused by the measurements being stochastic samples of the true mean density, and systematic error, which affects all the observations equally. Examples of sampling error include survey design, variation in the mean TS over the surveyed region; species discrimination through echogram partitioning; and sampling echogram marks by fishing to provide species proportions (Simmonds and MacLennan, 2005). As these sources of error are applicable to stock assessments we consider such effects to be minimized. Examples of systematic error include equipment sensitivity, transducer motion, the surface bubble layer, etc. (Simmonds and MacLennan, 2005). As the latter affect all measurements equally we consider such effects to be negligible.

The largest source of error in radiometric measurements is orientation of the instrument underwater (Jerlov, 1976). Although the radiometer we used was not mounted on gimbals, we consider the effect of orientation to be minimized because we did not consider individual casts to be absolute measurements, i.e., data for each cast were analyzed as part of a series of data.

4.5.2. Effect of light on DVM

The most obvious trend is that pollock DVM paralleled the isolume necessary for visual foraging in November, but not in August. The first question that comes to mind is whether this was due to seasonal differences in the underwater light environment. The appropriate comparison is between days with similar weather conditions. On August 26 dusk, August 27 dawn and Nov 11 dawn it was 100% cloudy/rainy. PAR values in the hour before (after) sunset (sunrise) were on the order of 10^{-6} μE/s/cm^2 on all 3 days; while downwelling irradiance at 490, 510 and 555 nm was on the order of 10^{-2} to 10^{-3} μW/cm^2 on all 3 days. PAR values 30 min after (before) sunset (sunrise) were on the order of 10^{-7} μE/s/cm^2. As the underwater light environment was roughly the same in August and November, it is clear that light alone cannot explain the seasonal differences in DVM of adult pollock.

4.5.3. Effect of temperature on DVM

The trawl catch data for August 26 dusk clearly demonstrate that pollock had passed through the thermocline during their ascent. In contrast, pollock appear to have stayed below the thermocline on November 7 dusk, although observations were not continued after civil twilight. The lack of a clear thermocline on November 11 dawn makes it difficult to assess the role of temperature, although the targets did appear to have stayed within temperatures around 6° C. Given that pollock passed through the thermocline in August, and assuming they remained in water of relatively constant temperature in November, temperature alone cannot explain the seasonal differences in DVM

4.5.4. Possible biological effects on DVM

The diet and prey selectivity of pollock in our study area has been reported previously (Adams et al., 2007), and likely has a direct bearing on the observed patterns of DVM in the present paper. There was no evidence of cannibalism in our study area, so adult pollock were not rising to within 20 m of the surface in August to feed on juvenile pollock. Pollock consumed primarily euphausiids in August, and the shrimp *Pandalus borealis* in November. Euphausiids typically migrate to the surface at night (Brinton et al., 2000) while shrimp DVM, if it occurs, is diffuse throughout the water column (Barr, 1970). It is our conclusion that the previously reported diet and prey selectivity, in conjunction with the physical factors described in this study, can be used to explain the DVM of adult pollock in the northern GOA.

4.5.5. Synthesis

We propose the following working model to explain the DVM of adult pollock in the northern GOA: in August, adults ignore the isolume/thermocline and simply track the movements of their prey (euphausiids) to feed upon them near the surface at night; in November, when euphausiids are no longer in patches (Alexei Pinchuk, personal communication) denser pollock shoals migrate up and down with the isolume necessary for visual foraging, feeding on decapods. It is important to note that this model does not apply to all adult pollock in the GOA, only those individuals that are vertical migrators.

Feeding is central to our model, as it is to the DVM of juvenile pollock. Bailey (1989) hypothesized that when food is abundant juveniles will remain in warm surface waters to feed and avoid being cannibalized; on the other hand if prey are not abundant juveniles will descend to the bottom at dawn to digest at colder temperatures, where they risk being cannibalized by adults. Similarly, Schabetsberger et al. (2000) concluded that a strategy of "eat and avoid being eaten" most likely explained the DVM patterns of juvenile pollock at a front in the Bering Sea. As cannibalism has not been observed in our study area (Adams et al., 2007), this factor drops out of the equation, further underscoring the importance of feeding in the DVM of adult pollock.

Duffy–Anderson et al. (2003) suggest that adult pollock are unable to pass through thermoclines and are therefore obligate demersals. Our August 26 dusk trawl catch demonstrates that this is not the case, as pollock ascended through an approximately 6° C thermocline. This is consistent with observations of juvenile pollock passing through thermoclines in the GOA (Brodeur and Wilson, 1996)

In the absence of euphausiids, pollock appear to be following the isolume necessary for visual foraging on decapods. This is consistent with observations on the pearlside, which migrates according to the rate of change of light (Baliño and Aksnes, 1993), thus maintaining position around a relatively constant level of light (Rasmussen and Giske, 1994).

Seasonal differences in DVM patterns have also been reported for Atlantic cod. Brunel (1965) found that cod in the Gulf of St. Lawrence performed Type–II DVM in spring, rising during the day and descending to the bottom at night, followed by the more typical pattern of ascending at dusk and descending at dawn later in the season. However, it is important to note that samples in this study were obtained with an otter trawl and gill nets fished simultaneously within 9 m of bottom, and so these patterns are not nearly the same magnitude as what we report here for pollock.

It should be noted that our isolumes of minPAR are deeper than the maximum depths of visual foraging predicted by Ryer and Olla (1999). This is because our measurements were done during crepuscular periods, while their calculations were done for nighttime conditions. It should also be noted that threshold light intensities and depths for visually mediated feeding are prey–species specific (Ryer and Olla, 1999).

There is circumstantial evidence in our data that pollock have evolved to exploit wavelengths of light with the best transmission in coastal waters. The fish eye is differentially sensitive to the various wavelengths of light (Douglas and Hawryshyn, 1990). Looking at Fig. 4.2 one can see that 490 and 510 nm light penetrates the deepest in our study area. The principal visual pigment of pollock occurs at 498 nm (Beatty, 1969). Together, these two things suggest that the visual system of pollock has evolved to exploit the wavelengths of light that will maximize the depths at which pollock can forage visually. It should also be noted that the principal visual pigment of pollock is close to the peak wavelength of light (~ 472 nm) transmitted during euphausiid bioluminescence (Boden and Kampa, 1959). Thus, the pollock eye is well adapted to cue in on this visual signal, and visual foraging may be possible even when there is insufficient ambient light.

Four major hypotheses have been proposed to explain the adaptive significance of DVM in the freshwater environment. The foraging hypothesis predicts that fish will track the vertical migration of their prey, resulting in increased foraging opportunities and higher growth rates (Begg, 1976). The bioenergetic hypothesis predicts that fish will migrate to depths with temperatures that increase digestion rates (Wurtsbaugh and Neverman, 1988) or maximize net growth efficiency (Brett, 1971). The predator avoidance hypothesis predicts that fish will increase survival by migrating to depths that minimize exposure to predators (Eggers, 1978). The antipredation window hypothesis predicts that fish will time their vertical migrations so as to minimize the ratio of mortality risk to feeding rate, and that this window will occur at intermediate light levels, i.e., dusk and dawn (Clark and Levy, 1988). Our working model for the DVM of adult pollock is a descendant of the foraging hypothesis.

The DVM patterns we observed may not be representative of other years. Duffy–Anderson et al. (2003) hypothesize that vertical mingling of different size classes of pollock occurs in the GOA because the shelf is relatively narrow (compared to the eastern Bering Sea), forcing the size classes to "pile up." There were relatively strong year classes of pollock in the GOA in 1999 and 2000 (Dorn et al., 2004), which would have corresponded to age–4 and age–3 fish, respectively, during our study. Thus, the DVM patterns of adults we observed in 2003 may be due in part to the strength of the 1999 and 2000 year classes, causing some adults to migrate to the surface along with younger pollock in August.

In conclusion, we found that adult pollock followed the isolume necessary for visual foraging when euphausiids were not available, but otherwise ignored both light and temperature in pursuit of euphausiid prey. This agrees with the conclusion of Neilson and Perry (1990) that DVM is a facultative process, not an obligate one. Sampling a vertically migrating species both during the day and at night can be a source of bias in the estimation of stock abundance and indices of recruitment (Walsh, 1988). Our findings demonstrate that incorporating seasonal variations in DVM behavior, and ultimately why certain members of the population are vertical migrators, will improve ecosystem based fisheries management.

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Table 4.1. TS–length equations from Gauthier and Horne (2004) used to partition echograms.

Capelin	$24.9 \log L - 75$
Eulachon	$27.3 \log L - 94$
Pacific herring	$13.3 \log L - 55.9$
Walleye pollock	$19.2 \log L - 66$

Table 4.2. Number of casts yielding PAR and downwelling irradiance data (upper), or PAR and upwelling radiance data (lower). Numbers in bold indicate data that were compared with the respective PAR data for a difference in slope.

			Samples			
	PAR	412	443	490	510	555
Aug 26 dusk	7	0	3	4	3	4
Aug 27 dawn	9	0	**6**	**8**	**5**	**7**
Nov 7 dusk	10	**6**	**7**	**9**	**5**	**6**
Nov 11 dawn	9	4	4	**8**	4	**7**
Aug 26 dusk	7	0	0	4	3	1
Aug 27 dawn	9	0	0	**7**	5	2
Nov 7 dusk	10	0	4	**8**	**7**	**7**
Nov 11 dawn	9	0	2	**5**	3	3

Table 4.3. PAR and downwelling irradiance values at 30 m. PAR is in units of μE/s/cm^2 and the three discrete wavelengths (490, 510 and 555 nm) are in units of μW/cm^2. SR: sunrise. SS: sunset.

Date	Time	PAR	490 nm	510 nm	555 nm
26 Aug	2038	5.28×10^{-6}	1.01×10^{-2}	1.08×10^{-2}	8.11×10^{-3}
26 Aug	2048				
26 Aug	2058	2.47×10^{-6}	5.38×10^{-3}		3.69×10^{-3}
26 Aug	2107	3.66×10^{-6}	7.39×10^{-3}	7.39×10^{-3}	4.79×10^{-3}
26 Aug	2118 SS				
26 Aug	2127	1.18×10^{-6}			1.48×10^{-3}
26 Aug	2139	2.29×10^{-7}	6.72×10^{-4}	4.98×10^{-4}	
26 Aug	2149	9.36×10^{-8}			
26 Aug	2159	2.89×10^{-8}			
27 Aug	0556	1.79×10^{-8}			
27 Aug	0606	6.08×10^{-8}			
27 Aug	0615	1.69×10^{-7}			
27 Aug	0626		2.02×10^{-3}	1.34×10^{-3}	
27 Aug	0636	1.12×10^{-6}	2.69×10^{-3}		1.48×10^{-3}
27 Aug	0646 SR	2.05×10^{-6}	5.44×10^{-3}	5.44×10^{-3}	3.49×10^{-3}
27 Aug	0656		8.06×10^{-3}		5.16×10^{-3}
27 Aug	0706	7.12×10^{-6}	1.63×10^{-2}	1.41×10^{-2}	9.96×10^{-3}
27 Aug	0716	8.67×10^{-6}	1.91×10^{-2}	2.02×10^{-2}	1.59×10^{-2}
27 Aug	0726	8.27×10^{-6}	1.81×10^{-2}		1.29×10^{-2}
27 Aug	0736	1.34×10^{-5}	2.72×10^{-2}	2.49×10^{-2}	2.10×10^{-2}
07 Nov	1551	5.23×10^{-5}	1.32×10^{-1}		8.81×10^{-2}
07 Nov	1610	3.74×10^{-5}	9.25×10^{-2}	9.98×10^{-2}	5.13×10^{-2}
07 Nov	1619	3.12×10^{-5}	8.69×10^{-2}	6.89×10^{-2}	3.44×10^{-2}
07 Nov	1629	2.54×10^{-5}	5.26×10^{-2}	5.44×10^{-2}	
07 Nov	1639	1.66×10^{-5}	3.45×10^{-2}	3.36×10^{-2}	1.64×10^{-2}
07 Nov	1649 SS	7.59×10^{-6}	2.09×10^{-2}		7.38×10^{-3}
07 Nov	1700	4.32×10^{-6}	9.41×10^{-3}		
07 Nov	1710	1.03×10^{-6}	3.63×10^{-3}		1.11×10^{-3}
07 Nov	1719	3.45×10^{-7}	9.07×10^{-4}	6.72×10^{-4}	
07 Nov	1729	9.07×10^{-8}			
11 Nov	0757	8.35×10^{-9}			
11 Nov	0808	3.44×10^{-8}			
11 Nov	0817	1.64×10^{-7}	4.78×10^{-4}	3.29×10^{-4}	1.03×10^{-4}
11 Nov	0827	5.24×10^{-7}	1.58×10^{-3}	1.06×10^{-3}	
11 Nov	0837	1.18×10^{-6}	3.31×10^{-3}		4.98×10^{-4}
11 Nov	0848 SR	2.66×10^{-6}	6.12×10^{-3}		1.49×10^{-3}

Table 4.3 continued.

11 Nov	0857				
11 Nov	0907		2.15×10^{-2}		7.39×10^{-3}
11 Nov	0917	7.84×10^{-6}	2.08×10^{-2}	1.63×10^{-2}	7.97×10^{-3}
11 Nov	0927	1.36×10^{-5}	4.16×10^{-2}		1.59×10^{-2}
11 Nov	0937	1.71×10^{-5}	4.41×10^{-2}	3.45×10^{-2}	1.84×10^{-2}

Table 4.4. Summary of DVM stations. OK: denotes that both dusk and dawn data were collected. *: denotes that dusk and dawn data were collected, but analysis revealed that the dusk data were too noisy too extract any useful information.

August	Acoustic data	Light data	Trawl data
Three Hole Bay	OK	OK	Dusk only
Central Aialik	OK	OK	Dusk only; insufficient catch (11 pollock)
Pony Cove	OK	OK	Dusk only; 95% herring (13 pollock)

November	Acoustic data	Light data	Trawl data
Three Hole Bay	OK*	OK*	OK
Dora Passage	Dusk only	Dusk only	Dusk only
Pony Cove	OK	OK	Dusk only; 99% herring (0 pollock)

Table 4.5. Trawl catch data for DVM stations. Min HR = minimum headrope depth during tow. Max FR = maximum footrope depth during tow. Note that Min HR and Max HR were recorded at the start and end of acoustic data collection and do not include deployment and retrieval of the net. Number for each species is presented.

	Min HR (m)	Max FR (m)	Capelin	Eulachon	Herring	Pollock	Surf smelt	Other
8/26 dusk	18.3	43.9	–	–	127	315	–	2[1]
11/7 dusk	100.6	170.1	1	157	12	794	–	1[2]
11/11 dawn	190.2	236.0	–	9	3	288	84	8[3]

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[1] Prowfish (*Zaprora silenus*)
[2] Spiny dogfish (*Squalus acanthias*)
[3] Unidentified eelpouts

Table 4.6. Data used to partition August and November echograms. Note that the August 27 dawn data were partitioned using the August 26 dusk data. Other category is presented so the mix column sums to 100%.

	TS (dB)	TL (cm)	Weight (g)	% mix
Aug 26 dusk				
Age–0 pollock	–48.16	8.5	4.8	4.05
Age–1 pollock	–41.27	19.4	53.0	0.68
Adult pollock	–36.60	34.0	271.4	66.22
Herring	–37.33	24.9	147.6	28.60
Other	NA	NA	NA	0.45
Nov 7 dusk				
Age–0 pollock	–45.21	12.1	13.4	2.46
Age–1 pollock	–39.78	23.2	89.3	37.58
Adult pollock	–35.03	41.0	467.9	42.25
Capelin	–50.21	9.9	5.5	0.10
Eulachon	–58.84	19.4	41.3	16.27
Herring	–42.54	10.1	9.4	1.24
Other	NA	NA	NA	0.10
Nov 11 dawn				
Adult pollock	–34.28	44.9	609.4	73.47
Eulachon	–59.09	19.0	38.7	2.30
Herring	–41.95	11.2	12.9	0.77
Surf smelt	–48.59	11.5	10.4	21.43
Other	NA	NA	NA	2.04

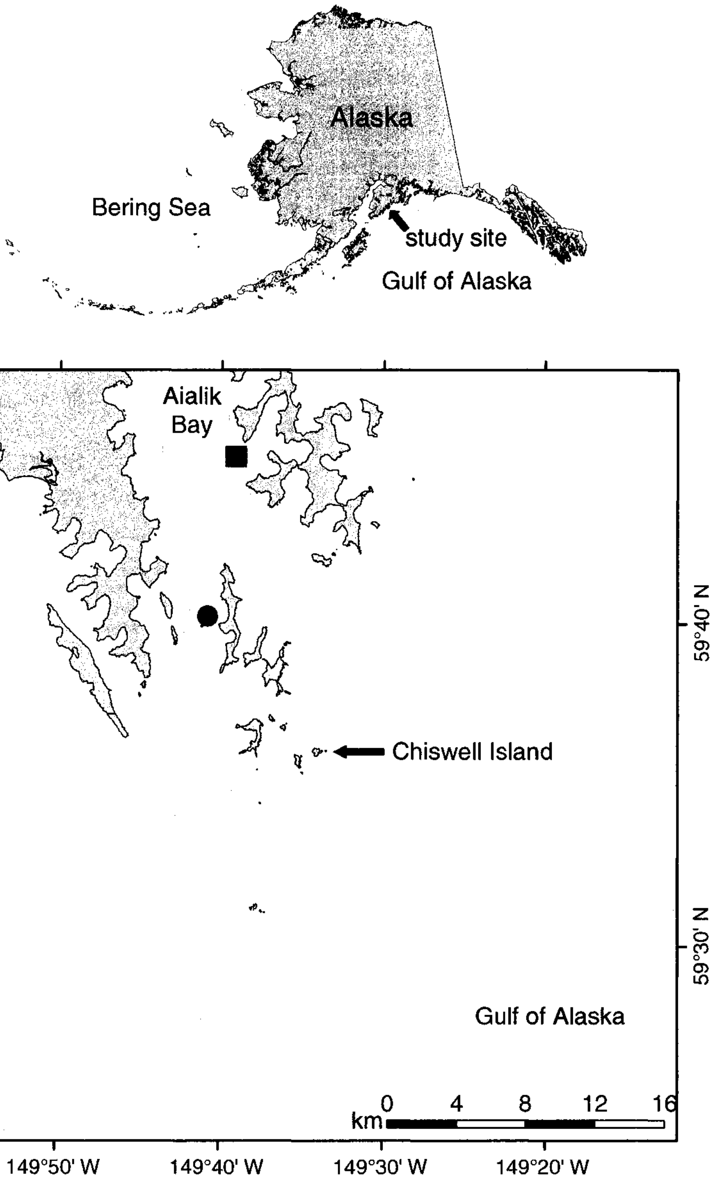

Figure 4.1. General map of Alaska (above), with close up of study area (below), centered around Chiswell Island. The solid black square (■) depicts Three Hole Bay, location of the August 26 dusk, August 27 dawn and November 11 dawn stations. Solid black circle (●) shows Dora Passage, location of the Nov 7 dusk station. Solid bathymetry contour is 100 m, while dashed contour is 200 m.

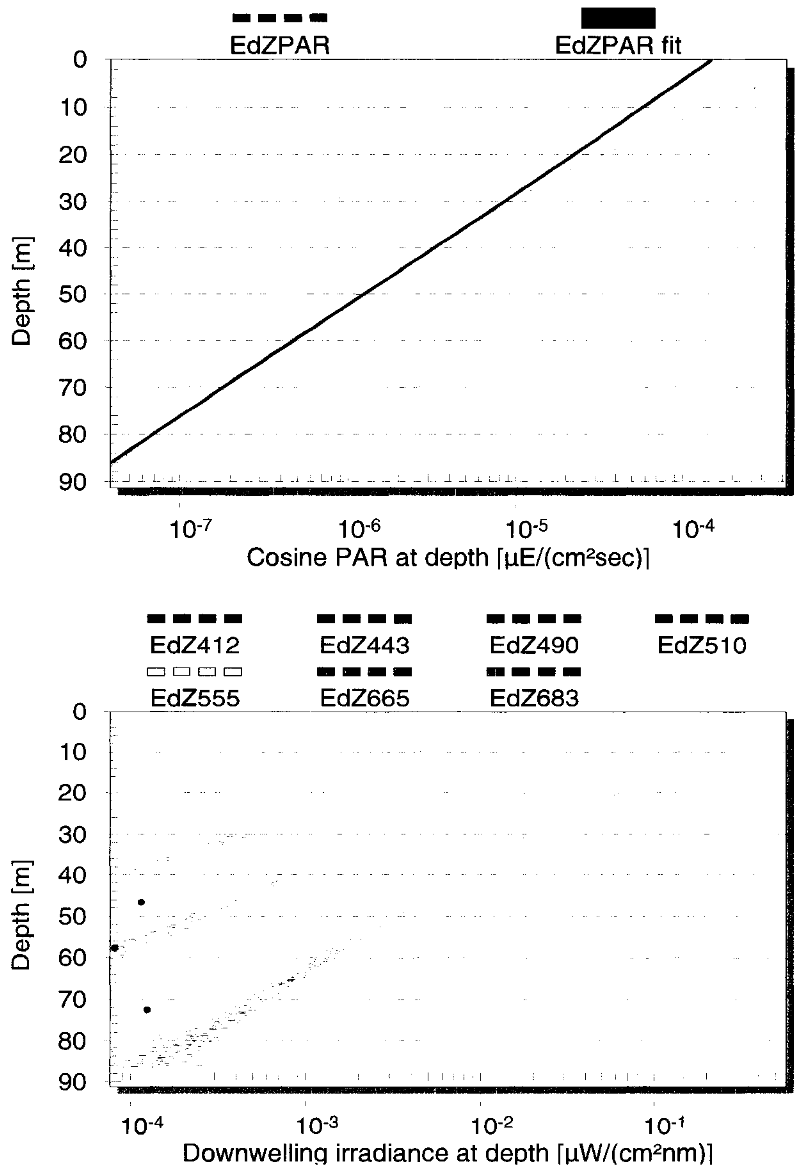

Figure 4.2. Plot of PAR (upper) and downwelling irradiance (lower) illustrating the transition zone in the upper 30 m of the water column. An exponential fit for the PAR data is provided to highlight the increased attenuation that occurred around 30 m. The same pattern can be observed in the irradiance data. Data for both panels were recorded on 27 August 2003 at 07:16 hrs (Alaska Standard Time), 34 min after local sunrise. EdZPAR: PAR. EdZPAR fit: exponential fit to the EdZPAR data. EdZ412: downwelling irradiance at 412 nm. EdZ443: downwelling irradiance at 443 nm. EdZ490: downwelling irradiance at 490 nm. EdZ510: downwelling irradiance at 510 nm. EdZ555: downwelling irradiance at 555 nm. EdZ665: downwelling irradiance at 665 nm. EdZ683: downwelling irradiance at 683 nm.

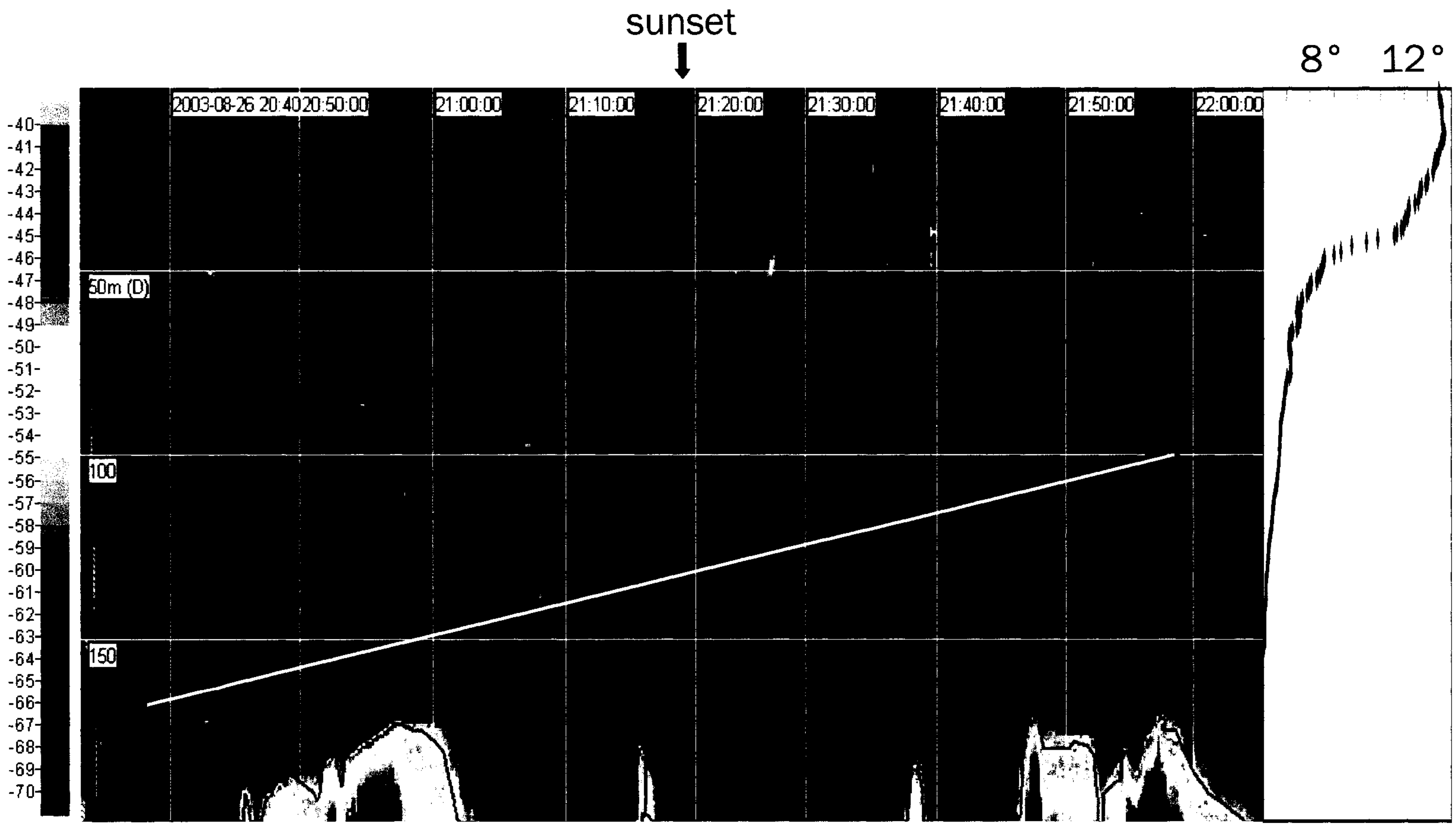

Figure 4.3. Echogram for August 26 dusk. The red line indicates the WMD for pollock biomass, while the yellow line depicts the isolume of minPAR. Color legend is in units of S_v (dB re m^2/m^3). Temperature data, collected to 152 m, are presented on the right.

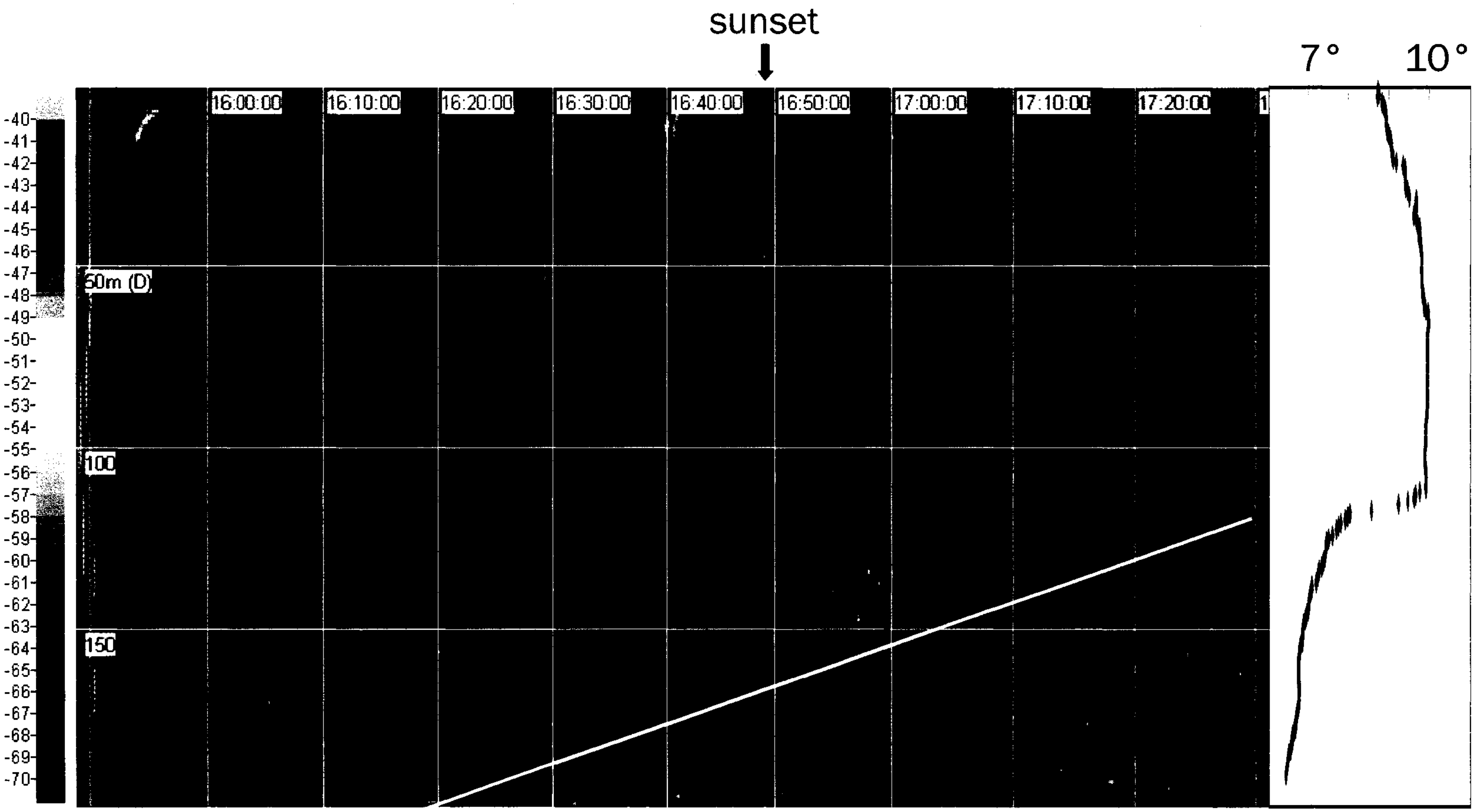

Figure 4.4. Echogram for November 7 dusk. The yellow line depicts the isolume of minPAR. Color legend is in units of S_v (dB re m^2/m^3). Temperature data, collected to 191 m, are presented on the right.

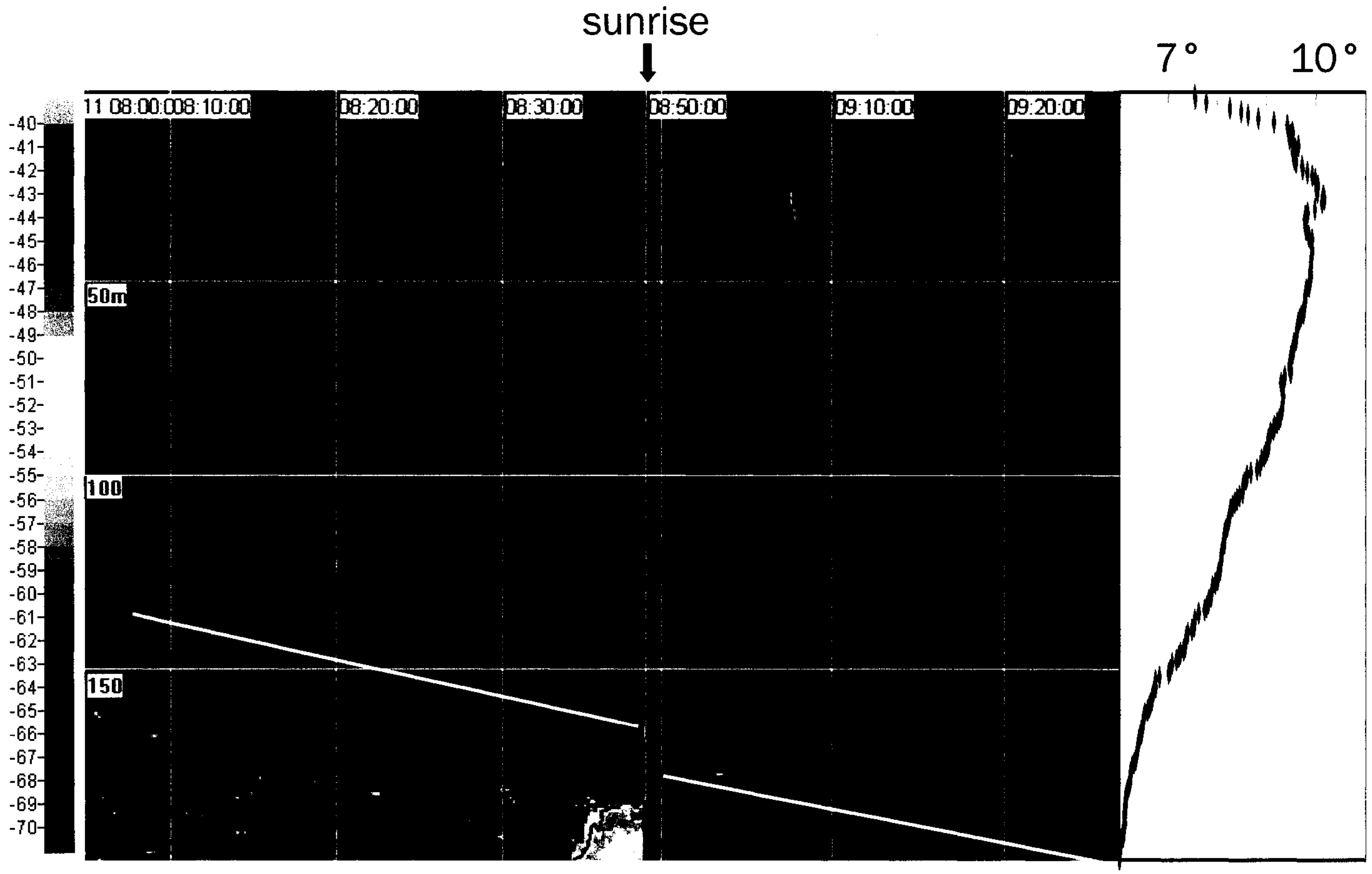

Figure 4.5. Echogram for November 11 dawn. Note the break in acoustic data collection, which is depicted as a discontinuity in the isolume of minPAR (yellow line). Color legend is in units of S_v (dB re m^2/m^3). Temperature data, collected to 227 m, are presented on the right.

Chapter 5 General Conclusions

5.1. Objective 1: Document the vertical distribution of adult pollock within 10 nmi of the Chiswell Island rookery at night

The vertical distribution of adult pollock around Chiswell Island at night was documented primarily through trawl catch data.

Trawls < 80 m in April, and < 50 m in August, suggested that at least some portion of the pollock population was ascending to within 20 m of the surface in spring and summer. In contrast, all November hauls were > 100 m, suggesting that adult pollock were not ascending to the surface at night, and that if they were performing DVM behavior it was occurring at depth.

5.2. Objective 2: Determine the role of prey availability and cannibalism on the DVM of adult pollock

The role of prey availability and cannibalism on the DVM of adult pollock was examined through stomach content analysis, resource selection statistics and comparisons with DVM patterns.

Euphausiids were the primary component of the diet in April and August. Resource selection analysis demonstrated that consumption of euphausiids in both of these months was disproportionate to their availability, relative to other taxa.

Decapods, primarily the shrimp *Pandalus borealis*, were the main component of the diet in November. Although no resource selection analysis was done for this month, it was assumed that pollock shifted their diet due to the absence of euphausiids patches at this time.

It was concluded that prey availability is a key element in the DVM of adult pollock. In April and August they ascend to within 20 m of the surface at night, presumably to feed on vertically migrating euphausiids. In November pollock performed

DVM at depth, presumably to remain within the isolume necessary for visual foraging on decapods.

No evidence of cannibalism was found during the stomach content analysis, and thus this biological factor is assumed not to play a role in the DVM of adult pollock in the northern GOA.

5.3. Objective 3: Determine the role of light and temperature on the DVM of adult pollock

The role of light and temperature on the DVM of adult pollock was examined by comparing acoustic backscatter records with light and temperature data.

Light and temperature did not play a role in the DVM of pollock in August. There was no relationship between the mean depth of pollock and the isolume necessary for visual foraging. Pollock passed through the thermocline during their ascent to the surface.

In contrast, light played a role in the DVM of adult pollock in November. There was a significant relationship between the biomass of adult pollock above the 200 m isobath and the isolume necessary for visual foraging. Pollock did not pass through the thermocline during their ascent (descent) above (below) the 200 m isobath.

5.4. General conclusions

This study has advanced our knowledge of pollock biology with 5 major findings:

1. Clear documentation of adult pollock rising to within 20 m of the surface at night in April and August in the northern GOA.
2. Showing a seasonal shift from feeding on euphausiids in spring and summer to feeding on decapods in late fall. No previous study has examined the spring and fall diets of pollock in the northern GOA.

3. Demonstrating that spring/summer feeding on euphausiids is due to prey selection, not just random feeding. Prey selectivity by adult pollock has not been examined previously.
4. Demonstrating seasonal changes in the role of light on the DVM of adult pollock. No study has ever compared underwater light measurements with the vertical migration of adult or post–larval juvenile pollock.
5. Demonstrating that adult pollock will pass through a 6° C thermocline.

This study has also advanced our understanding of DVM in general, by adding to a growing body of literature that this behavior is a facultative process in marine fishes. Furthermore, insights have been gained on the seasonal effects of physical and biological factors that affect the DVM of adults of a species that is generally thought to be demersal.

This research suggests several possibilities for future studies. The role of light was studied based on the minimum amount of light necessary for visual foraging in juvenile pollock. Laboratory determination of the minimum amount of light necessary for visual foraging by adults is necessary to more adequately address this issue. As visual acuity increases with growth in fishes (Fernald, 1989) it is anticipated that adults would require even less light to forage visually.

Laboratory confirmation of the field observation that adults passed through a 6° C thermocline would also be useful, as this will help to revise current thinking about adults being obligate demersals (e.g., Duffy–Anderson set al., 2003). My own personal observation with captive pollock is that adults will readily pass through a thermocline if food is offered (Adams, unpublished observations).

The importance of prey availability should be addressed further. Stomach contents from pollock sampled before and after the dusk vertical migration will more clearly establish whether pollock undergo DVM in pursuit of euphausiid prey. If pre–vertical migration samples contain no euphausiids, or partially digested euphausiids, while post–vertical migration samples contain fresh euphausiids, this would provide strong evidence that the purpose of DVM in adult pollock is to feed on euphausiids.

Interannual studies are needed to address whether DVM is common to pollock in the region, or whether the observed behaviors were isolated to 2003. Understanding interannual differences in pollock population biology, available prey fields, and oceanographic conditions will provide further insights as to why some individuals in a population undergo DVM, while others do not.

5.5. References

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