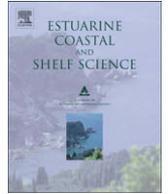




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## Nekton distribution and midwater hypoxia: A seasonal, diel prey refuge?

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## ABSTRACT

Hypoxia affects the distribution of pelagic nekton (i.e., fish and large invertebrates) in both marine and freshwater systems. Bottom hypoxia is common, but midwater oxygen minimum layers (OMLs) also develop in marine offshore regions, fjords, and freshwater lakes. Studies of nekton responses to OML in marine ecosystems have primarily occurred in deep, offshore regions with thick, persistent OMLs. Our study examined the response of pelagic nekton to an OML in a shallow temperate fjord, Hood Canal, WA, U.S.A. Using acoustics, we quantified vertical distribution of nekton at two sites (Hoodsport and Duckabush) before (July) and after (September) OML development. Both Hoodsport and Duckabush had strong OML between 10 and 35 m in September, with lower (minimum  $0.63 \text{ mg L}^{-1}$ ) oxygen levels at Hoodsport compared to Duckabush ( $1.58 \text{ mg L}^{-1}$ ). The OML did not affect daytime distribution of fish or invertebrates, with both occupying depths  $>60 \text{ m}$ . At night in July, with no OML, invertebrates migrated into waters  $<20 \text{ m}$  and fish dispersed to within 15 m of the surface at both sites. In the presence of the September OML, invertebrates migrated into waters  $<20 \text{ m}$ , but the upper limit of fish vertical distribution stopped at the base of the OML (35 m) at Hoodsport. Fish vertical distribution at Duckabush was less pronounced within and above the OML (10–35 m) than it had been in July. Our results suggest that the OML did not affect invertebrate vertical distribution, but did affect fish vertical migration, and may provide a seasonal, diel prey refuge.

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## 1. Introduction

Low dissolved oxygen conditions occur in both marine and freshwater ecosystems. Definitions vary, but water with  $\leq 2 \text{ mg L}^{-1}$  oxygen is generally considered to be hypoxic (Keister et al., 2000; Fontenot et al., 2001). Bottom hypoxia is common, but midwater oxygen minimum layers (OMLs) can also occur in marine offshore regions, fjords, and freshwater lakes (Hutchinson, 1957; Childress and Seibel, 1998; Fujiwara and Yamada, 2002). OMLs in lakes may result from midwater oxygen consumption by zooplankton (Shapiro, 1960) or from hypolimnetic (cold, deep water) oxygenation programs (Fast et al., 1975). In marine offshore regions, OMLs develop due to slow oxygen replenishment relative to biological demand and the presence of slowly circulating, low oxygen source waters (Childress and Seibel, 1998 and references therein). In fjords or marine embayments with sills that limit water exchange, OMLs occur when an inflow of dense water displaces the hypoxic bottom water into the water column (Fujiwara and Yamada, 2002; Arneborg et al., 2004).

Hypoxia can affect the ecology of aquatic systems by altering nekton (i.e., fish and large invertebrates) distributions. Nekton may alter their horizontal and/or vertical locations based on oxygen levels (Horppila et al., 2000; Keister et al., 2000) or modify their schooling/swimming behavior (Bertrand et al., 2006; Taylor et al., 2007). Differences in species-specific oxygen tolerances (Keister et al., 2000; Taylor and Rand, 2003; Bell and Eggleston, 2005) may also separate predators from their prey in low-oxygen refuges (Horppila et al., 2000; Klumb et al., 2004; Bertrand et al., 2006). In offshore marine areas that experience chronic hypoxia, organisms may also develop physiological adaptations to low dissolved oxygen and remain within OML zones (e.g., Childress, 1995; Herring et al., 1998; Cornejo and Koppelman, 2006).

For pelagic species, that undergo diel vertical migration, an OML has the potential to represent both an upper and/or a lower barrier to movement. Unlike offshore marine systems where a persistent, high-volume, OML may facilitate physiological nekton adaptations (e.g., Childress, 1995; Herring et al., 1998; Cornejo and Koppelman, 2006), OML in fjords or marine embayments are seasonal and based on the timing of deep-water renewal (Fujiwara and Yamada, 2002; Arneborg et al., 2004). For that reason, we surmise that an OML in a fjord is more likely to function as a seasonal barrier to nekton vertical distribution as it develops.

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Our study in a shallow (<200 m deep) temperate fjord (Hood Canal, WA) examined the response of pelagic nekton to changing oxygen conditions. The objective was to characterize day and night vertical distributions of nekton before and after the development of an OML.

## 2. Methods

### 2.1. Study site

Hood Canal (Fig. 1) is a fjord in Puget Sound, WA, that has experienced late-summer low dissolved oxygen conditions since the 1950s (Newton et al., 1995). The shallow sill (45 m) precedes a deep channel (120–180 m) and limits water exchange. Residence times, estimated for summer and winter transport scenarios, range from 40 to 250 days (Babson et al., 2006).

### 2.2. Oceanography

Physical oceanography in Hood Canal is regularly monitored through two efforts by the Hood Canal Dissolved Oxygen Program (HCDOP): the Citizen's Monitoring Program (CMP; HCDOP, 2007a) and Oceanic Remote Chemical-optical Analyzer moorings (ORCA; Dunne et al., 2002; HCDOP, 2007b). The CMP collects weekly water column measurements at six stations associated with the University of Washington PRISM program ([www.prism.washington.edu](http://www.prism.washington.edu)). The four ORCA moorings collect multiple water column measurements per day (Dunne et al., 2002). We focused on two sites, Hoodsport and Duckabush (Fig. 1), as dissolved oxygen, temperature, and salinity data were available from either CMP or the ORCA within 12 h of each acoustic survey. Water column depth in the middle of the channel was ~120 m at Hoodsport and ~160 m at Duckabush.

### 2.3. Acoustic surveys

Canal-wide day and night acoustic surveys (~75 km systematic, zig-zag) were conducted during 26–27 July and 13–14 September 2006. For this analysis, ~2 km of transect data from Hoodsport and

Duckabush (Fig. 1) were extracted from the Canal-wide survey, providing a single day and night survey in July and September. Nautical twilight periods (90 min before and after sunset) were avoided. All surveys were performed from the University of Washington Applied Physics Laboratory's R/V Mackinaw (7 m length), operated by the Hood Canal Salmon Enhancement Group. A 38 kHz echosounder (Simrad EK60 38-12; pulse duration 0.512 ms; ping rate  $0.5\text{ s}^{-1}$ ) was deployed at 0.5 m depth on a towed body at a survey speed of  $3\text{ m s}^{-1}$ .

### 2.4. Day/night nekton distribution

Acoustic data were analyzed using two approaches: (1) quantifying the vertical distribution of all nekton (i.e., fish and large invertebrates) and (2) quantifying the vertical distribution of fish using single target detection.

To characterize the vertical distribution of all nekton, water columns at Hoodsport and Duckabush were divided into 2 m vertical bins. Data analysis was restricted to between 4.5 m below the surface and 0.5 m above the bottom due to the presence of acoustic "deadzones" (regions that cannot be accurately assessed with an echosounder; Ona and Mitson, 1996). We applied an  $-80\text{ dB re } 1\text{ m}^{-1}$  threshold to the reflected acoustic energy (i.e., backscatter) measurements, measured as mean volume backscattering strength ( $S_v$ ,  $\text{dB re } 1\text{ m}^{-1}$ ) to remove background noise. An  $-80\text{ dB re } 1\text{ m}^{-1}$  threshold will include invertebrates, such as euphausiids and dense patches of smaller zooplankton, as well as stronger targets such as fish (McKelvey and Wilson, 2006). Thresholded acoustic backscattered energy (nautical area backscattering coefficient (NASC,  $\text{m}^2\text{ nmi}^{-2}$ )) values were exported for each 2 m vertical bin.

Fish vertical distribution was examined by detecting all single targets in the Hoodsport and Duckabush segments. Criteria for single target detection included echo intensity (i.e., target strength,  $\text{dB re } 1\text{ }\mu\text{Pa @ } 1\text{ m}$ ), which provides a relative measure of fish length. Although we did not conduct direct sampling to confirm species composition or length, *in situ* target strength is frequently used as an estimate of relative fish length (Barange et al., 1996). All single targets down to  $-100\text{ dB}$  were detected using Echoview 4.1 software default detection values (Pulse length determination level: 6 dB; Minimum normalized pulse length: 0.8; Maximum normalized pulse length: 1.5; Maximum beam compensation: 6.0 dB; Maximum standard deviation:  $1.0^\circ$ ; SonarData, 2007). After examination of target strength frequency distributions, we selected a  $-65\text{ dB re } 1\text{ }\mu\text{Pa @ } 1\text{ m}$  minimum target strength value for single fish. Based on a published target strength to fish length relationship (Foote, 1987),  $-65\text{ dB re } 1\text{ }\mu\text{Pa @ } 1\text{ m}$  represents a fish length of ~4 cm and should exclude euphausiids and zooplankton (Trevorrow et al., 2005). As single fish cannot be accurately detected if packing density (density of fish within a single transmission volume of the beam) is too high, we used the  $N_v$  index (Sawada et al., 1993) to verify that fish could be detected in dense backscatter regions at Duckabush and Hoodsport. In the calculation of Sawada et al.'s (1993)  $N_v$  index, we used the minimum target strength detected in the 10 m bin immediately below the dense region.

## 3. Results

### 3.1. Oceanography

Oceanographic profiles are presented for Hoodsport (Fig. 2A.i–A.iv) and Duckabush (Fig. 3A.i–A.iv). At Hoodsport, the July day profile was collected at 14:12 (Fig. 2A.i; acoustic data began at 14:30) and the July night profile was collected at 02:13 (Fig. 2A.iii; acoustic data began at 02:30). In September, the Hoodsport day

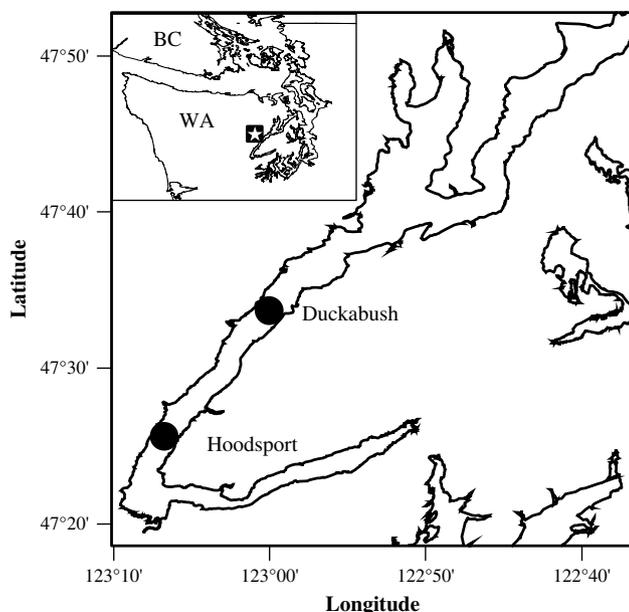
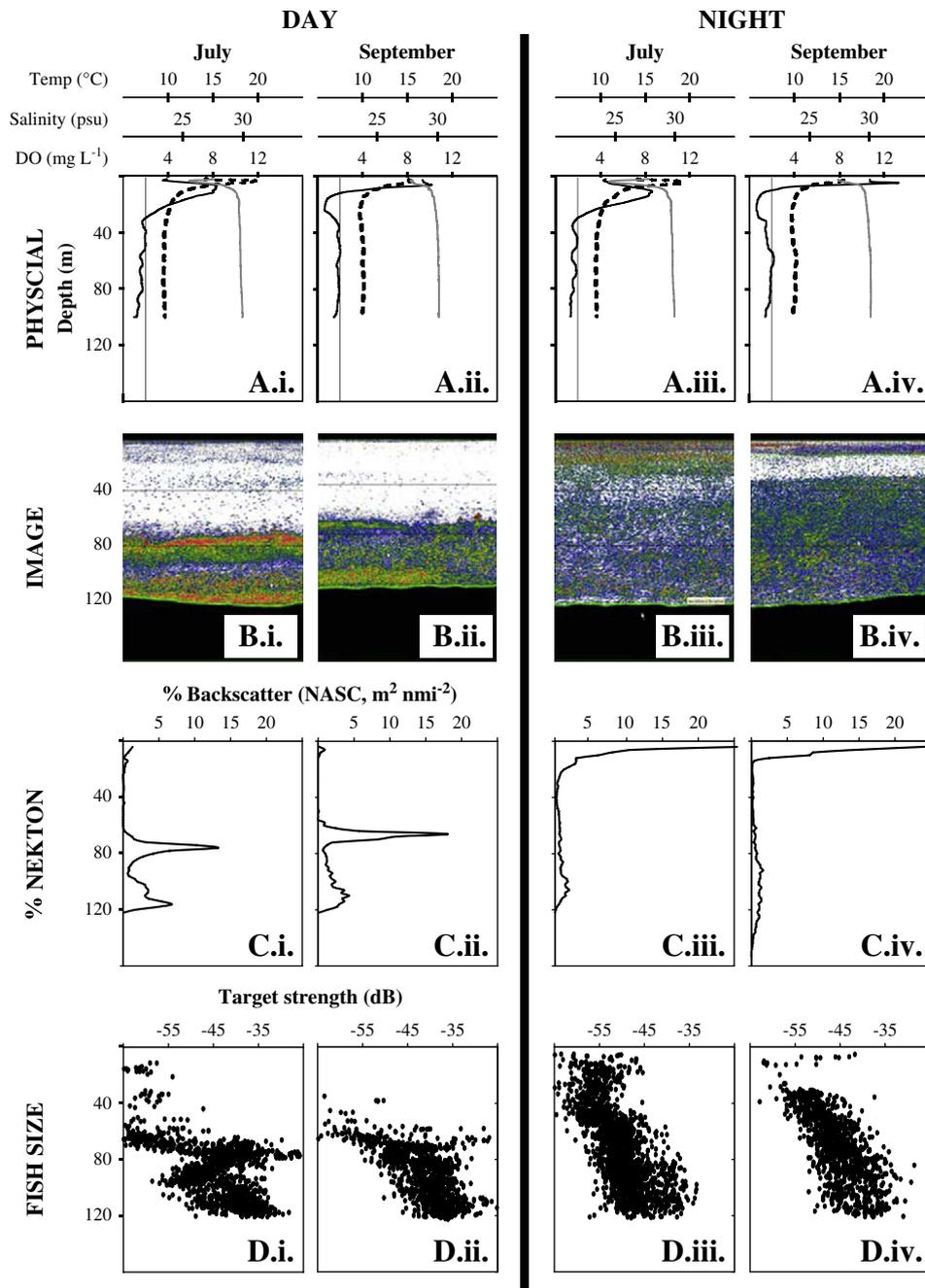


Fig. 1. Map of Hood Canal, WA showing the location of acoustic survey data and oceanographic profiles for Hoodsport and Duckabush (circles) with an inset showing the location of Hood Canal in the Pacific Northwest.

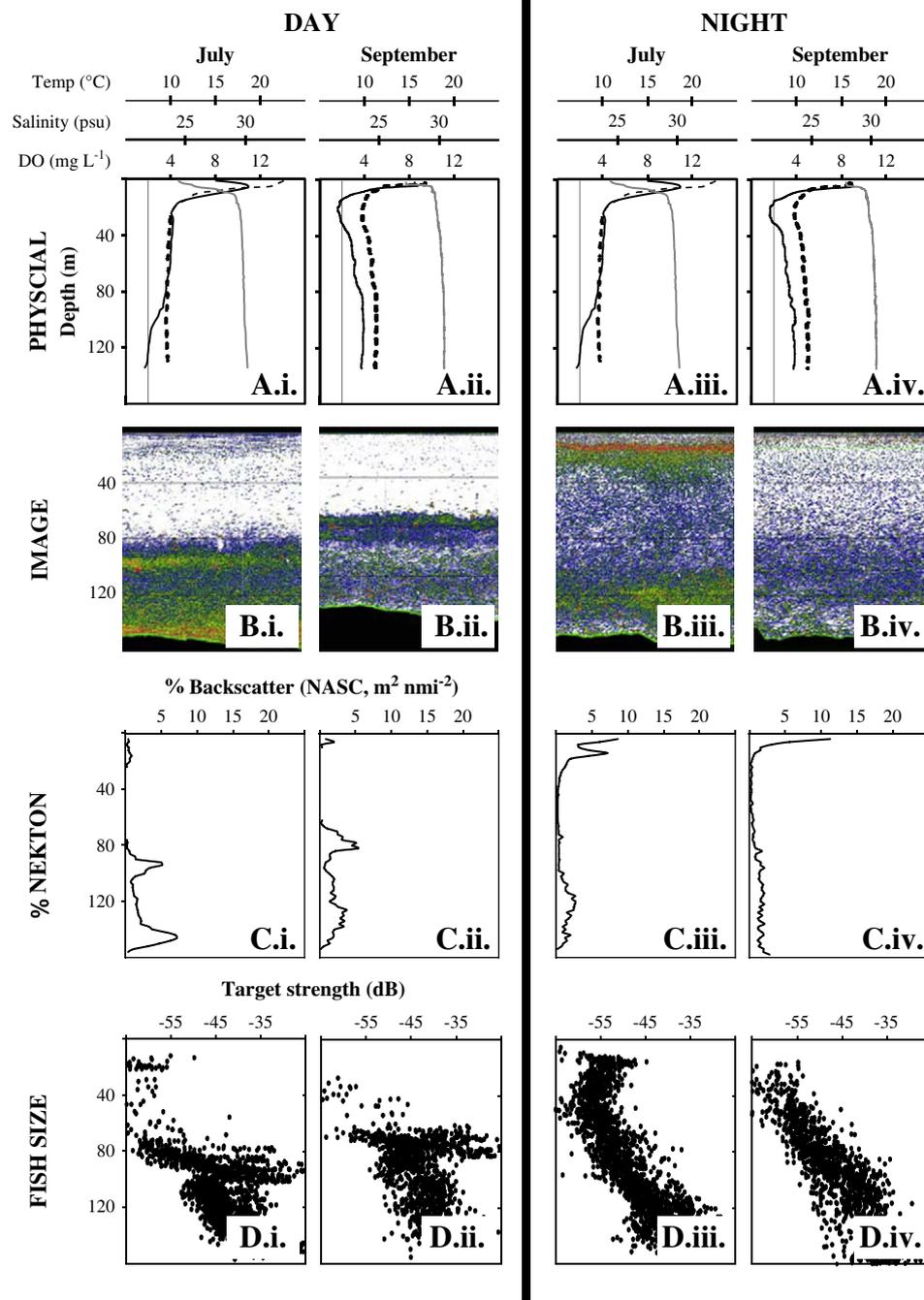


**Fig. 2.** Hoodspout July day (i), September day (ii), July night (iii), and September night (iv) oceanographic profiles (temperature (dashed black), salinity (solid grey), and dissolved oxygen (solid black)) with  $2 \text{ mg L}^{-1}$  hypoxia value marked as fine vertical black line (A), acoustic image with bottom shown as lower black region (B), % depth distribution of nekton (C, % NASC,  $\text{m}^2 \text{ nmi}^{-2}$ ), and individual fish size distribution (D, Target strength, dB).

profile was collected at 10:00 (Fig. 2A.ii; acoustic data began at 14:41), but an equipment problem prevented a night profile. To show the relative stability of the water column, in place of the night profile a profile is shown from a day later (Fig. 2A.iv; acoustic data began at 00:00 on September 14, profile is from 12:12 on September 15). At Duckabush, the July day profile was collected at 17:25 (Fig. 3A.i; acoustic data began at 17:25). As no night profile was available, the day profile, collected at 17:25 (acoustic data began 7.5 h later, at 00:55 the next day), is repeated in Fig. 3A.iii for comparison. In September, the Duckabush day profile was collected at 18:16 (Fig. 3A.ii; acoustic data began at 16:50) and the night profile was collected at 22:16 (Fig. 3A.iv; acoustic data began at 22:00).

Temperature and salinity profiles at Hoodspout and Duckabush were similar within and between months (Figs. 2A.i–A.iv and 3A.i–A.iv). Temperatures at depths  $>20$  m were slightly higher in September than in July at both sites (Fig. 2A.i–A.iv and 3A.i–A.iv). No dominant temperature or salinity features were evident at depths  $>20$  m at either site (Figs. 2A.i–A.iv and 3A.i–A.iv).

In July, both Hoodspout and Duckabush had dissolved oxygen concentrations of  $3\text{--}12 \text{ mg L}^{-1}$  in waters  $<20$  m with gradual declines in oxygen at depth (Figs. 2A.i, A.iii and 3A.i, A.iii). Oxygen concentrations at Hoodspout were below the  $2 \text{ mg L}^{-1}$  threshold at depths  $>40$  m (Fig. 2A.i, A.iii). Oxygen concentrations at Duckabush remained above  $2 \text{ mg L}^{-1}$  throughout the water column (Fig. 3A.i, A.iii). Between July and September, coastal upwelling lead to the



**Fig. 3.** Duckabush July day (i), September day (ii), July night (iii), and September night (iv) oceanographic profiles (temperature (dashed black), salinity (solid grey), and dissolved oxygen (solid black)) with  $2 \text{ mg L}^{-1}$  hypoxia value marked as fine vertical black line (A), acoustic image with bottom shown as lower black region (B), % depth distribution of nekton (C, % NASC,  $\text{m}^2 \text{ nmi}^{-2}$ ), and individual fish size distribution (D, Target strength, dB).

influx of dense bottom water and displacement of existing hypoxic bottom water into the water column (J. Newton, Applied Physics Laboratory, University of Washington, personal communication). In September, an OML zone between 10–35 m was present at Hoodspout and Duckabush (Figs. 2A.ii, A.iv and 3A.ii, A.iv). Hoodspout had lower dissolved oxygen values (minimum  $0.63 \text{ mg L}^{-1}$ , Fig. 2A.ii, A.iv) within the OML than Duckabush (minimum  $1.58 \text{ mg L}^{-1}$ , Fig. 3A.ii, A.iv) in September.

### 3.2. Day/night nekton distribution

Acoustic images illustrate day/night differences in nekton vertical distribution at Hoodspout and Duckabush (Figs. 2B and 3B).

During the day, nekton remained low in the water column regardless of site or survey month (Figs. 2B.i, B.ii and 3B.i, B.ii) and migrated into the water column at night (Figs. 2B.iii, B.iv and 3B.iii, B.iv). The images also illustrate differences in the extent of nighttime migration between July and September.

During the day, the highest proportion of nekton in the water column occurred in deep water (60–100 m) in July and September, regardless of oceanographic profiles (temperature, salinity, and oxygen) at both Hoodspout (Fig. 2C.i and C.ii) and Duckabush (Fig. 3C.i and C.ii). A bimodal nekton distribution was apparent in all daytime surveys (Figs. 2C.i, C.ii and 3C.i, C.ii). Target strengths of single targets, used as an index of fish length, were also comparable between the sites in July (Figs. 2D.i and 3D.i) and September (Figs.

2D.ii and 3D.ii), and coincided with peaks in nekton backscatter (Figs. 2C.i, C.ii and 3C.i, C.ii). Duckabush daytime nekton and fish distributions (Fig. 3C.i, C.ii, D.i, and D.ii) were deeper than the Hoodsport distributions (Fig. 2C.i, C.ii, D.i, and D.ii), possibly due to differences in site depth.

Nighttime vertical migration was evident in July and September at both sites (Figs. 2B.iii, B.iv and 3B.iii, B.iv). Regardless of the OML, most nekton migrated into surface waters <15 m deep at Hoodsport (Fig. 2C.iii and C.iv) and Duckabush (Fig. 3C.iii and C.iv).

Although nekton distribution was similar between surveys, fish vertical distributions differed between July and September nighttime surveys. Our calculation of Sawada et al.'s (1993)  $N_v$  index confirmed that single fish could be detected within regions of dense backscatter ( $N_v < 0.4$  fish per reverberation volume; Gauthier and Rose, 2001). In July, fish dispersed throughout the water column, coming within 10 m of the surface at both sites (Figs. 2D.iii and 3D.iii). During the September OML at Hoodsport (Fig. 2A.iv), the upper limit (~30 m) of the fish nighttime distribution coincided with the base of the OML (Fig. 2D.iv). The Hoodsport echogram contains a gap in backscatter, interpreted as a minimal presence of fish within the OML (Fig. 2B.iv). At Duckabush, where OML dissolved oxygen values were higher than at Hoodsport (Fig. 3A.iv), the distribution of fish to the surface was less pronounced than it was in July, but the upper limit of the nighttime distribution (~17 m; Fig. 3D.iv) did not end as abruptly as at Hoodsport (Fig. 2D.iv).

In both July and September night surveys, the upper peak (<10 m) in the nekton distribution at Hoodsport (Fig. 2C.iii and C.iv) and Duckabush (Fig. 3C.iii and C.iv) did not correspond with a high number of fish (Figs. 2D.iii, D.iv and 3D.iii, D.iv). As fish within the upper nekton peak were acoustically detectable, we surmise that the observed nekton distribution was dominated by backscatter from invertebrates.

#### 4. Discussion

Our study suggests that an OML affected the diel migration and vertical distribution of nekton. Based on evaluation of acoustic data, the OML did not change invertebrate vertical distribution but did affect fish nighttime vertical distribution. In September, the OML acted as an upper boundary to fish vertical migration. As there were no notable changes in either temperature or salinity at the base of the OML, we infer that avoidance of the OML explains the September fish vertical distribution.

Even though we did not sample acoustic targets, past studies in Hood Canal have shown that euphausiids, large copepods, and Pacific herring (*Clupea pallasii pallasii*) vertically migrate. Adult *Euphausia pacifica*, *Metridia pacifica*, and *Calanus pacificus* have been found at depths of 50–150 m in Hood Canal during the day with vertical migrations into surface waters at night (Bollens et al., 1992; Dagg et al., 1998; Hays et al., 2001). Both euphausiids and copepods have been shown to vertically migrate in and out of hypoxic zones in other aquatic systems (Decker et al., 2003; Cuzin-Roudy et al., 2004). Pacific herring also remain in deep water during the day and migrate toward the surface at night in this area (Bollens and Frost, 1991). Herring are considered to be nighttime predators of copepods (Bollens and Frost, 1991) and euphausiids (e.g., Onsrud et al., 2004) in Hood Canal and other ecosystems. Published depth ranges for *E. pacifica*, *M. pacifica*, *C. pacifica* and *C. pallasii pallasii* coincide with our observations of day and nighttime nekton and fish vertical distributions (Bollens and Frost, 1991; Bollens et al., 1992; Hays et al., 2001). As vertical migration observations for zooplankton species have been made between March and October (Bollens et al., 1992; Dagg et al., 1998; Hays et al., 2001), we assume that the same species were present during our July and September sampling. Although limited information exists on fish seasonality in

Hood Canal, the target strength distributions suggest that no major shifts in the fish community (i.e., based on relative fish length) occurred between our July and September sampling.

Species responses to an OML can change energy flow in an aquatic system. Studies of OML suggest that fish may move into shallower (Aku et al., 1997; Horppila et al., 2000) or deeper (Scott, 1931) waters to temporarily avoid low dissolved oxygen. Similarly, pelagic invertebrates may shift into shallower (Herring et al., 1998; Horppila et al., 2000) or deeper (Schram and Marzolf, 1994) waters to avoid the OML, or may use the OML as a prey refuge (Horppila et al., 2000). Horppila et al. (2000) observed that an OML facilitated the coexistence of an invertebrate (*Chaoborus falvicans* within the OML) and a fish predator (*Osmerus eperlanus* above the OML) that feed on common prey. In the absence of the OML, the fish would reduce the *Chaoborus* density through predation (Horppila et al., 2000). When the OML was present, both predators migrated into surface waters at night and depleted the zooplankton prey biomass (Horppila et al., 2000). In contrast, our study found that invertebrates and fish co-occurred in deep water during the day but were separated by the OML at night. The ecological importance of this finding depends on the feeding ecology of the fish. If a high proportion of a fish daily ration is from daytime feeding, the OML would have a reduced effect on energy flow in Hood Canal than if fish were primarily crepuscular/nighttime feeders. While Horppila et al. (2000) found that the OML resulted in a daytime *Chaoborus* prey refuge, our results suggest that the OML in Hood Canal is a seasonal nighttime invertebrate prey refuge.

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