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Spatial and temporal patterns of vertical distribution for three planktivorous fishes in Lake Washington

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Abstract – We sampled three limnetic fish species: juvenile sockeye salmon (*Oncorhynchus nerka*), three-spine stickleback (*Gasterosteus aculeatus*) and longfin smelt (*Spirinchus thaleichthys*) in Lake Washington to quantify species-specific patterns of diel vertical migration (DVM). Catch-per-unit-effort data analysed from 15 years of midwater trawling documented seasonal and diel differences in vertical distributions for each species. These results were consistent with the hypothesis that the patterns of DVM in Lake Washington were affected by life history, size and morphology. Sockeye salmon showed clear DVM in spring but essentially no DVM in fall, remaining in deep water, whereas three-spine sticklebacks were prevalent at the surface at night in both seasons. In fall, distribution patterns may be explained by differences in thermal performance (e.g., sticklebacks favouring warm water), but the patterns were also consistent with inter-specific differences in predation risk. Younger sockeye salmon and longfin smelt were present in greater proportions higher in the water column during dusk and night periods than older conspecifics. Compared with sockeye salmon, the greater use by three-spine sticklebacks of surface waters throughout the diel cycle during weak thermal stratification in spring was consistent with the hypothesis that sticklebacks' armour reduces predation risk, but use of this warmer, metabolically beneficial stratum may also have promoted growth. This study illustrates variation in the vertical distribution of three sympatric planktivores and offers broader implications for the DVM phenomenon and applied lake ecology.

Key words: diel vertical migration; temperature; predator avoidance; planktivores

Introduction

Fish need to feed, but foraging is seldom the only factor, and often not the primary factor, affecting their movements and distribution. Conflicts with reproduction, predator avoidance and optimisation of physiological conditions often limit foraging in time and space (Eggers 1978; Coutant 1985, 1987; Clark & Levy 1988; Appenzeller & Leggett 1995; Beauchamp et al. 1997). The costs and benefits of foraging in a

given area vary among species as a function of life history and among individuals as a function of size or other attributes that make them vulnerable to predation (Levy 1990). The vertical distribution of pelagic fishes can serve as a model for the study of such trade-offs (Clark & Levy 1988; Scheuerell & Schindler 2003; Hardiman et al. 2004; Jensen et al. 2006; Gjelland et al. 2009). Zooplankton densities are often higher in the epilimnion, but planktivorous fishes are more vulnerable to visual predators there than in deeper,

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darker waters where zooplankton are less abundant and detectable. In addition to vertical gradients in food availability and predation risk, vertical temperature gradients differentially affect the metabolic rates of predators and prey, further complicating the trade-offs associated with depth (Magnuson et al. 1979; Brandt et al. 1980; Wurtsbaugh & Neverman 1988). As foraging opportunities and predation risk vary with light levels over the 24-h period, planktivores often show diel vertical migrations (DVM).

Although temperature influences should be secondary to feeding and predation risk during daylight and crepuscular periods, thermal constraints could still be expressed as avoidance of temperatures that were stressful or detrimental to growth when the thermal experience of an individual is averaged over an entire diel cycle. At night, low light levels should inhibit feeding by both planktivorous and piscivorous fishes, so planktivores should occupy depths most beneficial for growth, unencumbered by the need to feed or avoid predators, although clear lakes under either high moon light (Luecke & Wurtsbaugh 1993) or excessive urban light pollution (Mazur & Beauchamp 2006; Kitano et al. 2008) may be exceptions to this pattern. Thermal optima vary among species (Coutant 1977; Magnuson et al. 1979), and the different DVM patterns of sympatric coregonids were best explained by differences in thermal ecology (Mehner et al. 2010). Temperatures above and below the optimum limit growth, but the limitation is generally more severe at incrementally warmer than cooler temperatures (Magnuson et al. 1979). The optimal temperature for growth also shifts to cooler temperatures for larger fish and at lower daily energy intake rates (Beauchamp 2009). These features of physiology suggest that DVM patterns should vary seasonally as a lake stratifies and mixes and as prey availability changes, but this seasonal shift was not observed in two coregonid species (Mehner et al. 2007).

Many fishes show DVM, but the patterns may differ among or within species in a given lake (e.g., Piet & Guruge 1997; Stockwell et al. 2010). Species less vulnerable to predation might be expected to spend more time feeding in profitable epilimnetic waters. The DVM patterns of two coregonids in Lake Superior revealed this pattern, as larger-bodied cisco had a shallower DVM than smaller kiyi (Stockwell et al. 2010). Moreover, fish of the same species may differ in the extent or timing of movement as a function of body size (Levy 1991). For example, a model indicated that older kokanee (nonanadromous sockeye salmon, *Oncorhynchus nerka*) tend to feed at and migrate to deeper depths than younger smaller fish in reservoirs where abundant large piscivorous lake trout *Salvelinus namaycush* imposed significant predation risk to all sizes of kokanee (Stockwell & Johnson

1999; Johnson & Martinez 2000). The opposite pattern was observed in lakes containing less abundant and smaller piscivores, presenting less predation risk for larger kokanee (Levy 1991).

Diel vertical migration of juvenile sockeye salmon has been closely studied in lakes around the Pacific Rim. These fish enter lakes in spring at a size of ca. 28 mm after emerging from gravel nests in streams or lake beaches (Quinn 2005), and they feed chiefly on zooplankton in the limnetic zone. They prey on large zooplankton if available (Eggers 1982) and display DVM to balance their foraging needs with predator avoidance (Eggers 1978; Clark & Levy 1988; Scheurell & Schindler 2003). Predator avoidance, prey distribution and temperature all affect the timing of movement and depth distribution (Brett 1971; Clark & Levy 1988; Levy 1990, 1991; Beauchamp et al. 1997). Because salmonids and their predators are primarily visual foragers, feeding should be confined to daylight and crepuscular periods, and their vertical distribution should be influenced by trade-offs between predation risk and the profitability of feeding at any given depth.

Lake Washington, in Washington State, USA, serves as a model body of water for comparative work on DVM. The lake's thermal regime and zooplankton community are well studied (Arhonditsis et al. 2004; Winder & Schindler 2004; Hampton et al. 2006a,b; Winder et al. 2009), as is the basic biology of the major planktivores (Chigbu 2000; Beauchamp et al. 2004). The lake has a narrow littoral zone and so the limnetic zone is the primary habitat, dominated by three planktivorous fishes native to the region (juvenile sockeye salmon, three-spine stickleback *Gasterosteus aculeatus* and longfin smelt *Spirinchus thaleichthys*), and two native midwater piscivores (cutthroat trout, *O. clarki*, and northern pikeminnow, *Ptychocheilus oregonensis*). Densities of *Daphnia* spp. are significantly higher in the upper 10 m of the water column than at deeper depths during both thermally stratified and destratified seasons (Edmondson & Litt 1982); therefore, the DVM patterns of the different planktivores determine their access to zooplankton.

The overall objectives of this study were to (i) quantify variation in planktivore catch-per-unit-effort (CPUE) related to season, diel period and depth and (ii) evaluate whether the diel vertical distributions of planktivores are similar among species and size classes of fish in Lake Washington. We predicted that the armoured species (three-spine stickleback) would exhibit shallower distributions throughout the diel cycle than the un-armoured species (longfin smelt and sockeye salmon) because they may be more willing to accept predation risk. Additionally, we expected to observe shallower distributions throughout the diel cycle for the shorter-lived longfin smelt than the

longer-lived and potentially more risk-averse, sockeye salmon. With respect to bioenergetic responses, we predicted that all three species should exhibit similar vertical distribution patterns during the cooler, weakly stratified period in April, but that juvenile sockeye salmon would occupy deeper, cooler strata than three-spine sticklebacks during the warmer fall stratification period. The range of near-optimal temperatures for juvenile sockeye salmon ($\geq 90\%$ maximum growth rate when food is unlimited at 8.0–19.5 °C; Beauchamp 2009) occurs over a cooler and broader range than the warmer, narrower range for three-spine sticklebacks ($\geq 90\%$ maximum growth rate when food is unlimited at 19.0–22.5 °C; Lefébure et al. 2011). Thermal optima are unknown longfin smelt, but the species is distributed farther to the south than sockeye salmon (i.e., to the Sacramento River), suggesting that they are more tolerant of warmer water. With respect to size within species, we evaluated the alternative hypotheses that (a) larger fish would forage more cautiously (i.e., move up in the water column later and be deeper overall) because they are already large and so have less to gain energetically, or (b) they would forage less cautiously because their larger size makes them less vulnerable to gape-limited visual predators.

Methods

Study site

Lake Washington is 32.2 km long, averages 2.5 km wide and has a maximum depth of 66 m. Thermal stratification in the lake begins in March and April, is fully established by late June–early July and persists through October, after which decreasing temperatures and wind destratify the lake through winter. From 1998 to 2010, surface temperatures (0–2 m) in April (spring) averaged 11.0 °C and bottom temperatures (52–54 m) averaged 7.3 °C (Fig. 1). October (fall) temperatures averaged 15.4 °C at the surface and 8.4 °C at the bottom. Dissolved oxygen levels during our study remained $>5 \text{ mg}\cdot\text{l}^{-1}$ throughout the water column, except in some years during August–November when localised benthic levels of 3–5 $\text{mg}\cdot\text{l}^{-1}$ were recorded at 50–60 m depths (King County Department of Natural Resources, WA, unpublished data).

The primary crustacean zooplankton species in the lake include the cladoceran *Daphnia pulicaria* and the copepods *Cyclops bicuspidatus*, *Leptodiptomus ashlandi* and *Epischura nevadensis*. *D. pulicaria* typically achieve moderate to high densities (5–35 organisms per l) from mid-May through November but are often below detection levels during winter and early spring (Hampton et al. 2006a,b). Copepod densities during winter and early spring are highly variable among years with either *C. bicuspidatus* or *L. ashlandi* pre-

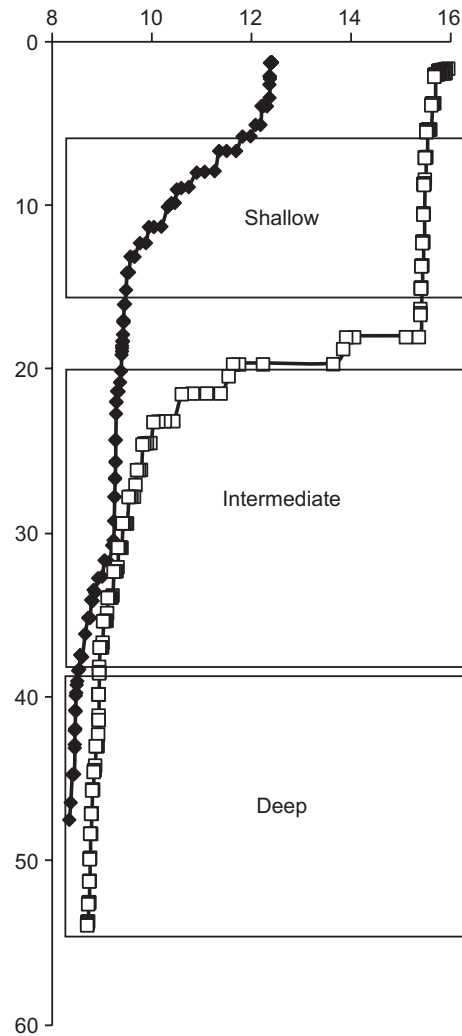


Fig. 1. Spring (April, solid diamonds) and fall (October, open squares) water temperature profiles from the sampling site in Lake Washington in a typical year (2005). Rectangles indicate the modal depth bins where fish were sampled.

dominating in the zooplankton assemblage (4–30 organisms per l for the predominant species; Beauchamp et al. 2004; Winder et al. 2009). In general, the dominant zooplankton (i.e., *D. pulicaria*) do not vertically migrate and are most dense in the upper 10 m of the water column and very scarce below 20 m, regardless of season (Edmondson & Litt 1982).

Fish sampling

From 1997 to 2011, sampling was conducted in the central basin of Lake Washington, east of Sand Point in water ca. 50 m deep from 14 to 26 April and 11 to 29 October. These months incorporate several ecological patterns. In April, juvenile sockeye salmon are present in two age classes, age-0 [fry, ca. 30–50 mm

fork length (FL)] and age-1 (fish *ca.* 110–130 mm FL that will migrate to sea later that spring; Fig. 2). Longfin smelt are present as age-1 fish (*ca.* 60–90 mm FL), because the age-2 fish have already spawned in rivers and died by this time of year while young-of-the-year have not yet recruited to the lake. In October, age-0 sockeye salmon (*ca.* 100–120 mm FL) are the only age class present, but both age-0 (*ca.* 40–60 mm FL) and age-1 (90–110 mm FL; Fig. 2) longfin smelt are present. Catches of limnetic three-spine sticklebacks are low in April because they breed in the littoral zone in late spring, but they are vulnerable to trawling in fall. In addition to these fish community dynamics, April and October present contrasts in thermal regime (cooler and weakly stratified in April; warmer and strongly stratified in October (Fig. 1)) without dramatic differences in overall prey availability. Zooplankton sampling from 25 m to the surface in the afternoon and at night on each date when fish were sampled revealed mean densities of 17.2 organisms

L^{-1} in spring and 13.3 in fall. The dominant taxa were *D. pulicaria*, *C. bicuspidatus*, *Bosmina* sp., *Epischura* sp. and *L. ashlandi* (T.P. Quinn, unpublished data). *D. pulicaria* were proportionally less abundant in April, although this varied among years. Independent sampling farther south in the lake revealed similar patterns. The mean depth-stratified densities (± 2 SE) of edible crustacean zooplankton during 2000–2007 were the following: $32.6 \pm 20.0 l^{-1}$ in 0–10 m and $19.6 \pm 8.9 l^{-1}$ in 10–20 m during April (1% *Daphnia*) versus $16.4 \pm 3.6 l^{-1}$ in 0–10 m and $11.3 \pm 2.1 l^{-1}$ in 10–20 m during October (31–38% *Daphnia*; D.E. Schindler, University of Washington, unpublished data).

Fish were captured using a Kvichak midwater trawl from 1997 to 2011, deployed for 15 min at three depths from mid-afternoon to night (Table 1). The net, held open by two horizontal metal bars, had a 2.5 m \times 2.5 m cross-section and mesh decreasing from 76- to 2-mm knotless mesh in the cod end. Diel

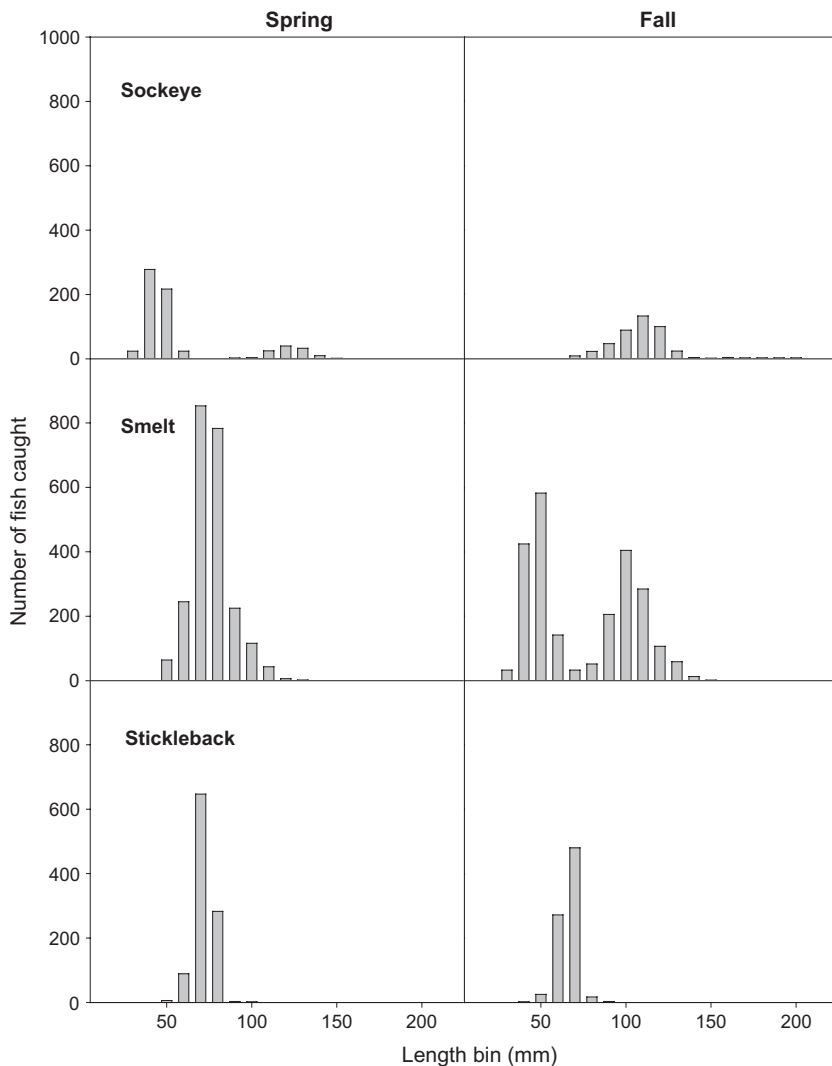


Fig. 2. Length frequency histograms for the three planktivore species sampled in Lake Washington in spring (April) and fall (October), pooling all samples from 1997 to 2011.

Table 1. Midwater trawl effort from 1997 to 2011, expressed as minutes towed (numbers of tows in parentheses) categorised by season, depth and period of the day.

Season	Depth category	Total trawl minutes (N tows)		
		Day	Dusk	Night
Spring	Shallow	679 (46)	317 (21)	151 (10)
	Intermediate	668 (45)	245 (16)	73 (5)
	Deep	811 (54)	226 (15)	105 (7)
Fall	Shallow	200 (14)	75 (5)	276 (19)
	Intermediate	247 (17)	46 (3)	293 (20)
	Deep	285 (20)	86 (6)	237 (16)

periods were categorised as day (before sunset), dusk (sunset to 1.5 h after sunset) and night (>1.5 h after sunset). Trawl depths were categorised as shallow (6–15 m), intermediate (20–38 m) and deep (38–54 m; depths shown in Fig. 1). Thermal exposure for fish averaged 9.5–12.0 °C in spring versus 15.5 °C in fall at shallow depths, 9.5 °C in spring versus 10–12 °C in fall at intermediate depths, and 8.5 °C in spring versus 9.0 °C in fall at deep depths. All captured fishes were counted in the field and measured to the nearest millimetre (FL) except in 2 years, when very large catches of age-0 longfin smelt were subsampled for length.

Catch analysis

To examine the general patterns in planktivore distribution, we calculated the mean number of fish caught per minute trawled across years for discrete depth × diel × season sampling cells. Catch data were normalised in this manner to account for slight variation in tow time and differences in effort across sampling cells (Table 1). We used generalised linear models (GLMs) to determine the relative importance of depth, diel period and season in explaining variation in planktivore CPUE for individual species. Model parameter coefficients were used to support species-specific patterns in diel vertical distribution. We then examined the CPUE data graphically, to describe differences in diel vertical distribution patterns among species and ages.

Many tows caught no fish; therefore, we used a delta approach to model CPUE because it is appropriate for zero-inflated data (Helsler et al. 2004; Maunder & Punt 2004). CPUE was modelled as a function of environmental variables in a two-stage process. First, the probability of capturing a species (i.e., frequency of occurrence in tows) was estimated using a GLM with a binomial error distribution. Then, the CPUE for nonzero tows was modelled using a negative binomial GLM with a log-link function. Thus, the overall CPUE may be determined as the product of the probability of a nonzero catch and the

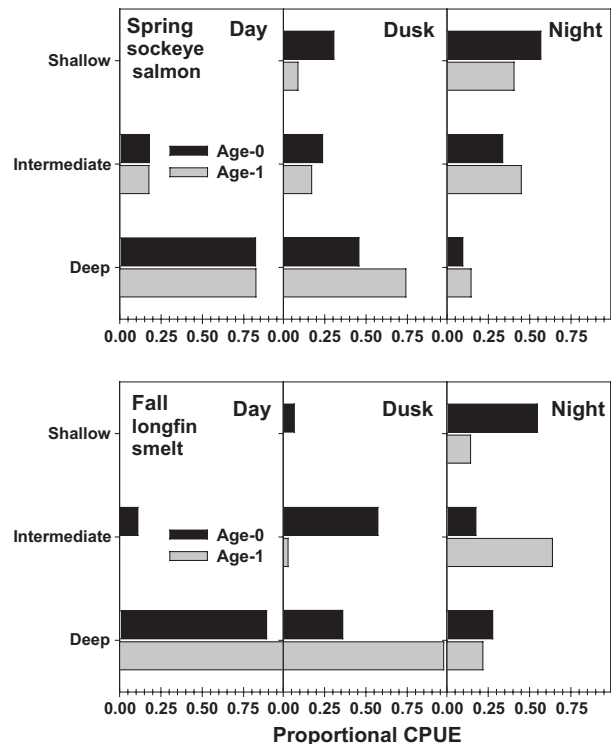


Fig. 3. Diel vertical distributions of age-0 and age-1 sockeye salmon in the spring (top) and longfin smelt in the fall (bottom). Catch-per-unit-effort (CPUE, $N \cdot \text{min}^{-1}$) was standardised by the total CPUE for each age class × diel period.

expected CPUE, given that the catch was nonzero. Models were fit separately to data for the three species. Age-0 and age-1 fish were combined in the analyses due to small sample sizes for individual age classes; however, we present graphical summaries of age-specific diel vertical distributions (Fig. 3).

Eight GLMs were evaluated for each species, including the null model (intercept only) and all possible combinations of three discrete predictor variables: depth (shallow, intermediate and deep); diel period (day, dusk and night); and season (fall and spring). Models provided reasonably good fits to the data; estimated dispersion parameters ranged from 0.60 to 1.43, indicating little evidence of over- or under-dispersion (Helsler et al. 2004). Additionally, diagnostic plots of deviance residuals versus fitted values from the full models showed constant variance, and half-normal plots of the residuals showed no outliers (Faraway 2006).

For each stage of the analytical process described earlier, we compared the eight candidate models using Akaike's information criteria, bias-corrected for small sample size (AICc), which balances model complexity (number of estimated parameters) with the goodness of fit, as determined by likelihood (Burnham & Anderson 2002). The ΔAICc was calculated for each model as its AICc minus the lowest AICc across all

models; by convention, models with $\Delta AICc$ within two of the minimum $AICc$ are classified as performing equivalently to the best approximating model (Burnham & Anderson 2002). We calculated the Akaike weight (w_i) for each model, interpreted as the weight of evidence (probability) that model i is the best approximating model from among the set of candidate models (Johnson & Omland 2004). As w_i approaches one, the weight of evidence in favour of model i increases (Burnham & Anderson 2002). The relative importance of each predictor variable j (w_j) was estimated by summing w_i across all models in the set that included variable j ; the closer w_j is to 1, the more important the variable in predicting the response across all models (Burnham & Anderson 2002).

Results

Longfin smelt were the most abundant species caught by midwater trawling during spring and fall sampling periods (71.7% of all fish caught), followed by three-spine stickleback (18.6%) and sockeye salmon (9.7%). Season, depth and diel period were important predictors of frequency of occurrence and density (nonzero CPUE) for all three species, based on their inclusion in the set of best approximating models (Table 2). For all species, observed spatial-temporal patterns in CPUE (Figs 4 and 5) were supported by coefficient values from best-fit models; coefficient estimates from the full models indicate the magnitude and direction of the effect of each parameter on planktivore CPUE (Table 3). For example, slope coefficients estimated from the full model for sockeye (Table 3) increased from day to night periods; this mirrors the graphical trend in sockeye CPUE (Fig. 4). Qualitative differences in patterns of age-specific CPUE were apparent in spring for sockeye salmon and in fall for longfin smelt. Generally, younger fish were caught in larger proportions higher in the water column during dusk and night periods than older conspecifics (Fig. 3).

Juvenile sockeye salmon demonstrated a seasonal shift in diel vertical distribution patterns. During spring, CPUE was highest in deep water during the day, intermediate depths at dusk and shallow depths at night (Fig. 4), whereas in the fall the highest CPUE was in deep water across all diel periods (Fig. 5). In both seasons, the frequency of occurrence and density increased dramatically from afternoon to dusk and night. Variation in sockeye salmon occurrence was related strongly to season, depth and diel period ($w_j = 1.0$); however, diel period and depth were more important than season in dictating the density of sockeye (Table 4). Sockeye salmon were encountered less frequently in fall surveys than in the spring but were captured in similar densities (nonzero CPUE) across seasons (Table 3).

Table 2. Diagnostic statistics for generalised linear models describing the relationships between catch-per-unit-effort (CPUE) and environmental factors. CPUE was modelled using a two-stage process, first estimating the probability of capturing a species (a) and then modelling the CPUE given that the species was caught (b). $AICc$ is Akaike's information criteria bias-corrected for small sample size, $\Delta AICc$ is the $AICc$ for each model minus the lowest $AICc$ from all possible models, and w_i is the model Akaike weight.

	(a) Frequency of occurrence			(b) CPUE, nonzero tows		
	$AICc$	$\Delta AICc$	w_i	$AICc$	$\Delta AICc$	w_i
Sockeye salmon						
<i>Model parameters</i>						
Depth + Diel + Season (full model)	332.0	0.0	1.00	821.9	2.2	0.22
Depth + Diel	367.1	35.0	0.00	819.7	0.0	0.67
Depth + Season	423.8	91.7	0.00	838.2	18.6	0.00
Depth	431.5	99.5	0.00	849.2	29.5	0.00
Diel + Season	380.6	48.6	0.00	825.4	5.7	0.04
Diel	406.4	74.4	0.00	824.1	4.4	0.07
Season	449.0	116.9	0.00	844.9	25.2	0.00
Intercept (null model)	455.2	123.2	0.00	853.1	33.4	0.00
Longfin smelt						
<i>Model parameters</i>						
Depth + Diel + Season (Full model)	303.0	0.0	0.98	1821.1	0.0	0.47
Depth + Diel	310.9	8.0	0.02	1834.3	13.3	0.00
Depth + Season	404.6	101.6	0.00	1825.1	4.1	0.06
Depth	431.2	128.2	0.00	1854.9	33.9	0.00
Diel + Season	349.3	46.3	0.00	1821.2	0.1	0.44
Diel	357.2	54.2	0.00	1832.3	11.3	0.00
Season	428.4	125.4	0.00	1826.3	5.3	0.03
Intercept (Null model)	453.8	150.8	0.00	1855.4	34.3	0.00
Three-spine stickleback						
<i>Model parameters</i>						
Depth + Diel + Season (Full model)	416.3	0.9	0.29	1028.0	2.0	0.26
Depth + Diel	415.4	0.0	0.46	1026.0	0.0	0.70
Depth + Season	464.6	49.3	0.00	1032.2	6.2	0.03
Depth	464.1	48.7	0.00	1034.6	8.6	0.01
Diel + Season	418.6	3.2	0.09	1062.6	36.6	0.00
Diel	417.5	2.1	0.16	1063.3	37.3	0.00
Season	463.6	48.3	0.00	1074.5	48.5	0.00
Intercept (null model)	463.1	47.7	0.00	1076.6	50.6	0.00

Variation in longfin smelt occurrence and density were related strongly to season and diel period ($w_j = 0.91-1.00$) and, to a lesser extent, depth ($w_j = 0.53-1.0$; Table 4). Longfin smelt demonstrated distinct DVM patterns during both spring and fall, with CPUE increasing in intermediate and shallow depths from day to night periods (Figs 4 and 5). Smelt were encountered more frequently and captured in higher densities in fall than in spring (Table 3).

Depth and diel period were more important than season in dictating the occurrence and density of three-spine stickleback (Table 4). The highest densities of three-spine stickleback occurred in shallow depths during all diel periods in the spring (Fig. 4) and at night in the fall, but they were captured in very low densities at all depths during daylight and dusk in the fall (Fig. 5).

Spatial and temporal patterns of vertical distribution

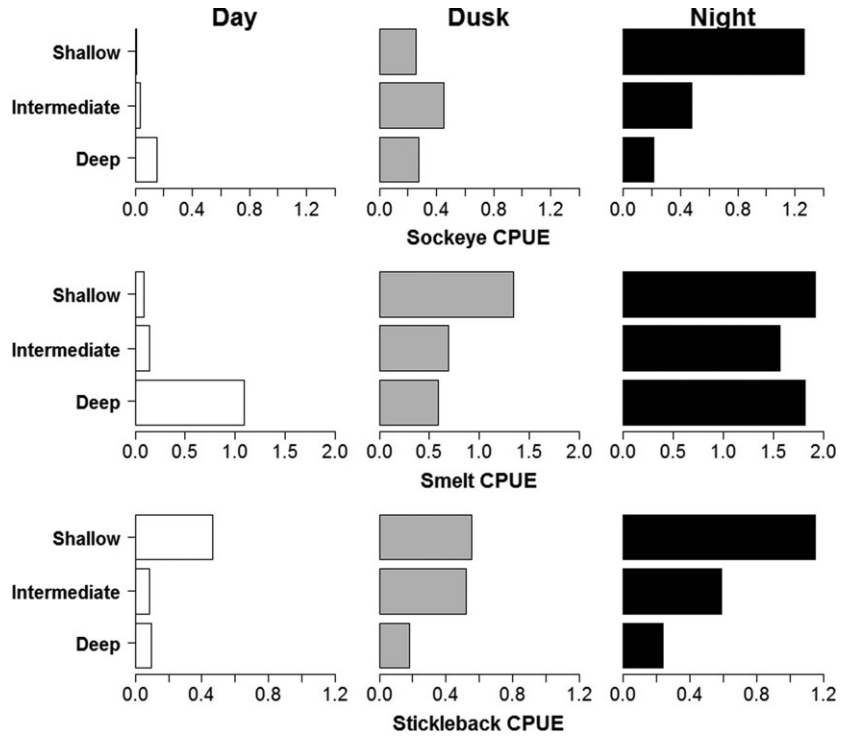


Fig. 4. Spring (April) depth distribution of sockeye salmon, longfin smelt and three-spine stickleback during day, dusk and night periods. Mean catch-per-unit-effort (CPUE, $N \cdot min^{-1}$) is shown for all sampling years combined (1997–2011).

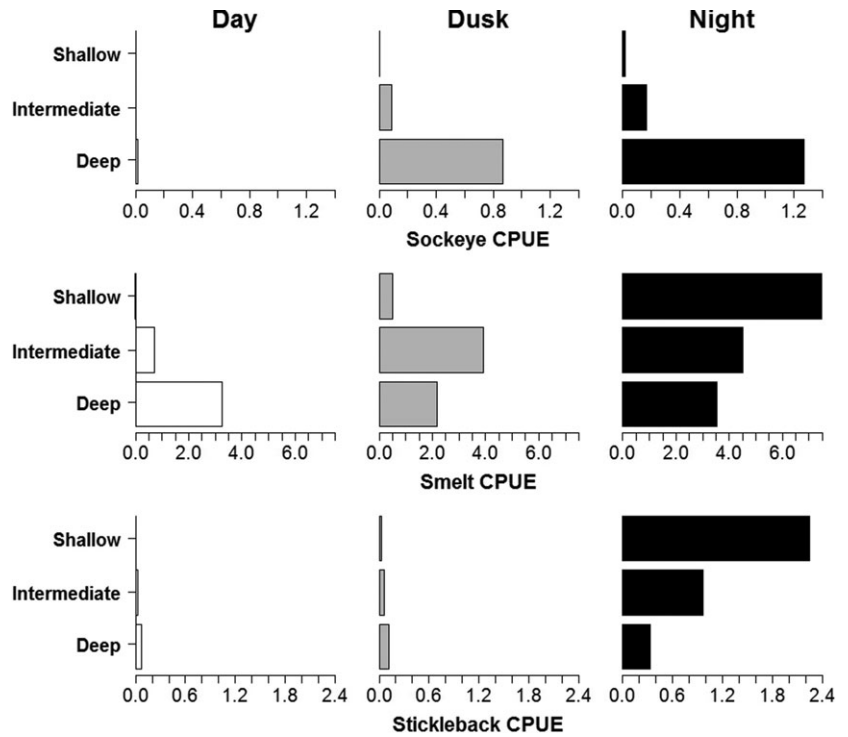


Fig. 5. Fall (October) depth distribution of sockeye salmon, longfin smelt and three-spine stickleback during day, dusk and night periods. Mean catch-per-unit-effort (CPUE, $N \cdot min^{-1}$) is shown for all sampling years combined (1997–2011).

In summary, CPUE data provided evidence of DVM from deep water during the day to shallow water at night for all planktivores, but the strength of this distributional pattern and consistency between seasons varied among species. Sockeye salmon demonstrated a strong DVM during the spring, but remained at highest densities in deep water across diel periods during the

fall. Longfin smelt exhibited DVM in both seasons and were more evenly distributed throughout the water column at night than the other species. Three-spine stickleback also showed increasing densities in shallow waters from day to night periods during both seasons, but were generally more abundant in shallow water across all diel periods.

Table 3. Parameter estimates from generalised linear models describing the (a) frequency of occurrence and (b) nonzero catch-per-unit-effort (CPUE) for three species. Coefficients (SE) are shown for the full model (Diel + Depth + Season).

	(a) Frequency of occurrence	(b) CPUE, nonzero tows
Sockeye salmon (full model)		
Intercept	-1.05 (0.41)	-1.04 (0.21)
Season: Oct	-2.16 (0.41)	0.01 (0.24)
Diel: Day	-2.62 (0.40)	-0.93 (0.24)
Diel: Night	0.69 (0.46)	0.47 (0.23)
Depth: Shallow	-1.54 (0.38)	0.44 (0.27)
Depth: Deep	0.99 (0.33)	0.64 (0.21)
Longfin smelt (full model)		
Intercept	-1.02 (0.44)	-0.22 (0.23)
Season: Oct	1.05 (0.34)	0.83 (0.20)
Diel: Day	-2.77 (0.43)	0.21 (0.24)
Diel: Night	0.93 (0.65)	0.74 (0.26)
Depth: Shallow	-0.99 (0.38)	0.52 (0.25)
Depth: Deep	1.52 (0.36)	0.33 (0.22)
Three-spine stickleback (Full model)		
Intercept	-2.28 (0.32)	-0.64 (0.26)
Season: Oct	-0.30 (0.28)	-0.14 (0.25)
Diel: Day	-1.38 (0.30)	-0.04 (0.27)
Diel: Night	0.69 (0.39)	0.86 (0.30)
Depth: Shallow	-0.11 (0.30)	0.84 (0.26)
Depth: Deep	0.57 (0.30)	-0.85 (0.26)

Table 4. Parameter Akaike weights (w_j) calculated from all candidate generalised linear models, describing the relationships between catch-per-unit-effort (CPUE) in biannual trawl surveys and environmental factors. CPUE was modelled using a two-stage process, first estimating the probability of capturing a species (a) and then modelling the CPUE given that the species was caught (b).

Parameter	(a) Frequency of occurrence	(b) CPUE, nonzero tows
	w_j	w_j
Sockeye salmon		
Depth	1.00	0.89
Diel	1.00	1.00
Season	1.00	0.26
Longfin smelt		
Depth	1.00	0.53
Diel	1.00	0.91
Season	0.98	1.00
Three-spine stickleback		
Depth	0.75	1.00
Diel	1.00	0.96
Season	0.38	0.29

Discussion

Midwater trawl data from Lake Washington demonstrated species-specific variation in the vertical distribution patterns of three planktivores across season and diel periods. The three species differed from each other, and in general, the hypotheses proposed for species-specific variation in DVM were supported. The DVM indicated by the sockeye salmon data was consistent with that of prior work on Lake Washington (Eggers 1978) and elsewhere (Levy 1987; Scheuerell

& Schindler 2003) on this species. Sockeye salmon reside in lakes for the first year or two of their lives, followed by migration to sea for the majority of their growth prior to return for spawning. In general, they grow slowly, as indicated by their smaller size at age when leaving freshwater compared with coho salmon, *O. kisutch*, a stream-rearing species, and smaller size for their age at sea than other Pacific salmon (Quinn 2005). In Lake Washington, age-0 sockeye salmon feed and grow much slower during their first months in the lake (Beauchamp et al. 2004) than sympatric lake-rearing Chinook salmon (Koehler et al. 2006). Where sympatric with pink salmon, *O. gorbuscha*, in lakes, sockeye salmon grow slower as well (Robins et al. 2005), and they seem to be generally unaggressive and risk-averse (Hoar 1954; Hutchison & Iwata 1997). Their nocturnal use of surface waters during spring was advantageous for growth, given the size and feeding rates exhibited by age-0 sockeye and to a lesser degree for the age-1 smolts (Beauchamp et al. 2004). In contrast, their strong avoidance of shallow strata during fall, when growth was insensitive to the range of temperatures available in deep (~9 °C) through shallow (ca. 15–16 °C) depths (Beauchamp 2009), was more consistent with predator avoidance.

There is less information on DVM by three-spine sticklebacks than by sockeye salmon, but DVM was reported in the Baltic Sea by Jurvelius et al. (1996) and Iliamna Lake, Alaska, by Quinn et al. (2012). In Alaska, significant numbers of sticklebacks were caught at the surface during the day, and their vertical shift in distribution was relatively subtle. In contrast, daytime catch rates of sockeye salmon at that lake were negligible compared with night-time catches (T.P. Quinn, unpublished data). Compared with sockeye salmon, three-spine sticklebacks are armoured (though still subject to predation from birds and fishes; Kitano et al. 2008), have a 1-year lifespan in Lake Washington (Eggers et al. 1978), and warmer optimal temperature for growth (Lefébure et al. 2011). During both spring and fall, the shallow stratum offered higher growth benefits for three-spine sticklebacks than either the intermediate or deep strata. These features likely all contributed to their greater proximity to the surface. Longfin smelt appeared to be intermediate between sockeye salmon and three-spine sticklebacks in their use of the epilimnion and extent of DVM. Like sockeye salmon, they lack defensive structures and are readily consumed by cutthroat trout in the lake (Beauchamp et al. 1992; Nowak et al. 2004), but their lifespan is much shorter, typically maturing at age-2 (Moulton 1974; Chigbu 2000).

Our age-specific samples of sockeye salmon in spring and longfin smelt in fall were insufficient for the rigorous statistical comparisons needed to test the two hypotheses concerning size effects on DVM, so

these results should be interpreted cautiously. However, the general patterns (Fig. 3) indicated greater proximity to the surface among the young-of-the-year, especially in longfin smelt. These fish would be more vulnerable to predation on the basis of size than the yearlings, and the use of the surface waters suggests that foraging to achieve growth was more important than predation risk. However, two features of the biology of smelt complicate this interpretation. First, the young-of-the-year are nearly transparent and so may be less vulnerable to visual predators than might be expected based on the size alone. In addition, the larger smelt feed more heavily on *Neomysis* than do smaller smelt (Chigbu and Sibley 1998), and *Neomysis* are closely associated with the bottom during the day, whereas zooplankton are primarily in the epilimnion. This difference in the locations of focal prey may also affect the vertical distributions of the age groups. Recently, Busch & Mehner (2012) reported earlier and more rapid ascent at dusk by smaller coregonids compared to larger ones, so the size-specific DVM patterns we saw may be genuine but further sampling is needed.

For all three species across all depths and seasons, there was a large disparity in CPUE among diel periods (lowest during daylight, intermediate at dusk and highest at night). Although light-mediated gear avoidance likely contributed to this disparity, this pattern was also observed in unbiased seasonal and diel hydroacoustic surveys (Beauchamp et al. 1999; Mazur & Beauchamp 2006). This disparity could be explained by schooling or a strong benthic association during daylight followed by partial or full dispersal into the water column at dusk and night. Our net was not designed to sample on the bottom, so close proximity to the bottom would greatly reduce vulnerability to the gear. Daylight schooling can be difficult to detect, much less quantify, by either small midwater trawls or narrow beam hydroacoustics. Nonetheless, occasional schools have been detected in the upper 10 m of the lake during hydroacoustic surveys in October (Mazur 2004; D.A. Beauchamp, unpublished data), and a single catch of nearly 17,000 three-spine sticklebacks was encountered when fishing at 15 m during daylight in October 2001 as well (Overman et al. 2006).

The seasonal and diel vertical distribution patterns of the three planktivores may reflect trade-offs between antipredation behaviour and bioenergetic benefits from behavioural thermoregulation. The low densities of nonschooling planktivores in the upper water column during daylight in both seasons, except for the armoured three-spine sticklebacks in spring, suggested that predator avoidance was a high priority during high-light periods. The depth distribution patterns during dusk were often intermediate between

day and night periods and could reflect either a critical feeding period during an antipredation window (e.g., Eggers 1978; Clark & Levy 1988; Scheuerell & Schindler 2003) or simply a transition from daylight to nocturnal distributions. Strong crepuscular feeding peaks were reported for longfin smelt (Dryfoos 1965) and juvenile sockeye salmon (Doble & Eggers 1978) in Lake Washington during the 1960s and early 1970s, before the emergence of *Daphnia* as the predominant zooplankton in the mid-1970s.

The depth distributions at night likely reflected thermoregulation, because darkness should minimise predation risk and inhibit feeding by the planktivores. The juvenile sockeye salmon moved into the epilimnion at night in spring, where the warmer temperatures offered a bioenergetic growth benefit. However, when the thermal benefit was neutral in fall, they remained in deep water at night. In contrast, the epilimnetic temperatures during both spring and fall were beneficial for growth of three-spine stickleback, and presumably for longfin smelt, and the highest catches of both species were in shallow depths at night during both seasons. Although little is known about the thermal preferences of longfin smelt, their optimal temperature is likely higher than for sockeye salmon, based on the much more southerly range of anadromous populations (Scott & Crossman 1973) and their generally shallower distribution in stratified lakes (Enzenhofer & Hume 1989; Chigbu et al. 1998). During peak thermal stratification in July–September, the 18–23 °C average epilimnetic temperatures in Lake Washington (Arhonditsis et al. 2004) would markedly reduce the growth of sockeye salmon, but optimise the growth of three-spine stickleback and possibly of longfin smelt.

The seasonal differences in DVM among species have implications for their vulnerability visually feeding limnetic predators. Using telemetry data on cutthroat trout (Nowak & Quinn 2002) and hydroacoustic data on nonschooling planktivores, a visual detection foraging model predicted that in spring, most predator–prey encounters would occur in the upper 12 m during all diel periods but rates were highest at dusk in the upper 6 m (Mazur & Beauchamp 2006). In fall, most predator–prey encounters would occur in the upper 21 m of the water column during all diel periods, with slightly higher maximum encounter rates in the upper 6 m at night (Mazur & Beauchamp 2006). These predicted encounter rates suggest that the planktivores were only vulnerable to predation in the shallow stratum. Thus in April, a larger fraction of the three-spine stickleback population was vulnerable to encounters with predators than in fall, followed by longfin smelt, and then sockeye salmon. In October, these species displayed the same ordering in terms of predicted encounter rates with predators, but sockeye

salmon were much less vulnerable than in the spring. Indeed, during 1995–2000, juvenile sockeye salmon represented larger fractions of the limnetic cutthroat trout diets in spring than in the fall, whereas longfin smelt contributed less to trout diets in spring than in fall, and sticklebacks contributed considerably less during any season for data spanning 1984–2000 (Beauchamp et al. 1992; Nowak et al. 2004). Following the recent fivefold increase in three-spine sticklebacks (Overman & Beauchamp 2006; Overman et al. 2006), they represented larger fractions of cutthroat trout diets (but low prey electivity indices) during spring and fall, while similar patterns in seasonal contributions by the other species persisted (D.A. Beauchamp, unpublished data).

In addition to the patterns documented by this study for the three planktivore species in Lake Washington, it offers broader implications for the DVM phenomenon and applied lake ecology. As noted by Piet & Guruge (1997), vertical distribution and DVM affect many aspects of community ecology in lakes, including the influences of non-native species. Assessment of these ecological interactions is greatly complicated by the variation in species-specific DVM patterns with season and size, and changing community composition at different trophic levels as species invade lakes and cascading effects occur. Lake Washington has had a particularly interesting and well-studied history of sequential effects of natural and human-related processes (Edmondson 1994; Winder et al. 2009), but it is certainly not unique. Modelling efforts directed at the conservation of species at risk and control of unwanted invasive species may hinge in part on complex trophic interactions affected by DVM patterns.

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