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Effects of prey abundance, distribution, visual contrast and morphology on selection by a pelagic piscivore

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SUMMARY

1. Most predators eat only a subset of possible prey. However, studies evaluating diet selection rarely measure prey availability in a manner that accounts for temporal–spatial overlap with predators, the sensory mechanisms employed to detect prey, and constraints on prey capture.
2. We evaluated the diet selection of cutthroat trout (*Oncorhynchus clarkii*) feeding on a diverse planktivore assemblage in Lake Washington to test the hypothesis that the diet selection of piscivores would reflect random (opportunistic) as opposed to non-random (targeted) feeding, after accounting for predator–prey overlap, visual detection and capture constraints.
3. Diets of cutthroat trout were sampled in autumn 2005, when the abundance of transparent, age-0 longfin smelt (*Spirinchus thaleichthys*) was low, and 2006, when the abundance of smelt was nearly seven times higher. Diet selection was evaluated separately using depth-integrated and depth-specific (accounted for predator–prey overlap) prey abundance. The abundance of different prey was then adjusted for differences in detectability and vulnerability to predation to see whether these factors could explain diet selection.
4. In 2005, cutthroat trout fed non-randomly by selecting against the smaller, transparent age-0 longfin smelt, but for the larger age-1 longfin smelt. After adjusting prey abundance for visual detection and capture, cutthroat trout fed randomly. In 2006, depth-integrated and depth-specific abundance explained the diets of cutthroat trout well, indicating random feeding. Feeding became non-random after adjusting for visual detection and capture. Cutthroat trout selected strongly for age-0 longfin smelt, but against similar sized threespine stickleback (*Gasterosteus aculeatus*) and larger age-1 longfin smelt in 2006. Overlap with juvenile sockeye salmon (*O. nerka*) was minimal in both years, and sockeye salmon were rare in the diets of cutthroat trout.
5. The direction of the shift between random and non-random selection depended on the presence of a weak versus a strong year class of age-0 longfin smelt. These fish were easy to catch, but hard to see. When their density was low, poor detection could explain their rarity in the diet. When their density was high, poor detection was compensated by higher encounter rates with cutthroat trout, sufficient to elicit a targeted feeding response. The nature of the feeding selectivity of a predator can be highly dependent on fluctuations in the abundance and suitability of key prey.

Keywords: pelagic, piscivore, predator–prey interactions, prey selection, visual detection

Introduction

Most predators are considered selective feeders, consuming particular species or sizes of prey more than expected from their abundance (Stephens & Krebs, 1986; Juanes, 1994; Isaac *et al.*, 2012). However, the realised diet of a predator in pelagic habitats could be influenced by a number of factors related to the distribution,

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detectability and vulnerability of the various prey (Hambright, 1991; Christensen, 1996; Mazur & Beauchamp, 2006). The apparent selectivity of a predator could range from random (opportunistic) feeding, reflecting the relative encounter rates with various prey types, to highly non-random (targeted) feeding, depending on the relative importance of the factors driving predator–prey interactions (Eggers, 1977; Jensen *et al.*, 2008). Studies evaluating feeding selectivity in natural systems rarely consider prey detectability and vulnerability explicitly, nor do they consider the spatial–temporal dimensions of predator–prey overlap when estimating prey abundance (Hyvarinen & Huusko, 2006; Jensen *et al.*, 2008; Isaac *et al.*, 2012; Jacobs *et al.*, 2013). Accounting for these factors could either help explain the diet selection of predators, or reveal greater selection for or against certain prey groups.

The predation sequence (search–encounter–capture) provides a useful framework for considering how physical and biological processes regulate the diets of predators (Beauchamp, Wahl & Johnson, 2007). Predators must first overlap with prey. In the pelagic zone of lakes, vertical gradients of temperature, oxygen, light, turbidity and zooplankton density structure the foraging environment for planktivores and piscivores (Hardiman, Johnson & Martinez, 2004; Jensen *et al.*, 2006). These variables are dynamic over time and space and can influence differentially the distribution of predators and prey, depending on species-specific or ontogenetic asymmetries in physiological tolerance and perception of the environment (Mackenzie-Grieve & Post, 2006; Hansen, Beauchamp & Baldwin, 2013a). For visually feeding piscivores, ambient photic conditions, body-size and visual contrast influence the detection of prey (an encounter) within overlapping habitats (Denton, 1970; Muntz, 1990; Hansen, Beauchamp & Schoen, 2013c). Given an encounter, species-specific behaviour (e.g. freeze, evade or school) and morphology (e.g. body shape, size or spines) can then regulate the capture and ingestion of prey when attacked (Christensen, 1996; Einfalt & Wahl, 1997; Scharf *et al.*, 1998; Reimchen, 2000). Predators often eat prey smaller than expected based on the sizes of prey present in the environment and gape limitation (Juanes, 1994). Such patterns could reflect size-dependency in prey capture success (Juanes, 1994). Therefore, the feeding selectivity of a predator may be driven by the behavioural and morphological constraints on prey encounter, capture and ingestion that follow sequentially from the processes that determine the spatial–temporal dimensions of prey abundance.

Lake Washington, Washington, U.S.A., contains a diverse assemblage of pelagic planktivores and is well suited for evaluating the influence of different factors on selection by top predators. Juvenile sockeye salmon (*Oncorhynchus nerka*), longfin smelt (*Spirinchus thaleichthys*) and threespine stickleback (*Gasterosteus aculeatus*) are the dominate planktivores (Eggers *et al.*, 1978). Coastal cutthroat trout (*O. clarkii clarkii*) is the most important offshore piscivore (Nowak & Quinn, 2002; Nowak *et al.*, 2004). The planktivores differ in life history, thermal tolerance and morphology (Quinn *et al.*, 2012). This diversity drives differences in the seasonal and diel depth distributions exhibited by each species (Quinn *et al.*, 2012), but may also translate into differences in detectability and vulnerability to predation. Juvenile sockeye salmon and longfin smelt achieve similar lengths over their lifespan in the lake (Hansen, Beauchamp & Lowery, 2013b) and are soft-rayed fish which are generally captured and ingested with greater success than spiny-rayed fish of a similar size (Savitz & Bardygula-Nonn, 1997; Scharf *et al.*, 1998). Threespine sticklebacks do not grow as large, but have spines and armour that may reduce the risk of predation (Scharf *et al.*, 1998; Reimchen, 2000; Kitano *et al.*, 2008). Additionally, longfin smelt are semelparous, have a two-year lifespan and exhibit cyclic variations in abundance where recruitment during even years (strong year classes) is typically five to 15 times greater than during odd years (weak year classes) (Beauchamp, 1994; Chigbu, 2000; Nowak *et al.*, 2004). New cohorts of age-0 longfin smelt become available offshore during summer and autumn (Chigbu & Sibley, 1998), but individuals are transparent at this time, which could limit their detection by visual predators (Hansen *et al.*, 2013c). Fluctuations in the abundance of different age classes of longfin smelt could alter the diet selection of piscivorous cutthroat trout.

Here, we examine whether adjusting the abundance of different prey for overlap with predators, and for differences in detectability and vulnerability to predation, can explain or modify patterns of diet selection for cutthroat trout during a weak and a strong year for longfin smelt recruitment. We then test for corresponding changes in the nature of the overall feeding selectivity (random or opportunistic versus non-random or targeted). We hypothesised that (i) cutthroat trout would select for different prey groups between the weak and strong year for longfin smelt, (ii) cutthroat trout would exhibit non-random patterns in diet selection when only considering prey abundance, both integrated across all depths, and specific to the depths occupied by cutthroat trout,

(iii) factors related to the visual detection, capture and ingestion of prey will help explain the diets of cutthroat trout and, therefore, patterns in diet selection would shift from non-random to random after adjusting prey abundance for these constraints, and (iv) the switch from non-random to random feeding would only emerge when considering depth-specific prey abundance, as this should better account for predator–prey overlap.

Methods

General approach

We estimated the offshore diet selection of piscivorous cutthroat trout during autumn 2005, when the abundance of age-0 longfin smelt was low (a weak year class), and autumn 2006, when their abundance was high (a strong year class). Both depth-integrated (standard approach) and depth-specific prey abundance (approach that accounts for overlap with predators during key feeding periods) within the study region of Lake Washington were used to estimate diet selection. Using a visual foraging model, we sequentially adjusted the depth-integrated and depth-specific density of each prey group for differences in visual detection, capture and ingestion by piscivores and re-evaluated diet selection. We could then evaluate changes in diet selection and the randomness of feeding of cutthroat trout across a range of definitions of 'prey availability' that progressively scaled down to the perceptual field of the predator.

Study system

Lake Washington is a large (32.2 km long by 2.5 km wide on average; maximum depth of 66 m), glacial lake adjacent to Seattle, Washington, U.S.A. (Fig. 1). Thermal stratification begins in May and persists through early November. Epilimnetic temperature approaches 12 °C in spring, 23 °C in summer and 16 °C in autumn. Dissolved oxygen typically remains above 5 mg L^{-1} throughout the year over the whole water column (Beauchamp *et al.*, 2004). The primary crustacean zooplankton consists of *Daphnia pulicaria*, *Cyclops bicuspidatus*, *Leptodiaptomus ashlandi* and *Epischura nevadensis*. *Daphnia* pre-dominates and achieves moderate to high densities (averaging 2–15 L^{-1}) from mid-May to November, but is below detection limits in winter and early spring. Cyclopoid copepods dominate during winter and densities during early spring vary among years (4–30 L^{-1}) (Edmondson & Litt, 1982; Beauchamp *et al.*, 2004; Quinn *et al.*, 2012).

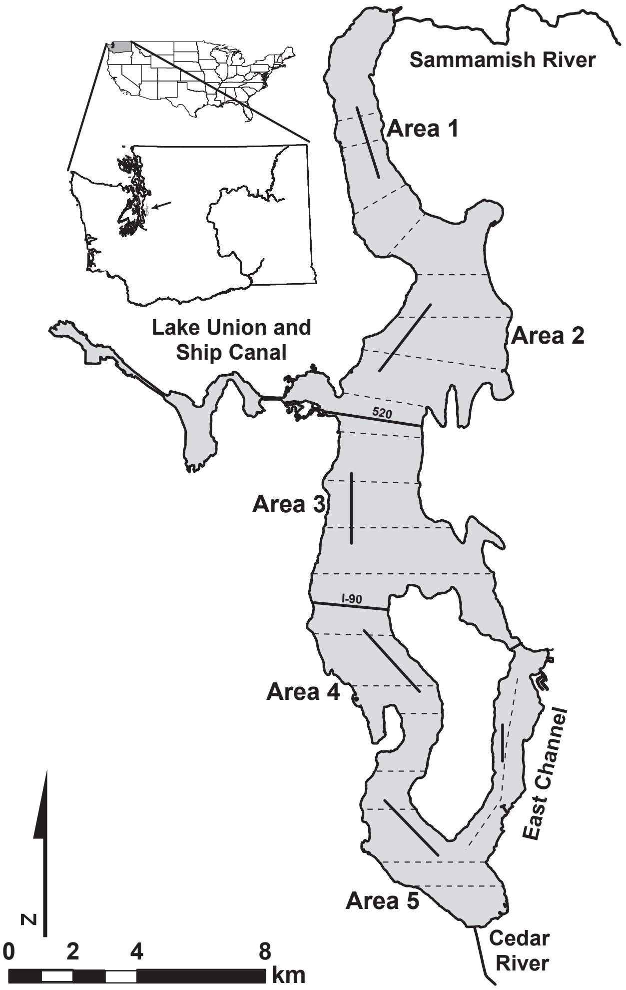

Fig. 1 Map of Lake Washington showing the different stratified sampling regions (areas 1–5 and the East Channel), hydroacoustic transects (dashed lines), mid-water trawling tracks (solid lines) and bridges (I-90 and 520).

The offshore density of different size or age classes of planktivores in Lake Washington changes seasonally. Sockeye salmon enter the lake as 25–30 mm fry during the spring (February–May), grow and develop offshore, then migrate as 120–150 mm smolts to the ocean the following May. Longfin smelt mature after 2 years and spawn in tributaries between January and March, then die (Chigbu, 2000). At this same time, a large and variable fraction of the age-1 cohort associates with benthic habitats nearshore, but the population is mostly pelagic during summer and autumn (Beauchamp, 1987; Chigbu, Sibley & Beauchamp, 1998). Longfin smelt exhibit strong density-dependent growth. Individuals from weak year classes are larger than those from strong year classes (Overman, Beauchamp & Mazur, 2006;

Hansen *et al.*, 2013b). Threespine stickleback have a 1 year lifespan in the lake, spawn nearshore during late spring and die within days to several months later (Eggers *et al.*, 1978). During the autumn, age-0 and age-1 longfin smelt, age-0 sockeye salmon parr, and age-0 threespine stickleback reside offshore (Quinn *et al.*, 2012).

Abundance of prey

In autumn 2005 and autumn 2006, paired mid-water trawl and hydroacoustics surveys were conducted at night in Lake Washington. These surveys were part of an ongoing programme that monitors the density, distribution, total abundance, growth and survival of the different pelagic planktivores (Hansen *et al.*, 2013b). Prey density is expanded to a total abundance using area and depth-specific water volume estimates for Lake Washington (Dawson, 1972). We used information from surveys conducted on 19–22 October 2005 and 16–20 October 2006 to obtain a depth-integrated and depth-specific density for each species and age class of planktivore (Overman & Beauchamp, 2006; Overman *et al.*, 2006).

The autumn pelagic fish surveys were stratified by depth and area of the lake. Trawls were deployed at three to five discrete depth intervals in five areas of the main lake basin. Parallel hydroacoustics transects ($N = 3$–4) were completed in each area prior to trawling (Fig. 1). Hydroacoustics surveys used a side-looking transducer in addition to a down-looking transducer to detect single targets and schools of fish near the surface (Yule, 2000; Beauchamp, Parrish & Whaley, 2009). Size- and depth-specific fish density was estimated using echo-counting procedures for single targets, supplemented with echo integration for schooling fish (Simmonds & MacLennan, 2005). Size- and depth-specific fish density was partitioned into different species and age classes based on the sizes and proportions of each prey group netted in the trawls (Love, 1977; Overman & Beauchamp, 2006; Overman *et al.*, 2006).

Cutthroat trout diet

Cutthroat trout in Lake Washington move offshore at around 250 mm fork length (FL) (Nowak *et al.*, 2004). Individuals greater than 250 mm are the most piscivorous and consume prey up to 40% of their body length (Nowak *et al.*, 2004). The percentage of fish in the diet by mass can approach 50% for individuals 250–299 mm, 80% for individuals 300–399 mm, and exceed 95% for individuals greater than 400 mm (Beauchamp *et al.*, 1999; Nowak *et al.*, 2004; McIntyre *et al.*, 2006). For this study, we netted cutthroat trout offshore with a purse seine primarily in area 2 (Fig. 1) on 9–10 November 2005 ($N = 7$ sets; two sets in area 3) and 8–9 November 2006 ($N = 10$ sets; three sets in area 3). The 17.7 m *FV Chasina* deployed the purse seine, which fished down to 25 m, over a single dusk-night sequence from 1625 to 0025 h in both years. We counted and identified to species fish found in the stomachs of cutthroat trout greater than 250 mm ($N = 19$ of 42 in 2005 and 27 of 38 in 2006). Longfin smelt were assigned to an age class by comparing standard lengths or lengths of intact vertebral columns in the diets and converted to fork length to the range of fork lengths estimated for each age class from catches in the seines and trawls (Table 1). When only partial vertebral columns were present, age classes were assigned through visual comparison of the remains with prey of known age. Thermocline depths (20–25 m) and epilimnetic temperatures were similar during late October (15.3–16.0 °C) and early November (12.8–13.6 °C) in both years (D. A. Beauchamp, unpublished data). This improved our confidence that the prey would not redistribute markedly between periods. Given the broad range of depths over which the cutthroat trout are likely to forage (see below), a large shift would be needed to alter substantially the prey field for cutthroat trout.

Diel depth distribution of cutthroat trout

We modified existing ultrasonic telemetry data to determine the range of depths occupied by cutthroat trout in Lake Washington during different periods of the day in the autumn (Nowak & Quinn, 2002). This analysis identified the appropriate depth intervals for estimating depth-specific prey density during key feeding periods for cutthroat trout. We focussed on the night, since most cutthroat trout with fish in their stomachs were captured ($N = 17$ of 19 or 89% in 2005 and $N = 25$ of 27 or 93% in 2006) and prey abundance was estimated at this time. Per cent frequency of fish in the diet of cutthroat trout was also higher at night than at dusk in both years (Fig. 2). Depth and time recordings from telemetry were assigned to a diel period (day, dusk, night or dawn) based on the start and end of twilight on the dates during October and November when cutthroat trout were tracked (Nowak & Quinn, 2002). Cutthroat trout occupied depths above and below the thermocline by day and night, but were mostly located within the upper

Table 1 Total number (*N*), mean length and range of lengths of piscivorous cutthroat trout (>250 mm) and different planktivore groups netted offshore in purse seines and mid-water trawls in Lake Washington during autumn 2005 and 2006

		Fork length (mm)							
Season and year	Predator–prey group	*N* netted	Range netted	*N* in diet	Range in diet	Mean netted	2 *SE*	PPR	CS
Autumn 2005	Cutthroat trout	19	278–488	–	–	347	29.0	–	–
	Age-0 longfin smelt	4	36–72	2 (2)	66–69	55	15.7	0.16	1.00*
	Age-1 longfin smelt	818	76–136	36 (16)	80–124	101	0.7	0.29	0.83*
	Threespine stickleback	107	53–88	11 (9)	73–85	64	1.1	0.18	0.81†
	Sockeye salmon	237	68–156	1 (0)	92‡	110	1.7	0.32	0.79*
Autumn 2006	Cutthroat trout	27	261–499	–	–	365	28.0	–	–
	Age-0 longfin smelt	964	29–80	108 (65)	26–80	45	0.5	0.12	1.00*
	Age-1 longfin smelt	49	94–142	6 (3)	109–130§	123	2.7	0.34	0.77*
	Threespine stickleback	199	35–73	38 (22)	51–73	60	0.7	0.16	0.85†
	Sockeye salmon	26	66–144	2 (2)	89–118	107	7.5	0.29	0.83*

The range of reconstructed fork lengths from prey observed in the diets of cutthroat trout are also shown. Values for *N* in the diet in parentheses indicate the number of prey for which fork lengths were reliably reconstructed. Estimates of piscivore capture success (CS) based on the ratio of mean prey length to mean predator length (PPR) are from the predictive equations of Scharf *et al.* (1998).

*Estimated using the predictive equation for Atlantic silverside (*Menidia menidia*) from Scharf *et al.* (1998): CS = 1.245–1.419(PPR), $r^2 = 0.42$, $P < 0.001$.

†Estimated using the predictive equation for striped bass (*Morone saxatilis*) from Scharf *et al.* (1998): CS = 1.166–1.926(PPR), $r^2 = 0.41$, $P < 0.001$.

‡Partial vertebral column only.

§Upper extent of range estimated from a large partial vertebral column.

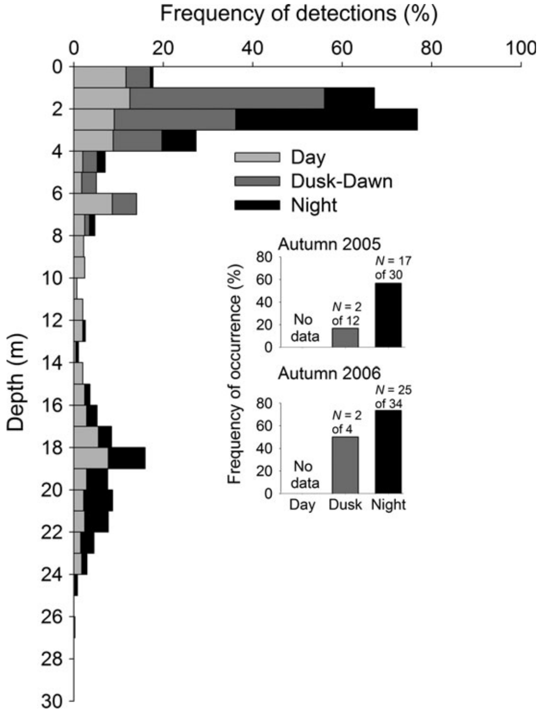

Fig. 2 Autumn (October and November) diel depth distribution of piscivorous cutthroat trout in Lake Washington based on the frequency of ultrasonic telemetry detections at different depths and times of day. Data were modified from Nowak & Quinn (2002). The inset panels show the frequency of occurrence of fish in the diet of piscivorous cutthroat trout netted offshore in the purse seine during autumn 2005 and autumn 2006. Sample sizes are indicated above each bar.

5 m of the water column during dusk and dawn (Fig. 2). Because cutthroat trout occupied depths down to 25 m at night, could be netted by the purse seine at those depths, and the nocturnal light environment in Lake Washington is sufficient for encountering prey down to 20 m (Mazur & Beauchamp, 2006), we used the density of each prey group within the 0–20 m depth stratum to evaluate diet selection for the depth-specific analysis. We pooled density estimates from areas 2 and 3, because almost equal numbers of piscivorous cutthroat trout were netted each year in each location.

Constraints on prey detection, capture and ingestion

The density of each prey group was adjusted for differences in detectability and vulnerability to predation to test whether these processes could explain diet selection. The mean fork length of each prey group (Table 1) in this study exceeded the sizes that limit visual detection by salmonid piscivores (Vogel & Beauchamp, 1999; Hansen *et al.*, 2013c), but the transparency of age-0 longfin smelt could limit detection (Denton, 1970; Muntz, 1990; Hansen *et al.*, 2013c). We accounted for transparency by generating relative measures of 'visual contrast' for each prey group using digital photography (Stevens *et al.*, 2007). We relied on the best information in the literature to adjust for constraints on prey capture and ingestion (Scharf *et al.*, 1998).

The measures of visual contrast were generated from fish netted in mid-water trawls in autumn 2012 (Hansen *et al.*, 2013b). Raw, digital images of age-0 longfin smelt ($N = 15$; mean FL = 41 mm; FL range = 31–56 mm), age-1 longfin smelt ($N = 10$; 120 mm; 99–134 mm), sockeye salmon parr ($N = 14$; 94 mm; 72–126 mm) and threespine stickleback ($N = 10$; 51 mm; 40–59 mm) were taken with a Canon EOS Rebel XS camera (ISO = 400; F-stop = 7.1) immediately after the catch was onboard. Fish were placed on a standard 18% grey card under indirect fluorescent lighting. Using the grey card as a reference (Stevens *et al.*, 2007), we standardised image exposure in Adobe Photoshop CS5.1 and converted the images to 8-bit grey scale (TIFF). Using ImageJ 1.45s, we calculated the total difference between the grey values (range: 0–255) of pixels from the fish body to the mean grey value of the background (Fig. 3a). Differences were averaged for each prey group and scaled to the maximum. This analysis represents an important first step in quantifying the effect of transparency on visual encounter.

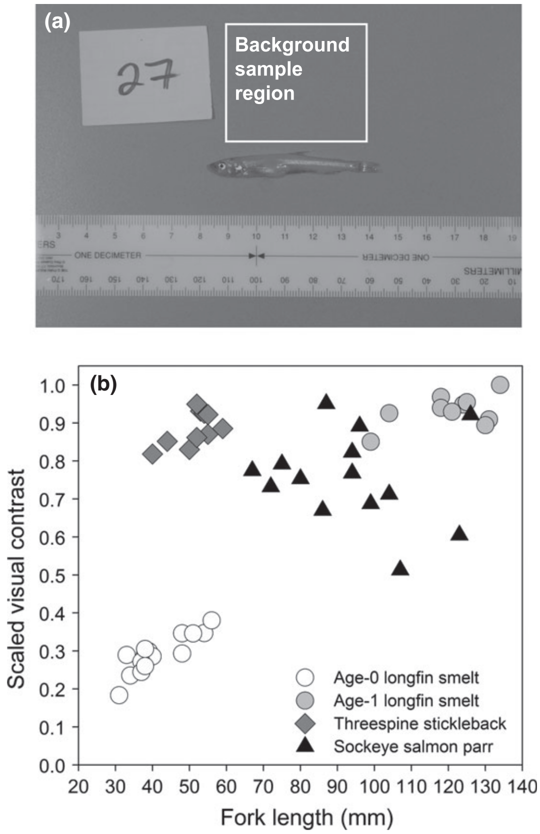

Fig. 3 A representative digital photograph (a) taken of individuals from each age class of planktivore present offshore in Lake Washington during October 2012. The white box shows where pixels were sampled to estimate the mean grey value of the background; (b) the scaled values of visual contrast generated for individuals from each age class of planktivore as a function of fork length.

To account for the potential effects of spiny-rayed versus soft-rayed prey on capture success, we applied capture success rates of juvenile bluefish (*Pomatomus saltatrix*) feeding on soft-rayed Atlantic silverside (*Menidia menidia*) and spiny-rayed striped bass (*Morone saxatilis*) (Scharf *et al.*, 1998). Capture rates of Atlantic silverside were used for longfin smelt and sockeye salmon. Capture rates of striped bass were used for threespine stickleback. Equivalent work using salmonid predators is fragmented and limited (Savitz & Bardygula-Nonn, 1997; Reimchen, 2000). However, the capture rates of similar sized threespine stickleback by adult cutthroat trout (~80%; Reimchen, 1991) were close to estimates (81–85%) from Scharf *et al.* (1998). Reimchen (1991) did not evaluate soft-rayed prey for comparison, but these data support the application of the more comprehensive work by Scharf *et al.* (1998). Capture rates estimated for the different prey groups, based on the ratio of mean prey length to mean predator length, ranged from 77–100% (Table 1).

We adjusted the density of each prey group with a visual foraging model. Visual foraging models link variability in feeding rate to changes in the environment and prey density, based on the prey encounter and behavioural responses of fish in pelagic habitats (Beauchamp *et al.*, 1999). We modified the general form of these models (Beauchamp *et al.*, 1999) by substituting the variable related to light- and turbidity-dependent visual reaction distance (R; see Hansen *et al.*, 2013a,c) with our measures of visual contrast (R_c) and then applying the capture rates of the different prey groups (c):

$$\text{Adjusted availability} = \pi R_c^2 \cdot \text{SS} \cdot T \cdot \text{PD} \cdot c, \qquad (1)$$

where SS is the swimming speed (m s^{-1}), T is time spent foraging (s) and PD is prey density (prey m^{-3}). The parameters SS and T were constants in our study and removed from the model, but these parameters are important in other studies using this approach (Hansen *et al.*, 2013a).

Diet selection and random versus non-random feeding

Numerous indices exist for evaluating diet selection (Lechowicz, 1982). We used the Jacobs index as it minimises some of the problems (e.g. nonlinearity and lack of symmetry) identified with other metrics (Jacobs, 1974):

$$D = \frac{r - p}{r + p - 2rp}, \quad (2)$$

where r is the numerical proportion of a prey group in the diet, and p is the numerical proportion of that prey group available in the environment. The index is centred on zero (neutral selection), and ranges from −1.0 (perfect selection against) to 1.0 (perfect selection for). To calculate r, we pooled counts of each prey group across diets of cutthroat trout during the autumn within each year. Assuming continuous feeding and gut evacuation, numerical diet proportions calculated in this way described the true diet of a population of piscivores better than other individually weighted methods in model simulations (Ahlbeck, Hansson & Hjerne, 2012). While the Jacobs index indicates which prey are selected for or against, using it for statistical inference regarding the overall randomness of feeding is cumbersome. For this, we relied on the χ^2 test for goodness of fit ($\alpha = 0.05$) (Lechowicz, 1982). Specifically, we tested whether the total number (not proportion) of each prey group eaten by cutthroat trout tracked what would be expected by the different definitions of prey availability (i.e. null hypothesis of random feeding).

Model robustness

Given uncertainty in our measures of visual contrast and estimates of capture success used in the foraging model, we tested if changes in these parameters could alter the outcome of random or non-random feeding after adjusting prey density for both constraints. Parameter values for each prey group, in each year, and under each abundance scenario (depth-integrated and depth-specific) were individually increased (to a maximum of 1.0) and decreased by 20% (Jensen *et al.*, 2006). We re-implemented the model with the new parameter value and repeated the χ^2 test to see whether diet selection still reflected random or non-random feeding.

Results

Relative visual contrast of prey

Visual contrast differed among the prey groups. Age-1 longfin smelt (mean scaled visual contrast = 0.93; 2 *SE* = 0.03), sockeye salmon (0.76; 0.06) and threespine stickleback (0.88; 0.03) contrasted significantly more (by factors of 2.6–3.2) from the standard grey background than the transparent age-0 longfin smelt (0.29; 0.03) (ANOVA, Tukey test, all $P < 0.001$). Threespine stickleback and age-1 longfin smelt were the only prey groups that did not differ (Tukey test, $P = 0.50$). In the modified foraging model, a threefold reduction in the visual contrast of age-0 longfin smelt translated into a ninefold reduction in the search volume of cutthroat trout. Visual contrast for age-0 longfin smelt also increased significantly with fork length ($r^2 = 0.74$, $N = 15$, $P < 0.001$):

$$\text{Scaled visual contrast} = 0.0055(\text{FL}) + 0.0624. \quad (3)$$

Similar length-dependent relationships were not observed for sockeye salmon and age-1 longfin smelt over the range of fork lengths examined (all $P \geq 0.12$), but threespine stickleback showed some evidence for a length-dependent relationship ($r^2 = 0.36$, $N = 10$, $P = 0.07$) (Fig. 3b).

Diet of cutthroat trout

The mean length of piscivorous cutthroat trout sampled did not differ between years (two sample t-test, $df = 44$, $P = 0.38$). Fewer prey fish were found in the diets of cutthroat trout in autumn 2005 ($N = 50$), when exposed to the weak longfin smelt year class, than in autumn 2006 ($N = 154$). Most prey eaten in 2005 were age-1 longfin smelt ($N = 36$; 72%), but age-0 longfin smelt ($N = 108$; 70%) dominated the diet in 2006. Sockeye salmon were almost absent in 2005 ($N = 1$; 2%) and 2006 ($N = 2$; 1%). Threespine stickleback represented intermediate fractions of the diet in 2005 ($N = 11$; 22%) and 2006 ($N = 38$; 25%). On average, all prey groups were within the gape limit (40% of FL; Nowak *et al.*, 2004) of the piscivorous cutthroat trout (Fig. 4). Additionally, there were no clear patterns of size selectivity within each prey group, except that cutthroat trout ate larger bodied threespine stickleback in 2005, but not in 2006 (Fig. 4c,d). Age-1 longfin smelt from a weak year class netted in 2006 were larger than age-1 longfin smelt from a strong year class netted in 2005 ($df = 865$, $P \ll 0.001$) and, therefore, were closer to the gape limit of cutthroat trout in 2006 (Fig. 4a,b).

Diet selection and random versus non-random feeding

Cutthroat trout differed in diet selection and randomness of feeding between autumn 2005, when a weak year class of age-0 longfin smelt represented 21–24% of the prey assemblage, and autumn 2006, when a strong year class represented 71–72%. Contrary to expectations, patterns of diet selection in each year did not depend on whether nocturnal prey abundance was measured over

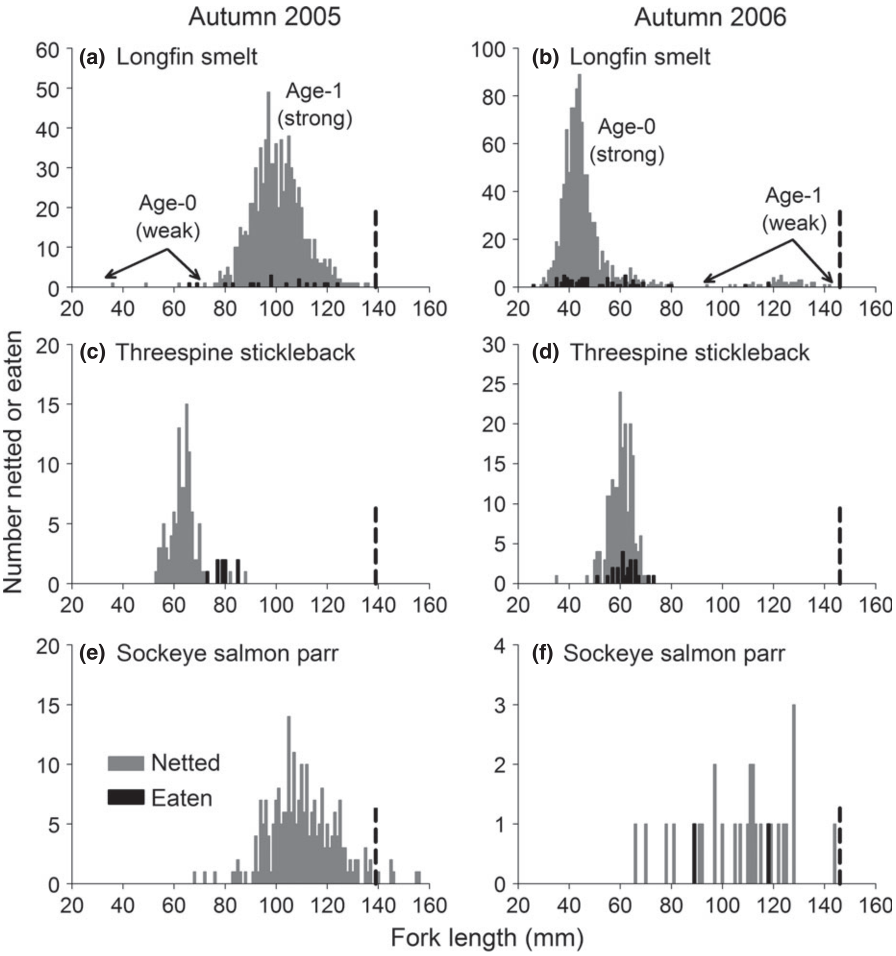

Fig. 4 Length–frequency distributions of prey fishes netted in purse seines and mid-water trawls and those eaten by piscivorous cutthroat trout in (a, c, e) autumn 2005 and (b, d, f) autumn 2006. For the prey eaten, only fish for which fork lengths were reliably reconstructed are shown. The dashed vertical lines indicate the gape limit (40% of fork length) of an average sized piscivorous cutthroat trout sampled in each year.

all depths (depth-integrated) or over just the upper 0–20 m (depth-specific) because 90% of the prey fish were concentrated in 0–20 m depths at night in both years. Consequently, only results from the depth-specific analysis are presented here.

Diet selection changed after accounting for differences in the detectability and vulnerability of each prey group (Fig. 5). For cutthroat trout in 2005, the Jacobs index indicated strong negative selection against age-0 longfin smelt (−0.77), but positive selection for age-1 longfin smelt (0.51). This was prior to accounting for detectability and vulnerability (Fig. 5a). At this stage, patterns in diet selection reflected non-random feeding ($\chi^2 = 18.31$, $df = 3$, $P \leq 0.001$). After adjusting prey density for the additional prey-specific constraints on detection, capture and ingestion, the selectivity of cutthroat trout became random ($\chi^2 = 3.32$, $P = 0.345$). Similarly, the Jacobs index shifted towards neutral selection, and all values fell between −0.31 and 0.35 (Fig. 5c). Taken alone, differences in the visual contrast of prey drove the shift from non-random to random feeding ($\chi^2 = 2.37$, $P = 0.50$). Differences in capture success alone could not produce the same shift to random feeding ($\chi^2 = 16.96$, $P < 0.001$). In general, differential capture success had a minor influence on the feeding selectivity of cutthroat trout, given their large average size (Table 1; Fig. 5).

Opposite patterns in diet selection and randomness of feeding were observed in autumn 2006, when the abundance of age-0 longfin smelt was nearly sevenfold higher than in autumn 2005. Prior to adjusting the density of each prey group for detectability and vulnerability, the Jacobs index indicated neutral selection for all prey groups (range: −0.21 to 0.08), except sockeye salmon, in which the index indicated strong positive selection (0.80) (Fig. 5b). However, like other proportional indices, the Jacobs index is overly sensitive to small proportions estimated for rare prey types in the environment and diet (Lechowicz, 1982), and strong selection for the rare sockeye salmon requires cautious interpretation. Overall patterns in diet selection reflected random feeding by cutthroat trout ($\chi^2 = 2.84$, $P = 0.42$), despite the apparent selection for sockeye salmon. After accounting for detectability and vulnerability, the feeding selectivity of cutthroat trout switched to highly non-

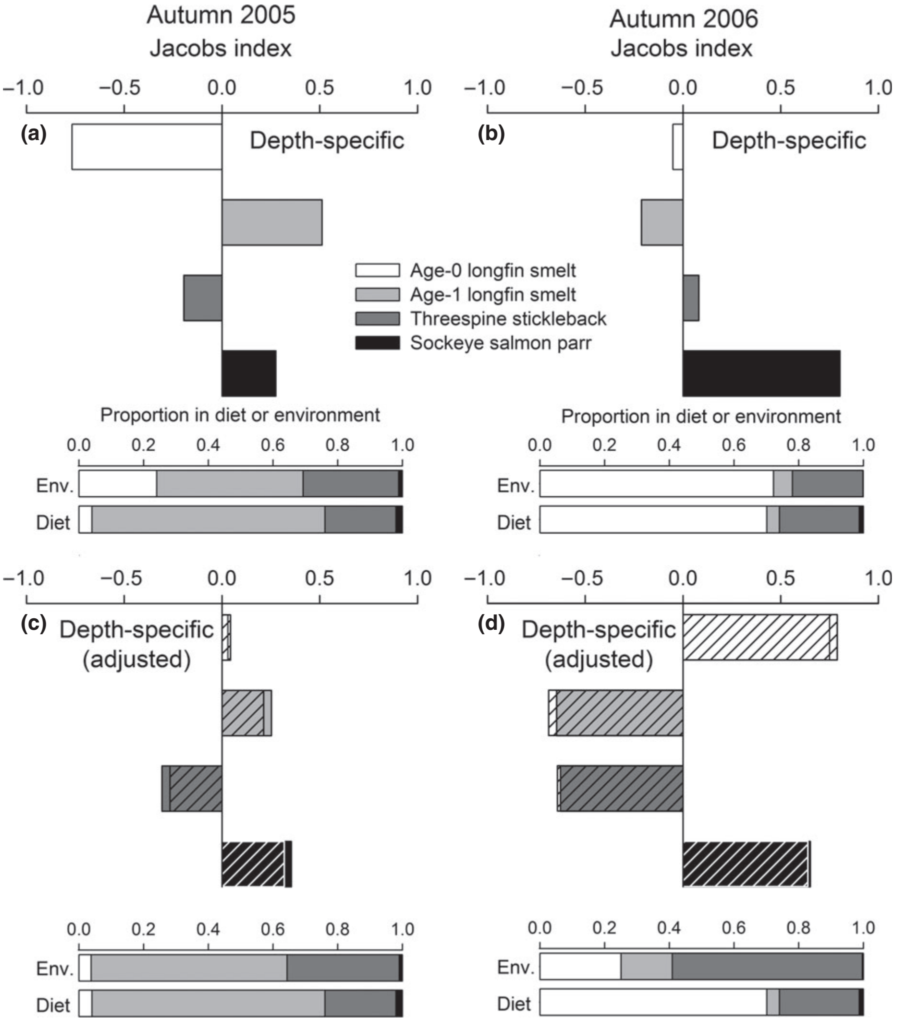

Fig. 5 Diet selection indices (shaded bars) calculated for cutthroat trout feeding on the dominant planktivores in Lake Washington during autumn 2005 and autumn 2006 using (a, b) prey abundance within the key depths occupied by cutthroat trout and (c, d) the same depth-specific abundance adjusted for constraints on detection, capture and ingestion by piscivores. The hatched bars overlaid on the shaded bars in panels (c) and (d) denote diet selection indices calculated after adjusting prey abundance for constraints on visual detection only. This is to show the minimal additional effect of differential capture success among the prey groups on diet selection. The corresponding stacked horizontal bars show the proportion of each prey group available in the environment versus what appeared in the diet.

random ($\chi^2 = 174.32$, $P << 0.001$). The resultant Jacobs indices indicated strong positive selection for age-0 longfin smelt (0.75) and sockeye salmon (0.65), but strong negative selection against age-1 longfin smelt (−0.65) and threespine stickleback (−0.63) (Fig. 5d).

Model robustness

The outcome of random feeding by cutthroat trout in autumn 2005 and non-random feeding in autumn 2006, after adjusting the density of each prey group for detectability and vulnerability to predation, was robust to the amount of uncertainty (±20%) we examined for the measures of visual contrast and estimates of piscivore capture success used in the foraging model. This amount of error was as great as or exceeded that observed in our measures of visual contrast and the estimates of capture success from Scharf *et al.* (1998). For parameters re-examined in 2005, corresponding χ^2 statistics (0.11–5.34) and P-values (0.15, 0.22, 0.35–0.99) all still reflected random feeding, except for when the visual contrast of age-1 longfin smelt was reduced by 20% ($\chi^2 = 8.23$, $P = 0.04$). In this year, 20% reductions in the visual contrast and capture success of threespine stickleback, but a 20% increase in the capture success of age-1 longfin smelt, improved the description of the diet ($\chi^2 = 0.11$–0.92 and $P = 0.82$–0.99). For parameters re-examined in 2006, corresponding χ^2 statistics (107.29–297.92) and P-values (all << 0.001) all still reflected non-random feeding. In this year, a 20% reduction in the visual contrast of age-0 longfin smelt worsened the description of the diet ($\chi^2 = 297.92$), whereas a 20% increase in the visual contrast of age-0 longfin smelt improved the description of the diet ($\chi^2 = 107.29$).

Discussion

Different perceptions of prey availability can alter the interpretation of whether predators feed randomly (i.e. opportunistically) or non-randomly (i.e. target certain prey). In this study, fluctuations in prey abundance interacted with differences in prey detectability to produce contrasting patterns in selection by piscivorous cutthroat trout. Differential capture success had a minor influence on selection by large-bodied cutthroat trout in this study. Whether cutthroat trout fed randomly or non-randomly before or after accounting for differences in detectability hinged on the presence of a weak versus a strong year class of the transparent age-0 longfin smelt. Prior to adjusting the abundance of prey for differences in detectability, results suggested that cutthroat trout were feeding non-randomly in autumn 2005, selecting against age-0 longfin smelt when their density was low, but randomly in autumn 2006, when their density was much higher. These patterns were reversed after accounting for differences in detectability. In 2005, reduced detection and a reduced encounter rate, relative to the other larger, more conspicuous planktivores, explained the rarity of age-0 longfin smelt in the diet of cutthroat trout. Conversely, reduced detection of age-0 longfin smelt was of minor importance in 2006, given their high relative abundance. Results from 2006 suggested that cutthroat trout were targeting age-0 longfin smelt. When compared to 2005, the less abundant, but larger age-1 longfin smelt approached the gape limit of cutthroat trout, which could have reinforced the targeted feeding response on the strong year class of age-0 longfin smelt in 2006. Therefore, in systems with diverse prey assemblages, the nature of the feeding selectivity of a predator can be a dynamic function of the interplay between fluctuations in prey abundance and prey suitability.

We sequentially adjusted estimates of total prey abundance (i.e. total prey availability) for predator–prey overlap (i.e. spatial–temporal availability), differences in detectability (i.e. availability due to visual encounters), and differences in vulnerability to predation (i.e. availability due to ease of capture and ingestion after an encounter) to estimate progressive changes in the diet selection of piscivorous cutthroat trout. Our hypothesis that the diet selection of cutthroat trout would reflect non-random feeding when representing prey availability by a depth-specific abundance, but random feeding after accounting for differences in detectability and vulnerability among prey groups was supported in autumn 2005. Counter to our initial hypothesis, this shift from non-random to random feeding also emerged when considering depth-integrated prey abundance. This was because the nocturnal prey fields in 0–20 m depths contained 90% of total prey numbers over all depths. The piscivores were already spatially overlapping with the majority of prey at night; therefore, the definition of prey availability for cutthroat trout changed little when trying to contrast total prey abundance throughout the water column with the realised prey abundance that overlapped with predators in 0–20 m depths. Results from 2005 demonstrated that random feeding by cutthroat trout and differential visual encounter rates among prey, not strictly non-random feeding, were the processes underlying the apparent strong selection against age-0 longfin smelt and for age-1 longfin smelt observed prior to accounting for prey detectability and vulnerability.

The shift between random and non-random feeding before and after adjustment of the depth-specific prey abundance for differences in detectability and vulnerability was reversed in autumn 2006, when the density of age-0 longfin smelt was nearly seven times higher. In this year, the targeted feeding response by cutthroat trout on age-0 longfin smelt was masked by defining prey availability as depth-specific abundance only. This definition of prey availability indicated apparent neutral selection for all prey groups (with the exception of sockeye salmon). The observed shifts between random and non-random feeding by cutthroat trout in response to fluctuations in the size structure, density and composition of the prey assemblage in Lake Washington suggests that pelagic piscivores are flexible predators. They can adapt their feeding behaviour to take advantage of large influxes of highly catchable prey (i.e. develop a search image), as might be anticipated from optimal foraging theory (Stephens & Krebs, 1986; Sih & Christensen, 2001; Jensen *et al*., 2008). Important questions that remain are (1) is there a critical density of age-0 longfin smelt needed to elicit this targeted feeding response and (2) does this critical density change in response to shifts in other ecological or environmental conditions?

Some predators may remain inflexible by continuing to select for certain prey types, despite continued reductions in the density of those prey. For example, Chinook salmon (*O. tshawytscha*) in Lake Michigan have become increasingly reliant on alewives (*Alosa pseudoharengus*) amid an overall reduction in alewife density in recent years (Jude *et al*., 1987; Jacobs *et al*., 2013), but the nature of this selection (random versus non-random) requires more in-depth evaluation of the temporal–spatial dimensions of these predator–prey interactions. Selection for alewife by Chinook salmon has remained relatively inflexible to the ecological changes in the lake over the past three decades (Bunnell, Madenjian & Claramunt, 2006), which suggests that these predators are targeting alewife. Therefore, Chinook salmon are expected to depress alewife populations substantially before switching to alternative prey (Madenjian *et al.*, 2006; Jacobs *et al.*, 2013). Under changing environmental and ecological conditions, more or less flexibility in the feeding selectivity of top predators could have different consequences for the dynamics of different prey populations.

Apparent, strong selective feeding on specific prey could be driven by the temporal–spatial structure of predator–prey interactions. If prey are highly aggregated, and predators can consistently exploit these aggregations, then prey abundance could be strongly depressed before a switch to alternative prey would be needed to maintain growth. Consumption rates estimated for lake trout (*Salvelinus namaycush*) in Lakes Superior, Michigan and Ontario did not respond to three to fivefold increases in prey density within the lakes, and were similar across a 100-fold difference in prey density among the lakes (Eby, Rudstam & Kitchell, 1995). These results demonstrated that piscivores can maintain adequate feeding rates at low average prey densities and highlighted the importance of evaluating prey abundance at temporal–spatial scales appropriate for understanding predator–prey interactions (Eby *et al.*, 1995). If aggregations of alewife form at low total abundance and if Chinook salmon can effectively exploit these aggregations, this mechanism could also explain the seemingly persistent, targeted selection for alewife by Chinook salmon in Lake Michigan (Jacobs *et al.*, 2013).

Lake Washington is heavily influenced by urban light pollution at night. Nocturnal light is sufficient for cutthroat trout to see fish prey, and turbidity in the lake is generally too low (≤1 NTU) to limit prey detection (Mazur & Beauchamp, 2006; Hansen *et al.*, 2013c). When compared to other salmonids, coastal cutthroat trout exhibit some of the greatest reaction distances to fish prey (behavioural proxy for visual detection) at light intensities prevalent at dusk and night (Hansen *et al.*, 2013c), suggesting that they are effective low-light piscivores. Although most fish are dispersed at night, light pollution can cause age-0 longfin smelt and threespine stickleback to form dense aggregations or schools near the surface where cutthroat trout actively feed (Mazur & Beauchamp, 2006; Overman & Beauchamp, 2006; Overman *et al.*, 2006). Presumably, a school is somewhat easier to detect than individual prey if a predator encounters one (Dunlop *et al.*, 2010; Hansen *et al.*, 2013c), even if the fish that form the school are transparent. The suggestion that cutthroat trout targeted the strong year class of age-0 longfin smelt in autumn 2006 could be misleading if cutthroat trout were able to exploit schools or aggregations of these fish near the surface. However, few schools or aggregations were detected by hydroacoustics in the study area during 2006, and the majority (95.5%) of age-0 longfin smelt surveyed were dispersed single targets (Overman & Beauchamp, 2006). Therefore, limited visual detection of individual age-0 longfin smelt, as represented by our measures of visual contrast, was probably an important factor influencing selection by cutthroat trout in 2006.

Seasonal shifts in environmental conditions influence the distribution of pelagic predators and prey (Hardiman *et al.*, 2004; Hansen *et al.*, 2013a). Selection by cutthroat trout was only evaluated during the autumn at night, when data on cutthroat trout diet, predator–prey distribution, and prey abundance coincided in space and time. The feeding selectivity of a predator could change if seasonal or diel shifts in distribution alter the temporal–spatial dimensions of predator–prey overlap. In Lake Washington, thermal conditions, along with other ecological and life-history related factors, alter the diel depth distributions of the planktivores between spring, when the lake is nearly isothermal, and autumn, when the lake is still thermally stratified (Quinn *et al.*, 2012). The spring is a dynamic period. Sockeye salmon fry (25–30 mm) enter the lake and are numerous offshore at night. Contrary to the autumn, age-1 sockeye salmon are much more dense near the surface at night in spring, where they are more accessible to cutthroat trout, whereas age-1 longfin smelt are more benthic (Nowak & Quinn, 2002; Overman *et al.*, 2006; Quinn *et al.*, 2012). Information on the distribution of pelagic prey fish during peak thermal stratification in summer is sparse for Lake Washington (Beauchamp, Vecht & Thomas, 1992; Chigbu *et al.*, 1998). Limited mid-water trawling data suggest that threespine stickleback are the only planktivore that can tolerate the warm epilimnion, whereas piscivorous cutthroat trout (Nowak & Quinn, 2002) and the other planktivores remain below the thermocline at all times of day (Hansen, Beauchamp & Lowery, 2014). Patterns of diet selection could be particularly sensitive to diel depth-integrated versus depth-specific prey abundance during this period of the year. For that reason, there is a need to extend the analyses presented in this study over a broader range of environmental conditions as well as predator–prey assemblages.

Key assumptions

The results of this study rest on two key assumptions. First, is that our measures of visual contrast match the perception of cutthroat trout. Controlled experiments evaluating the light- and turbidity-dependent reaction distances of cutthroat trout to transparent and non-transparent prey (e.g. see Hansen *et al.*, 2013c) have not been conducted. However, transparency has been repeatedly flagged as an important factor limiting the visual detection of predators (Denton, 1970; Muntz, 1990; Hansen *et al.*, 2013c), and our measures of visual contrast explained the rarity of age-0 longfin smelt in the diets of cutthroat trout when their density was low in autumn 2005. This outcome was robust to uncertainty in those measures. Second, is that the number of diets collected over a single dusk-night sequence in 2005 ($N = 19$) and 2006 ($N = 27$) characterised the autumn feeding of piscivorous cutthroat trout. Most variation in the seasonal dietary composition of large predators is captured with seven to 15 stomachs containing prey per size class (Beauchamp *et al.*, 2007), which we obtained for the large-bodied cutthroat trout. Autumn is also relatively stable in terms of fish distribution in Lake Washington (Quinn *et al.*, 2012), and interactions between cutthroat trout and prey persist over the duration of this period (Nowak *et al.*, 2004). A lower sampling frequency can adequately capture predator–prey interactions under these conditions, compared to when predation on focal prey is brief and acute or very dynamic (Beauchamp *et al.*, 2007). The autumn dietary composition we observed for cutthroat trout in 2005 and 2006 was very similar to previously published studies for this population (Beauchamp *et al.*, 1992; Nowak *et al.*, 2004; McIntyre *et al.*, 2006).

Implications for conservation and management

Evaluating how the feeding selectivity of a predator responds to natural fluctuations in temporal–spatial overlap with prey, and the abundance, detectability and vulnerability of prey over a range of environmental conditions should improve our understanding of the dynamic role of predators in regulating different prey groups in diverse aquatic communities. Such analyses are helpful if trying to identify when, where and under what conditions species of conservation or management concern might be threatened by predators, buffered from predation, or eaten in accordance with the rate at which they are encountered. Flexibility in the feeding selectivity of a top predator may complicate conservation or management efforts if attempts at boosting ecologically or economically important prey species correspond with ecological conditions that trigger a shift to non-random feeding on the prey group of interest.

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