

**Persisting in the pelagic: environmental, behavioral, and morphological
controls on predator-prey interactions**

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Abstract

Persisting in the pelagic: environmental, behavioral, and morphological controls on predator-prey interactions

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Persisting in the pelagic is not easy. The physical environment of pelagic ecosystems is highly dynamic. Unlike terrestrial systems where habitat complexity is driven by physical structure (e.g., vegetation and terrain), habitat complexity in the pelagic is driven by vertical gradients in light, turbidity, temperature, and oxygen. All of these factors change over time, and can mediate predator-prey interactions given ontogenetic or asymmetric responses of predators and prey to diel and seasonal changes in these factors. Additionally, pelagic predators and prey rely primarily on vision for feeding. Therefore, changes in photic conditions (light and turbidity) in particular can have a strong impact on the structure of predator-prey interactions. Yet, it remains unclear how habitat heterogeneity over different dimensions of time and space interacts with perception, behavior, and physiological tolerance to mediate the foraging success of predators and predation risk for prey in pelagic ecosystems. Pelagic environments are not static. They will change given continued human-induced alterations to the landscape, shifts in climate, and unanticipated introductions of nonnative predators and prey. Knowing how the pelagic foraging-risk environment changes in response to shifts in physical habitat over many different temporal-spatial scales should improve predictions regarding how aquatic food webs will respond to different perturbations.

For my dissertation I addressed the following series of questions: 1) how do light and turbidity effect the visual prey detection responses of pelagic planktivores and piscivores, and do the consumer groups differ?, 2) how does natural variation in photic conditions (diel and seasonal light regimes at different latitudes and turbidity) shape the foraging-risk environment for visually-feeding planktivores and piscivores in pelagic ecosystems?, 3) in addition to photic conditions, how do seasonal shifts in the thermal environment shape the foraging-risk

environment for pelagic planktivores and piscivores?, and 4) do fluctuations in the abundance, distribution, visual detectability, and vulnerability to predation of different prey groups alter the diet selection of piscivores and relative predation risk for planktivores in diverse pelagic communities? To address the first question, I conducted a series of controlled laboratory experiments and measured light- and turbidity-dependent reaction distances by piscivores. To address the remaining questions, I linked individual-based, mechanistic models (visual foraging and bioenergetics models) that capture important fine-scale behavioral and physiological processes with empirical data on physical habitat, predator diet, movement, and distribution (from netting, ultrasonic telemetry, and hydroacoustics) to estimate changes in feeding rates for piscivores and planktivores and predation risk for planktivores over time and space.

First, reaction distance responded asymptotically with increasing light, but declined quickly with increasing turbidity for both planktivores and piscivores. The maximum reaction distance for piscivores was 5-6 fold greater than for planktivores, but planktivores achieved their maximum reaction distance at a much lower light level, and the decline in reaction distance with turbidity was much steeper for piscivores. Second, based on these asymmetric visual prey detection responses, the foraging-risk environment for pelagic planktivores and piscivores changed considerably in systematic ways with changes in diel patterns of illuminance along a broad latitudinal gradient and to increases in turbidity. These changes have different implications for the structure of pelagic predator-prey interactions over a broad latitudinal gradient. Third, like shifts in photic conditions, seasonal shifts in the thermal environment also mediated the foraging success of piscivores and predation risk for planktivores. Here, periods of environmental stress (i.e., high temperature and low dissolved oxygen) greatly reduced both the foraging success of piscivores and predation risk for planktivores by creating thermal refugia for the planktivores. Lastly, the nature of the feeding selectivity (random or opportunistic versus non-random or targeted) of visually-oriented piscivores was highly dependent on fluctuations in the abundance and susceptibility of key prey to visual detection and capture. Results suggested that pelagic piscivores are flexible predators, and can adapt their feeding behavior to take advantage of large influxes of highly catchable prey. Overall, by observing through the eyes of pelagic predators and prey, my results show that the foraging-risk environment for piscivores and planktivores can look very different as physical habitat changes over many different dimensions of time and space.

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DEDICATION

To my parents, Gary and Pat, brothers, Andy and Jesse, and nephew, Gavin Hansen.

Chapter 1.—Persisting in the pelagic

Introduction

Heterogeneity through time and three-dimensional space present unique challenges to visually-feeding pelagic predators and prey (Loew and McFarland 1990). Pelagic environments lack structural features that physically inhibit access to different habitats, provide refugia for prey, or limit the searching efficiency of predators or prey (Kauffman et al. 2007). Instead, vertical gradients in abiotic factors (temperature, oxygen, light, and turbidity) create the predominant physical structure (Hardiman et al. 2004). These variables are dynamic over time and space, and can differentially influence the distribution of predators and prey depending on species-specific or ontogenetic asymmetries in physiological tolerance and perception of the environment (Hardiman et al. 2004; Mackenzie-Grieve and Post 2006). Forage fishes must balance the need to feed and grow with the metabolic demands of foraging in different habitats and associated risk of predation within those habitats (Eggers 1978; Clark and Levy 1988). Moreover, the costs and benefits of foraging may depend on life history requirements, and other morphological attributes (e.g., size, armoring, and pigmentation) that make different species more or less vulnerable to detection or predation, or influence their perceived risk of predation (Kitano et al. 2008; Quinn et al. 2012). Apex predators can forage without risk of predation, but must balance the need to feed and grow with the energy requirements of foraging efforts (Jensen et al. 2006). Therefore, as environmental conditions change, the spatial-temporal dimensions of tradeoffs confronting predators and prey change, creating complex patterns of distribution, foraging success, and predation risk in pelagic ecosystems.

Evaluating these dynamics has been of continual interest to ecologists. However, an ongoing challenge is understanding how habitat heterogeneity interacts with behavior and

physiological tolerance to mediate the foraging success of predators and predation risk for prey, and how the relative importance of different factors changes with shifts in environmental or ecological conditions. Apex predators complicate this task because data on their movement at scales necessary for capturing important fine-scale processes are difficult to collect (Baldwin et al. 2002). Mechanistic tools that operate at spatial-temporal scales pertinent to the perceptual fields of predators and prey offer an effective approach for exploring these types of interactions (Beauchamp et al. 1999). Pelagic environments are not static. They will likely change given continued human-induced alterations to the landscape, shifts in climate (Ficke et al. 2007), and unanticipated introductions of nonnative predators and prey (Johnson et al. 2009). Knowing how the foraging-risk environment for different species changes in response to shifts in physical habitat over many different dimensions of time and space should improve predictions regarding how the extent of predation mortality on key prey will likely respond to these perturbations.

Pelagic predators and prey are primarily visual foragers (Loew and McFarland 1990). Consequently, the photic environment plays a strong role in structuring pelagic communities (Appenzeller and Leggett 1995; Gjelland et al. 2009; Kahilainen et al. 2009; Mehner 2012). Therefore, the purpose of the research presented in this dissertation is to both develop and link individual-based, mechanistic models (visual foraging and bioenergetics models) that capture important fine-scale behavioral and physiological processes with empirical data on physical habitat, fish diet, movement, and distribution (from netting, ultrasonic telemetry, and hydroacoustics) to explore: 1) how seasonal and latitudinal shifts in photic conditions (diel light regimes and turbidity) shape the foraging-risk environment for pelagic piscivores and planktivores, 2) the importance of other environmental factors (i.e., temperature and oxygen) in mediating the foraging success of piscivores and predation risk for planktivores, and 3) the

effects of prey abundance, distribution, pigmentation, and morphology on the apparent diet selection of piscivores and relative predation risk for planktivores. I use experimental, field, and model generated data to evaluate these different aspects of pelagic predator-prey interactions.

Goals and objectives from individual chapters

Chapter 2.—Visual prey detection responses of piscivorous trout and salmon: effects of light, turbidity, and prey size

Hansen, A. G., D. A. Beauchamp, and E. R. Schoen. 2013. Visual prey detection responses of piscivorous trout and salmon: effects of light, turbidity, and prey size. *Transactions of the American Fisheries Society* 142:854-867.

Goals and objectives: Visual foraging models provide a useful framework for predicting distribution, foraging success, and predation risk in pelagic communities. These models effectively link variability in feeding rate to changes in environmental conditions and prey availability, based on the optical conditions, visual prey detection capabilities, and behavioral responses of fishes in pelagic habitats (Beauchamp et al. 1999; Vogel and Beauchamp 1999; Mazur and Beauchamp 2006). However, the light- and turbidity-dependent visual prey detection capabilities of different predator species within and among taxonomic groups have not been sufficiently evaluated. The goal of this chapter was to increase the capacity of the visual foraging approach by supplying key parameters for additional ecologically and economically important species. The primary objective of this work was to more adequately characterize variation in the reaction distances (a behavioral proxy for prey detection) of piscivorous salmonids by evaluating important anadromous taxa. The approach and work presented in this chapter set the foundation for the remainder of my dissertation and provided important mechanistic building blocks for subsequent analyses.

Chapter 3.—Latitudinal and photic effects on diel foraging and predation risk in pelagic ecosystems

Goals and objectives: Despite the strong structuring force of light and turbidity on pelagic communities, it remains unclear how pelagic predator-prey interactions change over broad spatial-temporal scales with latitude in response to shifts in the diel and seasonal light environment and to increases in water turbidity. The goal of this chapter was to address the question: how does natural variation in photic conditions shape the foraging-risk environment for visually-feeding planktivores and piscivores in pelagic ecosystems? Clark and Levy (1988) described an antipredation window for smaller planktivorous fishes during crepuscular periods when light permits feeding on zooplankton, but limits visual detection by piscivores. I addressed the question above by using the antipredation window concept as an integrative representation of the foraging-risk environment. Here, I linked a sun illuminance model (Janiczek and DeYoung 1987) with the foraging rate model of Clark and Levy (1988) and with empirical relationships describing the light- and turbidity-dependent reaction distances of an idealized planktivore and piscivore (like those developed in *Chapter 2*) to estimate the size of the antipredation window under different photic conditions. The objective of this study was to evaluate changes in the size of the antipredation window across the full gradient of latitude and turbidity that characterize freshwater systems supporting visually-feeding pelagic planktivores and piscivores.

Chapter 4.—Environmental constraints on piscivory: insights from linking ultrasonic telemetry to a visual foraging model for cutthroat trout

Hansen, A. G., D. A. Beauchamp, and C. M. Baldwin. 2013. Environmental constraints on piscivory: insights from linking ultrasonic telemetry to a visual foraging model for cutthroat trout. *Transactions of the American Fisheries Society* 142:300-316.

Goals and objectives: *Chapter 3* focused on the effects of broad-scale changes in photic conditions (light and turbidity) on the foraging-risk environment for visually-feeding pelagic planktivores and piscivores. The goal of this chapter was to assess the interacting effects of all key physical habitat factors (light, turbidity, temperature, and oxygen) within a framework that

captures interdependencies among environmental factors, behavior, and the physiological tolerances of predators and prey. Specifically, I asked: how does the foraging-risk environment for pelagic planktivores and piscivores change in response to parallel, seasonal shifts in light regime, turbidity, water temperature, and dissolved oxygen? My primary objectives were to determine whether the foraging success of piscivores changes during periods of environmental stress (i.e., high temperature and low dissolved oxygen), and to identify the behavioral mechanisms that either lead to or buffer piscivores against shifts in foraging success. I addressed these objectives by linking observed movement patterns from previously published ultrasonic telemetry data (Baldwin et al. 2002) with a visual foraging model for piscivorous cutthroat trout.

Chapter 5.—Effects of prey abundance, distribution, pigmentation, and morphology on apparent selection by a pelagic piscivore

Goals and objectives: Predation risk for different prey within diverse pelagic communities also depends on the feeding selectivity of predators (Jensen et al. 2008). However, most studies evaluating the diet selection of predators rarely measure prey availability in a manner that accounts for 1) the temporal-spatial overlap between predators and prey, 2) how prey fields might be perceived by predators, 3) the primary sensory mechanisms employed by predators to detect prey (e.g., vision), and 4) the behavioral and morphological constraints on capture and ingestion after a predator encounters prey (Hyvarinen and Huusko 2006; Jensen et al. 2008; Isaac et al. 2012; Jacobs et al. 2013). The goal of this chapter was to evaluate the feeding selectivity of piscivores using estimates of prey availability that are more in-line with the perceptual fields of predators. My specific objectives were to determine whether fluctuations in the abundance, distribution, visual detectability, and vulnerability to predation of different prey groups can alter the diet selection of piscivores feeding on a diverse pelagic planktivore community.

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Chapter 2.—Visual prey detection responses of piscivorous trout and salmon: effects of light, turbidity, and prey size

Abstract.—Visual foraging models provide a useful framework for predicting distribution, foraging success, and predation risk in pelagic communities; however, the visual prey detection capabilities of different species within and among taxonomic groups of predators has not been sufficiently evaluated. Our primary objective was to more adequately characterize variation in the reaction distances of piscivorous salmonids by evaluating important anadromous taxa. We measured reaction distances of yearling Chinook Salmon *Oncorhynchus tshawytscha* and adult Coastal Cutthroat Trout *O. clarki clarki* to fish prey over a range of ecologically relevant light and turbidity levels, and prey sizes. Reaction distances for Cutthroat Trout increased rapidly with increasing light to a maximum averaging 187.1 cm above a light threshold of 18.0 lx. Reaction distances for Chinook Salmon increased at a slower rate to a maximum of 122.1 cm above a light threshold of 24.9 lx, declined exponentially with turbidity beyond a threshold (1.65 NTU), and declined for prey sizes at fork lengths < 50 mm. Reaction distances of Cutthroat Trout were consistently higher than for Chinook Salmon across all light levels. This difference could not be attributed to the greater lengths of the Cutthroat Trout. Results from this and previous studies show that the functional form of reaction distance is similar across species and life-stages of piscivorous salmonids, but the magnitude of the response can vary considerably. Therefore, in order to adequately predict the strength of predation effects in pelagic communities, species and life-stage specific responses must be considered.

Introduction

Dynamic environmental conditions can influence overlap between predators and prey in pelagic systems (Hardiman et al. 2004; Jensen et al. 2006). How perception and behavior

interact with the physical environment to mediate piscivory after overlap is achieved is less well understood. Pelagic piscivores are primarily visual foragers (Loew and McFarland 1990). As a result, optical conditions can limit the foraging success of piscivores, first by mediating their ability to detect prey (Beauchamp et al. 1999; Vogel and Beauchamp 1999), and second by affecting their capture rate of encountered prey (Petersen and Gadomski 1994; De Robertis et al. 2003; Mazur and Beauchamp 2003). By experimentally evaluating the influence of visibility on foraging behavior we can identify mechanisms at scales pertinent to the perceptual fields of predators and prey that help explain variability in the strength of predation effects. Here we focus on visual prey detection and reaction by piscivorous salmonids.

Reaction distance, the average point at which a predator first exhibits a response to prey, is a valuable behavioral metric for measuring the effects of visibility on prey detection for piscivores (Howick and O'Brien 1983; Miner and Stein 1996; Vogel and Beauchamp 1999). Declining light and increasing turbidity reduce reaction distances, search volumes, and prey encounters at disproportionately higher rates for piscivores than for their planktivorous prey (Breck 1993; De Robertis et al. 2003). These asymmetric responses interact with dynamic light environments (Gjelland et al. 2009), basin productivity (Beauchamp et al. 1999), and other abiotic factors (e.g., temperature and oxygen; Hardiman et al. 2004; Hansen et al. 2013) to create complex patterns of predator-prey distributions, foraging success, and predation risk that affect the growth and survival of pelagic fishes over time and space (Jensen et al. 2006; Gjelland et al. 2009; Kahilainen et al. 2009). The influences of light intensity and scattering on reaction distance also appear to vary markedly among piscivorous species, suggesting that competition and intraguild predation within this functional group may be influenced by optical conditions (see Henderson and Northcote 1985 and Mazur and Beauchamp 2003). However, these

responses have been described for only a small number of species, limiting the application and refinement of this approach.

Similarly, few studies have investigated the effect of prey fish size on the reaction distances by piscivores, and they have generated potentially conflicting results. Largemouth Bass *Micropterus salmoides* exhibited increasing reaction distance with increasing prey sizes (30-80 mm fork length; FL) of Bluegill *Lepomis macrochirus* and Redfin Shiners *Notropis umbratilis* (Howick and O'Brien 1983), whereas different prey fish sizes (55-139 mm FL salmonids) did not affect light-dependent reaction distances for Lake Trout *Salvelinus namaycush* (Vogel and Beauchamp 1999). Piscivores typically rely on the contrast between prey and the background for detection, whereas planktivorous fishes use an acuity-based system to detect small-bodied zooplankton (Breck 1993). Whether these differences among species resulted from different visual capabilities or foraging modes ascribed to different taxonomic groups of predators has yet to be determined. Nonetheless, there is presumably a size or transitional range of prey sizes that affect the detection/reaction distance of piscivorous salmonids to prey fishes (Vogel and Beauchamp 1999).

Despite the importance of visibility in mediating predation rates in pelagic communities, the visual prey detection capabilities of anadromous salmonids are unknown. Chinook Salmon *Oncorhynchus tshawytscha* are important visually-oriented predators in predominantly pelagic habitats of marine and some freshwater systems (e.g., Stewart and Ibarra 1991), become piscivorous early in life, and consume greater fractions of fish prey as they grow (Keeley and Grant 2001; Daly et al. 2009; Duffy et al. 2010). Recent evidence suggests that for juvenile Chinook Salmon, foraging conditions that promote rapid growth during early marine residence are critical for their overall marine survival (Duffy and Beauchamp 2011), and fish prey may

play a key role in achieving such growth (Daly et al. 2009; Duffy et al. 2010). Therefore, it is particularly important to understand how visibility affects prey detection for early life-stages of Chinook Salmon. Coastal Cutthroat Trout *O. clarki clarki* are top piscivores in many salmon-bearing lakes (Cartwright et al. 1998; Nowak et al. 2004) and are important piscivores in nearshore coastal marine waters (Loch and Miller 1988; Duffy and Beauchamp 2008). Measuring responses from these anadromous species expanded our understanding of the visual prey detection capabilities of piscivorous salmonids by complimenting the resident freshwater taxa that have previously been studied (Vogel and Beauchamp 1999; Mazur and Beauchamp 2003).

Visual foraging models are useful tools for predicting distribution, foraging success, and predation risk in pelagic communities, either under ambient conditions or in response to future management or environmental alterations (Beauchamp et al. 1999). However, the utility of such models relies on sufficient parameterization of the prey detection process (Gerritsen and Strickler 1977; Aksnes and Giske 1993; Mazur and Beauchamp 2003). Our primary objectives were to more completely characterize variability in the visual prey detection capabilities of piscivorous salmonids by evaluating important anadromous forms, and address lingering uncertainties regarding the effects of prey size on reaction distance. In this paper, we (1) experimentally measure reaction distances of yearling Chinook Salmon and adult Coastal Cutthroat Trout over a range of ecologically relevant light and turbidity levels in a large laboratory tank, (2) parameterize and compare species-specific reaction distances as functions of light and turbidity, (3) evaluate whether reaction distances of Chinook Salmon change across the range of prey sizes that they consume during early marine residence (Duffy et al. 2010), but smaller than prey fish sizes addressed in previous studies of piscivorous salmonids (Vogel and Beauchamp 1999), and

(4) qualitatively compare our results to those from previous studies evaluating inland salmonids (Vogel and Beauchamp 1999; Mazur and Beauchamp 2003).

Methods

We measured the effects of light, turbidity, and prey size on reaction distances by piscivorous, anadromous salmonids in freshwater tank experiments using video analysis. All experiments were conducted at the University of Washington's Big Beef Creek Field Station, Seabeck, Washington. We first measured reaction distances of yearling Chinook Salmon (194-288 mm FL; $N = 20$) and Coastal Cutthroat Trout (255-440 mm FL; $N = 13$) across a range of light intensities (0.03-250 lx; measured at the water's surface) in clear water (< 0.5 NTU). The light levels selected resembled a daylight-dusk-night cycle (Mazur and Beauchamp 2003). Next, we measured reaction distances of Chinook Salmon (182-241 mm FL; $N = 36$) to incremental increases in turbidity (0.4-7.2 NTU) under a constant surface light level (50 lx). Trials were designed to detect thresholds where reaction distance began to decline and limit search volume (Mazur and Beauchamp 2003). Prey fish for the light and turbidity experiments were Rainbow Trout (*O. mykiss*; mean $\pm 2 SE = 49 \pm 0.31$ mm FL), as this followed previous studies (Vogel and Beauchamp 1999; Mazur and Beauchamp 2003). Lastly, we measured reaction distances of Chinook Salmon (220-290 mm FL; $N = 12$) to a series of smaller prey fishes under low and high surface light levels (5 and 25 lx). Trials explored whether the contrast-based visual system of piscivores limited their reaction distances as prey size declined. We hypothesized that reaction distance would decline with prey size, but at a higher rate at low light given the likely greater difficulty in detecting smaller objects under more degraded visual conditions. Timing of prey availability and logistical constraints precluded using different sizes of the same prey species in these trials. Consequently, we used Threespine Stickleback *Gasterosteus aculeatus* for the

smallest prey treatment (23 ± 0.77 mm FL), juvenile Coastal Cutthroat Trout for a mid-sized treatment (35 ± 0.62 mm FL), and Rainbow Trout for the largest treatment (50 ± 0.59 mm FL).

Collection, maintenance, and acclimation of experimental fish

Yearling Chinook Salmon were obtained in spring 2010 and 2011 from Hoodspout Hatchery (Washington Department of Fish and Wildlife; WDFW), Hoodspout, Washington. Wild Coastal Cutthroat Trout were captured via hook-and-line from Big Beef Creek near its mouth on Hood Canal, Washington, during summer-fall 2009-2011. Captured Cutthroat Trout were held in outdoor circular tanks (4 m diameter) covered with netting and black mesh cloth to reduce direct sunlight. These tanks were supplied with stable 9.5-11.5°C well water and were subjected to a natural photoperiod through the duration of experimentation. Chinook Salmon were held indoors under identical conditions, except incandescent lights on a timer mimicked the natural photoperiod. Chinook Salmon were maintained on formulated feed (Silver Cup™ Fish Feed). Cutthroat Trout were maintained on a combination of formulated feed and frozen krill (Hikari Bio-Pure®). We conditioned the predators to feed on live prey fish for 1-5 months prior to experimentation. Rainbow Trout were obtained from Eells Springs Hatchery, Shelton, Washington (WDFW). Cutthroat Trout prey were spawned from the adults captured from Big Beef Creek and raised in the hatchery, and wild Threespine Stickleback were captured from the settling ponds at the Big Beef Creek facility. Animal care and handling for this research was performed under the auspices of University of Washington IACUC Protocol #3286-19.

Experimental arena

Reaction distances were measured in an indoor 4.1 m diameter \times 1.2 m high circular tank filled to a depth of 0.5 m. The diameter of our circular arena exceeded the maximum average reaction distances (\sim 0.5-1.0 m) measured for piscivorous salmonids in previous studies (Vogel

and Beauchamp 1999; Mazur and Beauchamp 2003) by 4-8 times. Additionally, unlike the narrow rectangular tank used previously (4.5 m long \times 1.0 m wide \times 1.0 m high), our arena provided a greater breadth of angles from which the predators could orient towards the prey fish. The arena was lined with a flexible gray PVC material to follow previous experiments (Vogel and Beauchamp 1999). A rectangular curtain made from the same material was used to split the arena into halves while acclimating predators. Prey were tethered inside one of four acrylic tubes (14 cm diameter) to eliminate non-visual stimuli. Two tubes were positioned vertically near the tank wall and about 1.0 m apart at the far end of the arena on both sides of the opaque acclimation curtain. The tether consisted of low visibility fishing line (4.5 kg test; 0.20 mm diameter) extending through each tube and held taut by a small weight.

The arena was illuminated by six fluorescent fixtures (two lamps per fixture) suspended 2.4 m above the surface of the water. We chose lamps (F32-T8-TL865 PLUS ALTO from Philips Lighting) designed to mimic natural daylight, but with a higher color temperature (6500 k) so that the spectral composition of emitted light was dominated by violet, blue, and green (range: 380-760 nm; Figure 2.1). These lamps best represented the underwater light environment of the types of systems inhabited by salmonids (Horne and Goldman 1994; Kirk 2010), and matched the rapid drop in sensitivity of fishes to longer, red wavelengths (Horodysky et al. 2010; Figure 2.1). Light intensity was controlled by adding multiple layers of fiber-glass window screen (Vogel and Beauchamp 1999) between the lamps and a diffuser plate on each fixture, and then fine-tuned using a series of dimming switches (Lutron Electronics, Inc.). Turbidity was controlled by mixing consistent amounts of pulverized kaolin clay (Acros Organics; particle distribution: 50-62% $<$ 2 μ m) into the arena with a submersible water pump. The arena was shrouded with a layer of black plastic sheeting to remove external sources of

light.

Trials were recorded using two fixed-focus, low-light black and white security cameras (model CVC-321WP from Speco Technologies[®]) mounted perpendicular to and 2.6 m above the surface of the water. Cameras were connected to a video capture card (model PV-183-8 from Bluecherry) in a desktop computer. We used video acquisition software from the Nonlinear Dynamics and Control Laboratory at the University of Washington that synchronized each camera and recorded video at 60 frames per second with 640×480 pixel resolution. To enhance camera sensitivity for trials at low light levels (≤ 1 lx), we recorded video with the addition of infrared light (850 nm) not detectable by humans or fishes (Douglas and Hawryshyn 1990; Mazur and Beauchamp 2003) from six strategically placed illuminators (model CM126-30 from Scene Electronics Co., Ltd.).

Experimental protocol and measurement of treatment variables

The predators were tested in pairs and deprived of food for at least 36 h prior to use to enhance their motivation to feed (Meager et al. 2005). Having multiple predators in the arena improved the fish's willingness to explore the arena (De Robertis et al. 2003). All predators were allowed to hunt free-swimming prey fish in the arena before being used in trials. Experience levels were controlled by cycling the predators through a series of "used" and "unused" holding tanks. Based on variability observed among trials in previous experiments (Vogel and Beauchamp 1999), two to four sets of predators were tested at each surface light level (0.03, 0.1, 1, 5, 10, 15, 20, 25, 50, and 250 lx; $N = 41$ for Chinook Salmon and $N = 31$ for Cutthroat Trout) and turbidity level (Chinook Salmon only; near 0.5, 1, 1.5, 2, 3, 4, 5, 6, and 7 NTU; $N = 30$). Six pairs of Chinook Salmon were tested at each combination of light and prey size ($N = 36$). Treatments were blocked such that one trial of each treatment or combination

thereof was completed in random order before replication as designated by the blocks to reduce time-varying effects.

For all trials, a single, live prey fish was tethered through the connective tissue underneath the maxilla (large prey) or through the lower jaw (small prey) in the middle of the water column, inside one of the four acrylic tubes. The tube was randomly selected for each trial. The tethering procedure allowed the prey to ventilate and rotate freely around a central pivot point (advantageous because movement of prey often elicits responses from predators; Howick and O'Brien 1983), yet maintain a fixed position to standardize measurements of reaction distance. Preliminary experiments (using 50 mm prey under clear water at 10 and 50 lx) showed no significant differences between reaction distances measured to prey tethered outside and inside the tubes ($F_{3,37} = 1.25$, $P = 0.271$). Predators were placed on the opposite side of the opaque curtain from the prey and allowed to acclimate to the light conditions for 1 h to ensure light-dark adaptation (Ali 1959). To minimize the amount of kaolin settling out of suspension during the turbidity trials, we reduced acclimation to 30 min. After acclimation, the curtain was lifted and the predators were allowed to respond to the tethered prey for 1 h.

Light levels were measured before and after each trial at the surface of the water from six locations around the perimeter of the arena using a calibrated LI-COR[®] LI-210 photometric sensor (cosine-corrected) and a LI-1400 data logger. We report the average of the before and after measurements ($N = 12$) to account for any minor deviations from the target irradiance (mean percent change $\pm 2 SE = 4.1 \pm 0.76$) that occurred during a trial. The photometric sensor measured visible radiation in lx (380-770 nm) using the spectral responsivity of an average human eye (Figure 1). We also recorded corresponding measurements of photosynthetically active radiation (400-700 nm; $\mu E \cdot s^{-1} \cdot m^{-2}$) using an LI-190 terrestrial quantum sensor (cosine-

corrected). Unlike the photometric sensor, the quantum sensor responded equally to all photons across the 400-700 nm range. The relationship ($I_x = 66.849\mu E \cdot s^{-1} \cdot m^{-2}$) between units under our fluorescent lamps was strongly linear ($N = 1,350$; $r^2 = 0.99$). The bottom of the arena reflected light back up into the water-column, causing slightly higher irradiance underwater than indicated by the surface light measurements. Therefore, we used a linear model (sub-surface light = $1.206 \times$ surface light; $N = 169$; $r^2 = 0.99$) generated by pairing surface light measurements (LI-190 quantum sensor) with subsurface light measurements (measured with an LI-193 underwater spherical quantum sensor) to correct all mean surface measurements to what the predators experienced at the depth of the prey.

Turbidity in NTU was measured with a LaMotte 2020e turbidity meter. A single water sample was integrated from three mid water-column points around the perimeter of the arena before and after each trial. We measured 5-8 subsamples of the before- and after-trial water samples and averaged the means from the before and after measurements to account for clay settling out of suspension over the duration of each trial. Clay settled by an average of 30% ($2 SE = 6\%$) over the 1.5 h long combined acclimation and trial period. Turbidity levels were highly reproducible ($NTU = 0.495g \text{ kaolin}/m^3 + 0.51$; $r^2 = 0.99$).

Oceanographic studies generally quantify turbidity in terms of beam attenuation (the sum of absorption and scatter; Kirk 2010). Therefore, we developed a conversion from turbidity in NTU to beam attenuation for our kaolin suspensions. We measured the percent of light at a wavelength of 660 nm transmitted through a 10 mm cuvette using a Spectronic 21 DV spectrophotometer (Milton Roy[®]). Beam attenuation was calculated using the standard formula: $T = e^{-cr}$, where T (%) is the light transmitted through a path length r (m) at an attenuation rate c (m^{-1}) (Kirk 2010). Beam attenuation of the kaolin suspensions was highly correlated to turbidity

in NTU across a range of 0-10 NTU ($c = 0.40\text{NTU}$; $N = 26$; $r^2 = 0.98$).

Camera model and estimation of reaction distance

Reaction distances were estimated from video recordings using two-dimensional camera tracking techniques. By using a 0.5 m water depth, we assumed that the predators always reacted to the tethered prey fish on the same two-dimensional plane in the middle of the water-column, thus simplifying measurements. The approximate position of the predators in the water-column relative to the prey, based on the fish's shadows that were created on the bottom of the arena (Laurel et al. 2005), supported this assumption.

Nodes of a 20 cm \times 20 cm reference grid ($N = 324$) were marked on the bottom of the experimental arena to calibrate the overhead cameras. Using ImageJ software (version 1.45s), we linked the coordinates of each node in pixels taken from still images with the known coordinates of each node in cm based on a defined grid origin. With this information, we fit a series of 3rd order polynomial regression models as applied by Hughes and Kelly (1996) that converted coordinates in pixels (x_c, y_c) taken from anywhere within the image of the reference grid to known coordinates in cm (x_g, y_g). The set of regression models fit to each camera specifically were:

$$(2.1) \quad x_g = p_1 + p_2x_c + p_3y_c + p_4x_c^2 + p_5x_cy_c + p_6y_c^2 + p_7x_c^3 + p_8x_c^2y_c + p_9x_cy_c^2 + p_{10}y_c^3,$$

$$(2.2) \quad y_g = p_1 + p_2x_c + p_3y_c + p_4x_c^2 + p_5x_cy_c + p_6y_c^2 + p_7x_c^3 + p_8x_c^2y_c + p_9x_cy_c^2 + p_{10}y_c^3,$$

where p_1 - p_{10} were fitted parameters. Parameters were estimated using least squares (unadjusted r^2 for all fits of the model > 0.998 ; computed as $1 - [\text{SSresidual}/\text{SStotal}]$) with a multi-dimensional optimization routine (function *optim*) in R (version 2.14.1; R Development Core team 2011).

We viewed the video recordings using Media Player Classic Home Cinema (freeware; v. 1.5.1.2903). When a reaction was noted, we recorded the coordinates in pixels (x_c, y_c) from the

predators position (eye region of head) in the associated video frame using ImageJ, and then converted those to coordinates in cm (x_g, y_g) using the regression models fitted to the camera that captured the reaction. Because the position of the tethered prey was known, we simply used the distance formula to estimate the reaction distance. The potential error in any reaction distance measurement using this technique was largely within $\pm 5\%$ (98.5% of the observations), as characterized by the distribution of percentage deviations between the known and predicted distances from all grid nodes to each tether location (pooled across each camera; $N = 1,772$; mean absolute percentage $\pm 2 SE = 0.92 \pm 0.10$).

Statistical analyses

We used a model selection approach to analyze the reaction distances of Chinook Salmon and Cutthroat Trout as functions of light, turbidity, and prey size. A candidate set of plausible models were fit to the mean reaction distances calculated from each trial (responses pooled across predators; Vogel and Beauchamp 1999; Mazur and Beauchamp 2003). For light, we selected four biologically meaningful functional relations that could capture the plateau response observed in reaction distance (see results). We included the two primary functions used in previous studies (Mazur and Beauchamp 2003): a linear hockey stick including a breakpoint, and a similar two-piece model where the increasing limb is a nonlinear power function. We also tested two continuous functions that exhibit asymptotic behavior; a power function and a Holling type II functional response (Holling 1959) that included a y-intercept to improve its comparability to the other models (Table 2.1). When analyzing the Chinook Salmon turbidity experiments, we only considered a declining exponential function (Miner and Stein 1996; Vogel and Beauchamp 1999). We tested for a significant turbidity threshold by fitting the model with and without a breakpoint, whereby reaction distance is a constant prior to the breakpoint, before

declining exponentially.

For light, different formulations of each candidate model were generated by iteratively sharing parameters between Chinook Salmon and Cutthroat Trout, starting with the most saturated formulation (i.e., a fully parameterized function fit to the data for each species), and ending with the most reduced formulation (i.e., a single function fit to the data combined across species). Models were fit to the data using maximum likelihood estimation (function *mle2* within the package *bbmle*; Bolker 2012) in R (R Development Core Team 2011). Error terms were assumed to be normally distributed and estimated separately for each species in all model formulations. We used the same methods to fit the turbidity model to the data for Chinook Salmon. This procedure allowed us to test for significant differences in parameter estimates between the species and for a significant turbidity threshold directly via model selection. We used Akaike's information criterion (AICc; Burnham and Anderson 2002) to select the best model.

The length distributions of the Chinook Salmon and Cutthroat Trout predators were overlapping, but not identical, limiting our ability to determine whether observed differences in reaction distance resulted from a species or an ontogenetic effect, based on the model selection results alone. Therefore, we used linear models (function *lm* in R; R Development Core Team 2011) with species as a grouping factor and fork length as a continuous explanatory variable to test whether mean reaction distance under non-limiting light conditions differed between the two species, after taking predator length into account. Reaction distances were pooled and fork lengths were averaged for each Chinook Salmon pair, but were analyzed separately for each Cutthroat Trout, which could be individually identified in the video recordings. Reaction distance data were centered (on fork length) and standardized (z-transformed) prior to fitting the

linear models (Schielzeth 2010). We started with a linear model containing all effects (including the interaction term), then iteratively reduced model terms based on AICc (Burnham and Anderson 2002).

Data from the prey-size experiment were analyzed using the same model selection procedures as the predator length analysis. Here we used linear models to test whether reaction distances of Chinook Salmon varied as a function of prey size (continuous explanatory variable) and light (coded as a factor level), and whether the effect of prey size depended on light level (interaction term). Models were fit to the mean reaction distances ($N = 6$) measured at each prey-size-light combination. Both reaction distance and prey size (fork length) were \log_{10} -transformed to improve linearity. We tested for a block effect using simple linear regression. Reaction distances showed no temporal trend during the course of the experiment at $\alpha = 0.05$ (i.e., no significant block effect; slope = -4.08, $r^2 = 0.076$, $P = 0.10$).

Results

Reaction distance as a function of light

Overall, reaction distances from Cutthroat Trout were higher than those from Chinook Salmon across all light levels (Figure 2.2). The best fitting model formulation ($\Delta\text{AICc} = 0$) for describing reaction distance as a function of light was the fully saturated (i.e., no parameters shared between species) piecewise linear hockey stick (Table 2.1). Based on the fitted equations, reaction distance was strongly dependent on light for both Chinook Salmon ($r^2 = 0.89$) and Cutthroat Trout ($r^2 = 0.84$) (Table 2.2; Figure 2.2). For both species, reaction distance increased rapidly with light to a breakpoint termed the saturation intensity threshold (SIT; Henderson and Northcote 1985), and these breakpoints differed significantly between the species (24.9 lx for Chinook Salmon and 18.0 lx for Cutthroat Trout; Table 2.2) based on the model selection results

(Table 2.1). As light increased from low levels to SIT, reaction distances for Cutthroat Trout increased at a significantly higher rate (slope = 5.66) and reached a much higher maximum (187.1 cm) than those from Chinook Salmon (slope = 2.68; maximum = 122.1 cm) (Table 2.2). After controlling for predator fork length, significant differences in the reaction distance above SIT (to remove the effect of light) between the species were still apparent (Figure 2.3). The best fitting linear model included species-specific y-intercept terms, but a shared slope equal to zero, supporting a strong species difference with no effect of fork length, and no interaction between species and fork length (Table 2.3). Reaction distances of Cutthroat Trout at higher light levels were 46% greater than those from Chinook Salmon.

Reaction distance as a function of turbidity

Reaction distances for Chinook Salmon were strongly dependent on turbidity ($r^2 = 0.96$; Table 2.2). The best fitting model for describing reaction distance as a function of turbidity included a breakpoint (1.65 NTU), or threshold beyond which reaction distance began to decline exponentially (Table 2.2; Figure 2.4). In contrast, the model excluding the breakpoint fit poorly ($\Delta AICc = 22.65$). Reaction distance decreased about 70% from the breakpoint to 7.2 NTU.

Reaction distance and prey-size effects

The best fitting linear model for describing reaction distance as a function of prey size and light included all terms, suggesting that light was an important factor, reaction distance varied as a function of prey size, and the extent to which reaction distance varied as a function of prey size depended on light level (Table 2.4). Based on the model selection results, reaction distances declined significantly with decreasing prey size at both the low and high light levels, but the rate of this decline was significantly greater at high light (slope = 0.71) than at low light (slope = 0.42). The significant interaction term was driven by the convergence of reaction

distances measured at low and high light at the smallest prey sizes examined (~23 mm Threespine Stickleback; Figure 2.5).

Discussion

These experiments show that the functional form of reaction distance over ecologically relevant levels of light and turbidity is similar across species and life-stages of piscivorous salmonids inhabiting both marine and freshwater; however the magnitude of the responses can differ. Reaction distance for Coastal Cutthroat Trout increased rapidly with increasing light to a maximum beginning at 18.0 lx. Reaction distance for yearling Chinook Salmon increased at a slower rate to a maximum beginning at 24.9 lx, declined exponentially with increasing turbidity after a low turbidity threshold (1.65 NTU) for light levels above SIT, and decreased with decreasing prey size. Previous experiments with adult piscivorous Lake Trout, Rainbow Trout, and Bear Lake strain Cutthroat Trout *O. clarki utah* observed the same plateau response and reported similar SIT values ranging from 17.00-18.75 lx (Vogel and Beauchamp 1999; Mazur and Beauchamp 2003; Figure 2.6). Results from these studies also suggested that the threshold value beyond which turbidity limits reaction distance ranged from 1-2 NTU, but this response has not been measured precisely until now. Lastly, reaction distances did not change with prey size over the 55-139 mm length range for Lake Trout in these studies (Vogel and Beauchamp 1999), but investigators did not evaluate whether this relationship held for smaller prey sizes that are more relevant to juvenile life-stages. We found that reaction distance for yearling Chinook Salmon was significantly reduced for prey < 50 mm. Therefore, models of encounter rate for juvenile piscivores may benefit from inclusion of prey size data.

The linear hockey stick model fit the light-dependent reaction distances for both Chinook Salmon and Coastal Cutthroat Trout the best. However, the other piecewise model utilizing a

power function for the increasing limb, and two formulations of the modified Holling type II functional response also fit the data well ($\Delta AICc \leq 2$). Previous studies with piscivorous salmonids have relied on both types of piecewise functions (linear and power) explored in this analysis for describing reaction distance as a function of light (Vogel and Beauchamp 1999; Mazur and Beauchamp 2003). Although beyond the scope of this study, further analyses evaluating whether a single functional form and SIT value is transferable among species, and quantifying resulting errors in estimates of reaction distance from using an alternative model for different species is warranted. However, visual foraging models for piscivores typically approximate search volume by a cylinder with radius equal to reaction distance and length equal to the product of the predators swimming speed and time spent foraging (Beauchamp et al. 1999). Since estimates of search volume depend on the square of the reaction distance within this formulation, visual foraging models are quite sensitive to errors in estimates of reaction distance. Therefore, when refining the visual foraging approach, generalizations regarding species-specific responses should be explored cautiously.

The observed threshold responses are important because they mark points above or below which reaction distance is no longer influenced by changes in the optical environment. As long as piscivores occupy depths with ambient light levels above SIT (e.g., > 24.9 lx for Chinook Salmon and > 18.0 lx for Cutthroat Trout), increasing light offers no additional advantage in terms of prey detection. Similarly, prey detection is not limited by turbidity until levels extend beyond a critical level (1.65 NTU). Therefore, under conditions where predator search is not limited, other components of the predation sequence or prey behavior become more important in mediating the magnitude of piscivory. For example, prey evasion is enhanced under improved visibility (Petersen and Gadomski 1994; Mazur and Beauchamp 2003; Meager et al. 2006), and

evasion distances of prey often exceed reaction distances of piscivores under these conditions (Howick and O'Brien 1983; Miner and Stein 1996).

Though the functional forms of reaction distance in response to light and turbidity observed in this study and others were similar across species, the magnitudes of the responses differed considerably. Reaction distances above SIT averaged ~50 cm for Rainbow Trout and Bear Lake strain Cutthroat Trout (Mazur and Beauchamp 2003), and ~100 cm for Lake Trout (Vogel and Beauchamp 1999) (Figure 2.6). In contrast, the reaction distances reported here averaged ~120 cm for yearling Chinook Salmon and ~185 cm for Coastal Cutthroat Trout. It is important to note that our measurements represent an average distance under optimal visual conditions, not the maximum possible reaction distance. For example, the Coastal Cutthroat Trout occasionally reacted to prey over 300 cm away. These distances are quite impressive when considering that the predators were responding to a single 50 mm prey fish which blended in well with the gray background (personal observation). The ability of fish to manipulate their coloration to better mimic their surroundings is common (reviewed by Leclercq et al. 2010), and helps minimize contrast. This apparent contrast must exceed the contrast threshold of a piscivore's visual system for successful detection (Muntz 1990; De Robertis et al. 2003).

Several factors could explain differences between our reaction distance measurements and those reported by Vogel and Beauchamp (1999) and Mazur and Beauchamp (2003). First, these differences could reflect dissimilarities in the experimental arena. For example, we used a circular tank as opposed to the narrower rectangular trough used in the previous studies. The greater space could have influenced recognition of orientation responses differently. Additionally, reaction distances can vary considerably depending on where prey are first detected within the visual field of the predator (e.g., transverse vs. lateral plane; Dunbrack and

Dill 1984). Although not evaluated in the present study, our larger circular arena provided a greater breadth of angles from which the predators could orient towards the prey, likely allowing the predators to utilize a greater fraction of their visual field. Lastly, we tethered a single prey inside a clear tube in such a manner that enabled restricted swimming around a central pivot point thereby offering a range of aspects to the predators. Previous studies confined 1-3 free-swimming prey to a predominately side-aspect within an aquarium. Despite these methodological differences, the variability in reaction distances reported in these three studies may reflect real differences in visual capabilities among salmonid taxa.

The differences in reaction distance between the two species in this study could reflect pressures associated with fulfilling different life history strategies (i.e., semelparity vs. iteroparity) or functional role as a piscivore. For example, anadromous Coastal Cutthroat Trout are iteroparous and remain nearshore in the marine environment (Trotter 1989). Chinook Salmon are semelparous, pelagic, and require rapid marine growth to optimize the tradeoff between mortality risk and body size for reproduction (Quinn 2005). Given these added pressures and operating under the assumption that reaction distance is largely a behavioral response, we expected Chinook Salmon to respond to prey at greater distances (both above and below SIT) than the Cutthroat Trout. Since eye diameter or area of the retina is correlated with body size, and inherently linked to the theoretical range at which objects can be visually resolved (Aksnes and Giske 1993), physiological mechanisms could also be contributing to differences in reaction distance between the two species. Chinook Salmon reach adult body sizes that are much larger than both the yearlings and adult Cutthroat Trout examined here. It is possible that their reaction distance increases with length or age, reflecting a visual or behavioral ontogeny of prey recognition. For logistical reasons, we could not measure responses from larger Chinook

Salmon and evaluate this hypothesis directly. Therefore, our measurements in this study were confined to represent their capabilities at a size where early foraging success is critical for overall marine survival. Conversely, we were able to evaluate a large range of sizes for the Cutthroat Trout, including smaller juveniles that overlapped with the lengths of the yearling Chinook Salmon. Because predator fork length did not influence reaction distance for either species over the range of lengths examined, results show that (1) differences in reaction distance were driven primarily by a species effect when comparing similarly sized Chinook Salmon and Cutthroat Trout, and (2) reaction distances of Cutthroat Trout did not exhibit an ontogenetic response over a broad range of lengths where this species can be highly piscivorous (Duffy and Beauchamp 2008).

Observed differences in reaction distance were unlikely attributable to differences in the spectral sensitivity of species because both the absorbance spectra for rods and cones and the spectral sensitivity curves are quite similar among species of salmonids (Parkyn and Hawryshyn 2000; Novales Flamarique 2005). Experiments by Henderson and Northcote (1985) provide empirical support for this view. Their study measured the effect of different colors of light (blue, green, yellow, and red) on the reaction distance of Coastal Cutthroat Trout and Dolly Varden *Salvelinus malma* to artificial prey. The effect of color on reaction distance was minimal (within the error bars of our measurements) for both species across the dominant range of wavelengths emitted by our lamps. The qualitative pattern in the effect of color on reaction distance was the same for both species, but Cutthroat Trout still exhibited higher reaction distances across all light conditions. Therefore, the authors concluded that differences in reaction distance were from an effect unrelated to the spectral sensitivity of the species.

Salmonid predators in the present study could perceive all wavelengths of light emitted

by the fluorescent lamps (Parkyn and Hawryshyn 2000; Novales Flamarique 2005), so it is important to consider which fraction of the light spectrum was measured by our light sensors and how this relates to the estimates of reaction distance. We measured lux using a photometric sensor as this: 1) allowed for direct comparison to previous experiments with salmonids, 2) incorporated wavelengths of light that pelagic coastal marine piscivores are generally most sensitive to (500-600 nm; Horodysky et al. 2010) with a higher relative response (Biggs 1984), and 3) is a more intuitive unit of measure based on vertebrate vision for evaluating differences among treatments and the extent to which visual conditions change in pelagic environments. The photometric sensor's spectral responsivity curve matches the CIE (Commission Internationale de l'Eclairage) photopic curve developed for the human eye (Biggs 1984). However, fishes are generally more sensitive to shorter, bluer wavelengths than are humans (Horodysky et al. 2010). Although our lux measurements discounted wavelengths in the blue region to a greater extent than likely perceived by the predators, these wavelengths were adequately captured by our corresponding measurements of photosynthetically active radiation (Biggs 1984). Given that the colors of light emitted from our fluorescent lamps should not have had a meaningful influence on reaction distance (Henderson and Northcote 1985), these measurements captured the true light environment experienced by the predators. When considering the purpose and utility of visual foraging models (Beauchamp et al. 1999), both units of measure are sufficient for characterizing the optical environment in natural systems and for quantitatively describing behavioral responses like reaction distance as a function of light.

Twilight is a period of high activity for piscivores (Helfman 1986), and peaks in piscivory under such conditions have been reported in lakes (Beauchamp 1990; Beauchamp et al. 1992; Malmquist et al. 1992; Kahilainen et al. 2009). During dusk, light declines rapidly with

depth over short time scales to levels well below the SIT values reported here (Henderson and Northcote 1985). Schools of prey often disperse during this time, increasing encounter rates with individual prey (Beauchamp et al. 1999; Mazur and Beauchamp 2006). Therefore, accurately measuring reaction distances to individual prey under degraded visual conditions is of particular importance. These measurements could be a better indicator of predatory performance than those that occur above SIT. An important question that remains is how reaction distance changes with aggregations of prey. However, the scale at which these types of experiments can be performed efficiently in the laboratory is likely insufficient for unbiased measurement. By linking telemetry with multi-beam acoustics, Dunlop et al. (2010) observed Lake Trout exhibiting rapid bursts of speed toward schools of Cisco *Coregonus artedii* (proxy for attack) at proximities of 2.4-6.4 m during daylight in Lake Opeongo, Ontario. Their study represents an important first step towards *in situ* measurement of such responses.

Turbidity strongly influences prey detection for piscivores. Turbidity reduced the reaction distance of yearling Chinook Salmon by ~70% from 0.4-7.2 NTU. For comparison, reaction distances of adult Lake Trout diminished by ~50% over the same range (Vogel and Beauchamp 1999). Direct observation from De Robertis et al. (2003) suggested that reaction distances of yearling Sable Fish *Anaplopoma fimbria* feeding on Chum Salmon *O. keta* dropped by ~85% from 0-10 NTU. These results show that the ability of piscivores to effectively detect fish prey declines rapidly with moderate increases in turbidity even under well-illuminated conditions. The range of turbidities used in this experiment reflected a wide range of oligotrophic to eutrophic salmonid habitats, excluding the higher turbidities experienced in glacial and some estuarine waters (Gregory 1994; Gregory and Levings 1998; Vogel and Beauchamp 1999). In productive coastal marine habitats during dense phytoplankton blooms

(Lovvorn et al. 2001) or in river plumes (Emmett et al. 2004) where turbidities may exceed those examined here, planktivory should be a more effective foraging strategy than piscivory for juvenile Chinook Salmon.

Prey size influenced measurements of reaction distance in our experiments. Reaction distances declined significantly by ~30-40% depending on light level for yearling Chinook Salmon as prey length declined from 50 to 23 mm. This experiment was intended only as an initial examination of the effect of declining prey size on the reaction distances of piscivorous salmonids, and we cannot determine whether differences among prey species contributed to this decline. However, the results suggest that sizes of prey representing post-larval fishes that have achieved full pigmentation can limit reaction distance, contrary to what was observed over a range of larger prey in previous studies (55-139 mm; Vogel and Beauchamp 1999). Since all prey were fully pigmented, this decline could reflect reductions in the cross-sectional area of the prey as length declined (Aksnes and Giske 1993). Body depth measurements from the prey supported this suggestion and ranged from 4-5 mm for the Threespine Stickleback, 5-6 mm for the Cutthroat Trout, and 9-11 mm for the Rainbow Trout treatments. The transition from a contrast-based to an acuity-based visual system for detecting prey (Breck 1993) may depend more on the onset of pigmentation for translucent larval fishes than on length alone.

Foraging models incorporating light-dependent reaction distance functions like those developed here provide a useful, mechanistic approach for exploring distribution, foraging success, and predation risk in pelagic communities (Scheuerell and Schindler 2003; Jensen et al. 2006; Gjelland et al. 2009; Kahilainen et al. 2009; Hansen et al. 2013). This study increases the capacity of the visual foraging approach by supplying key parameters for applications to additional ecologically and economically important species. Knowing how the environment

influences prey detection and the foraging success of different species of piscivores benefits fisheries managers by providing the means for quantitatively gauging which species may have a competitive or predatory advantage under certain conditions, or how the performance of any particular species and resulting predator-prey dynamics are likely to change with shifts in the environment. Our results highlight the need to evaluate species and life-stage specific responses. These differences have important implications for predicting how the magnitude of piscivory is likely to change through the ontogeny of a predator and across environmental conditions, communities, and systems.

The goal of most fisheries management agencies is to provide a suite of recreational fishing opportunities for the public, while conserving native species. Different species have been successfully introduced both legally and illegally into many salmonid-dominated western lakes in an attempt to meet these competing demands, and some introductions have greatly diminished the ecological integrity of the native fish communities. For example, introductions of Lake Trout into Yellowstone Lake, Flathead Lake, Bear Lake, and Lake Chelan, have threatened or diminished the native salmonid populations (Martinez et al. 2009; Ellis et al. 2011; Schoen et al. 2012), requiring that fisheries biologists develop creative management solutions for either reintroducing or conserving native species (Al-Chokhachy et al. 2009; Hansen et al. 2010). Additionally, illegal or unintended introductions of nonnative warm-water piscivores into western systems is an increasing problem (Johnson et al. 2009). Therefore, studies evaluating the light and turbidity-dependent prey detection capabilities of key pelagic warm-water piscivores (e.g., Walleye *Sander vitreus* and Striped Bass *Morone saxatilis*) are greatly needed. Armed with this type of information for key species, we will be better equipped for evaluating the potential success and food web implications of native species reintroductions and the

ecological impacts of current or looming illegal introductions of nonnative piscivores.

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Tables

Table 2.1. Results from the model selection analysis evaluating different functional relations ('Model' and 'f(x)' columns; I = light in lx) for describing light-dependent reaction distances for Chinook Salmon and Coastal Cutthroat Trout. The table shows ΔAICc and Akaike weight (w_i) values corresponding to each model formulation tested. These values are referenced to the results generated from different formulations within each candidate model ('Within model' columns), and across the entire set of candidate models ('Across models' columns). Results within each candidate model are listed beginning with the most saturated formulation where no parameters are shared between species ('—' symbol under 'Shared parameters' column), and ending with the most reduced formulation where all parameters are shared. The total number of parameters corresponding to each formulation (k) includes the species-specific error terms. Values in bold correspond to the best fitting models (i.e., ΔAICc values ≤ 2).

Model	f(x)	Shared parameters	k	$-2l$	AICc	ΔAICc		w_i	
						Within model	Across models	Within model	Across models
Hockey stick (linear)	RD = $a + bI$ for $I \leq t$ RD = $a + bt$ for $I > t$	-	8	574.377	592.66	0.00	0.00	0.9175	0.3669
		a	7	588.133	603.88	11.22	11.22	0.0034	0.0013
		b	7	593.429	609.18	16.52	16.52	0.0002	0.0001
		t	7	581.841	597.59	4.93	4.93	0.0780	0.0312
		a, b	6	626.317	639.61	46.95	46.95	0.0000	0.0000
		a, t	6	601.233	614.53	21.86	21.86	0.0000	0.0000
		b, t	6	593.245	606.54	13.87	13.87	0.0009	0.0004
		a, b, t	4	706.009	714.61	121.94	121.94	0.0000	0.0000
		-	8	580.453	598.74	4.11	6.08	0.0671	0.0176
Piecewise (power)	RD = aI^b for $I \leq t$ RD = at^b for $I > t$	a	7	613.444	629.19	34.57	36.53	0.0000	0.0000
		b	7	580.452	596.20	1.57	3.54	0.2386	0.0625
		t	7	581.129	596.88	2.25	4.22	0.1701	0.0446
		a, b	6	652.945	666.24	71.61	73.57	0.0000	0.0000
		a, t	6	615.929	629.22	34.59	36.56	0.0000	0.0000
		b, t	6	581.336	594.63	0.00	1.97	0.5241	0.1373
		a, b, t	4	706.608	715.21	120.58	122.54	0.0000	0.0000
		-	6	614.529	627.82	2.38	35.16	0.2331	0.0000
Power	RD = aI^b	a	5	648.964	659.87	34.43	67.21	0.0000	0.0000
		b	5	614.530	625.44	0.00	32.78	0.7669	0.0000
		a, b	3	716.125	722.48	97.04	129.82	0.0000	0.0000
		-	8	576.145	594.43	0.26	1.77	0.4485	0.1516
Holling type II (with y-intercept)	RD = $aI/(b + I) + c$	a	7	589.590	605.34	11.17	12.68	0.0019	0.0006
		b	7	578.425	594.17	0.00	1.51	0.5097	0.1723
		c	7	583.603	599.35	5.18	6.69	0.0383	0.0129
		a, b	6	593.796	607.09	12.91	14.42	0.0008	0.0003
		a, c	6	625.682	638.97	44.80	46.31	0.0000	0.0000
		b, c	6	593.859	607.15	12.98	14.49	0.0008	0.0003
		a, b, c	4	706.762	715.36	121.18	122.70	0.0000	0.0000

Table 2.2. Best fitting models developed for the reaction distances (RD; cm) of Chinook Salmon and Coastal Cutthroat Trout as functions of light (I; lx), turbidity (NTU), and prey size (fork length; FL). An equation describing the proportional decline ($P[RD_{max}]$) in reaction distance with turbidity is also shown for Chinook Salmon. The models fit to the reaction distances of Chinook Salmon as a function of prey size and light (SIT = saturation intensity threshold) in log-log space are presented in linear form.

Species	Variable	Limb or factor level	Model	Breakpoint (lx or NTU)	r^2	Parameter error		
						Parameter	SE	
Chinook Salmon	Light	Increasing Level	RD = 2.68*I + 55.39	≤ 24.9	0.89	Slope	0.222	
			RD = RD _{max} = 122.11	> 24.9		Y-intercept	2.608	
						Breakpoint	1.819	
	Turbidity	Level	Declining	RD = RD _{max} = 124.06	≤ 1.65	0.96		
				RD = 184.40e ^(-0.240*NTU)	> 1.65		Y-intercept	2.426
		Level	Declining	$P(RD_{max}) = 1.0$	≤ 1.65	0.96	Breakpoint	0.146
				$P(RD_{max}) = 1.49e^{(-0.240*NTU)}$	> 1.65			
	Prey size	Low light (< SIT)	High light (> SIT)	RD = (FL ^{0.415})*(10 ^{1.288})	-	0.65	Exponent 1 (low)	0.124
							Exponent 2 (low)	0.191
							Exponent 1 (high)	0.124
Exponent 2 (high)							0.190	
Coastal Cutthroat Trout	Light	Increasing Level	RD = 5.66*I + 85.31	≤ 18.0	0.84	Slope	0.477	
			RD = RD _{max} = 187.05	> 18.0		Y-intercept	6.105	
						Breakpoint	0.543	

Table 2.3. Results from fitting different linear models to test whether reaction distances (RD) above the saturation intensity threshold differed between Chinook Salmon and Coastal Cutthroat Trout after accounting for predator fork length. ΔAICc and w_i (Akaike weight) values in bold represent the best fit models (i.e., ΔAICc values ≤ 2). The total number of parameters fit in each linear model (k) includes the error term (ϵ).

Linear model	k	$-2l$	AICc	ΔAICc	w_i
RD ~ Species + ϵ	3	78.016	84.5613	0.00	0.4841
RD ~ Length + Species + ϵ	4	76.011	84.9413	0.38	0.4003
RD ~ Length + Species + Length:Species + ϵ	5	75.998	87.4268	2.87	0.1155
RD ~ Length + ϵ	3	134.61	141.153	56.59	0.0000

Table 2.4. Results from fitting different linear models to test whether reaction distances (RD) of Chinook Salmon varied as a function of prey size and light. ΔAICc and w_i (Akaike weight) values in bold represent the best fit models (i.e., ΔAICc values ≤ 2). The total number of parameters fit in each linear model (k) includes the error term (ϵ).

Linear model	k	$-2l$	AICc	ΔAICc	w_i
RD ~ PreySize + Light + PreySize:Light + ϵ	5	-89.53	-77.534	0.00	0.5396
RD ~ PreySize + Light + ϵ	4	-86.5	-77.208	0.33	0.4584
RD ~ PreySize + ϵ	3	-73.09	-66.337	11.20	0.0020
RD ~ Light + ϵ	3	-58.33	-51.577	25.96	0.0000

Figures

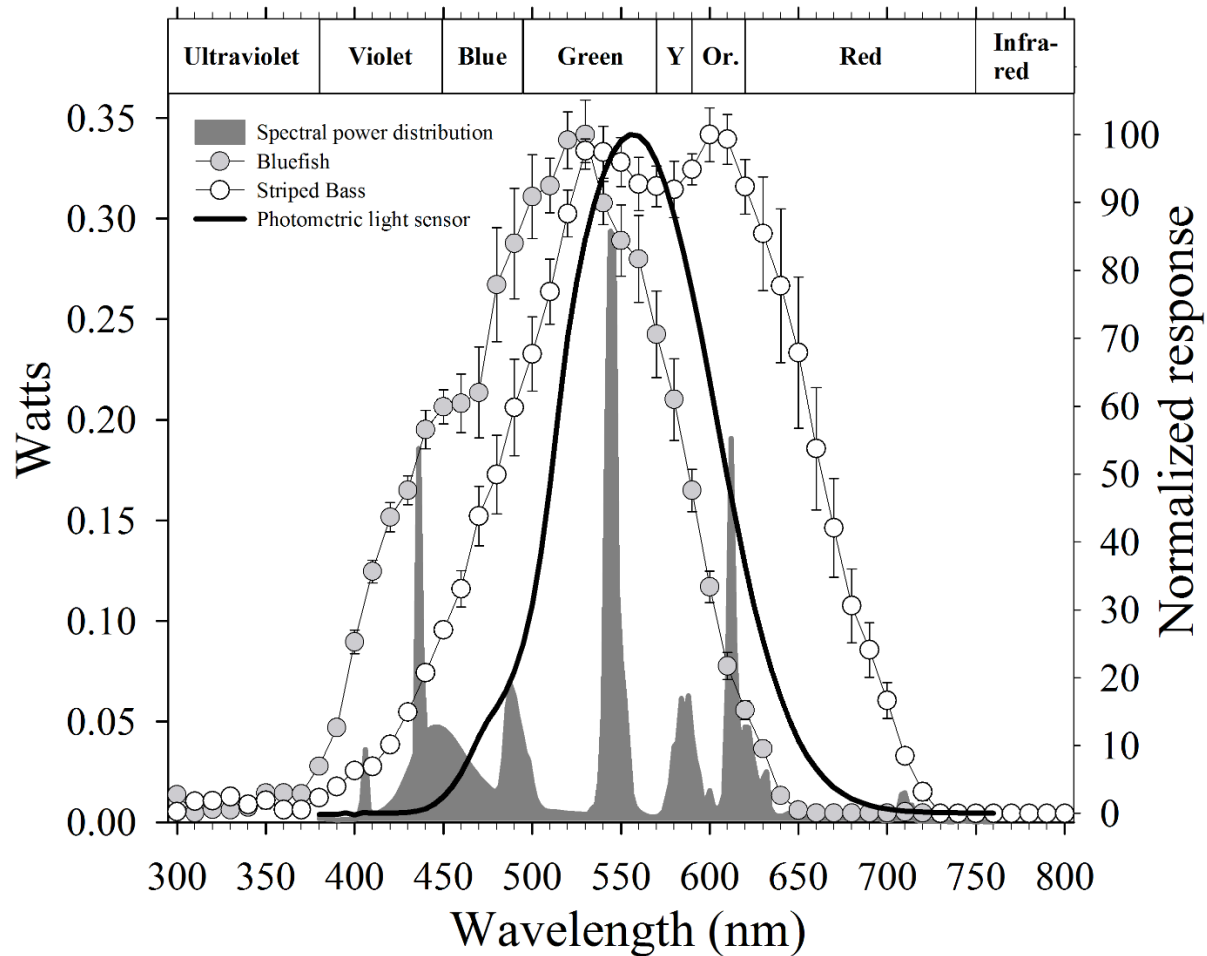


Figure 2.1. Spectral power distribution (watts) of the fluorescent lamps at maximum voltage (data from Philips Lighting) in relation to the normalized spectral sensitivity curves developed for Bluefish *Pomatomus saltatrix* and Striped Bass *Morone saxatilis* (circles are means of five individuals $\pm 1 SE$; data from Horodysky et al. 2010), and the normalized spectral responsivity curve of the LI-210 photometric light sensor (measures lux; data from LI-COR[®]). The Y stands for yellow and the Or. stands for orange.

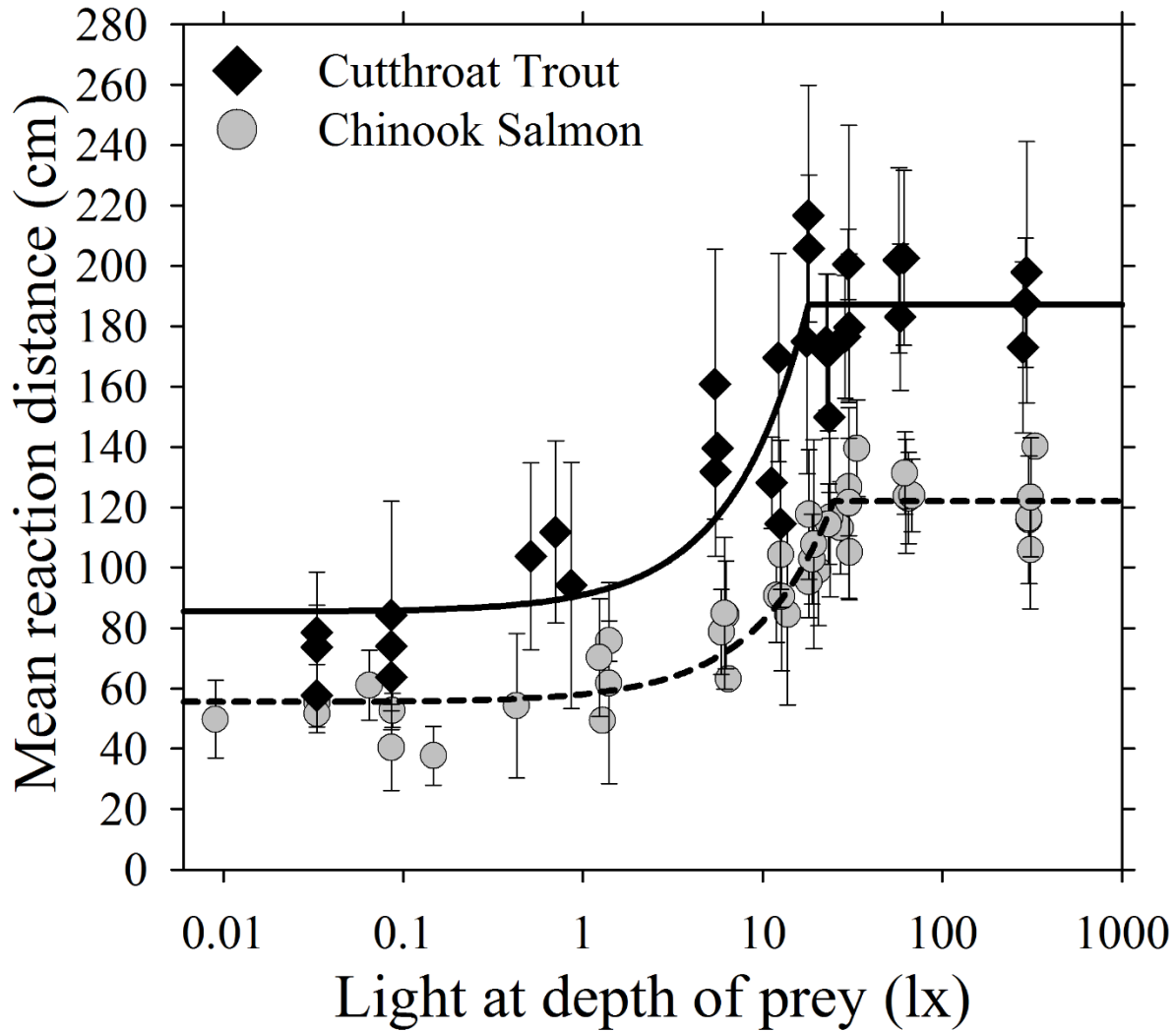


Figure 2.2. Reaction distance as a function of light for Chinook Salmon ($N = 41$) and Coastal Cutthroat Trout ($N = 31$) to 47-52 mm fork length Rainbow Trout. Data points represent the mean reaction distance $\pm 2 SE$ pooled across predators from each individual trial. Lines represent the fitted piecewise models (solid line for Cutthroat Trout and dashed line for Chinook Salmon). Note that the x-axis (light) is presented on a \log_{10} scale.

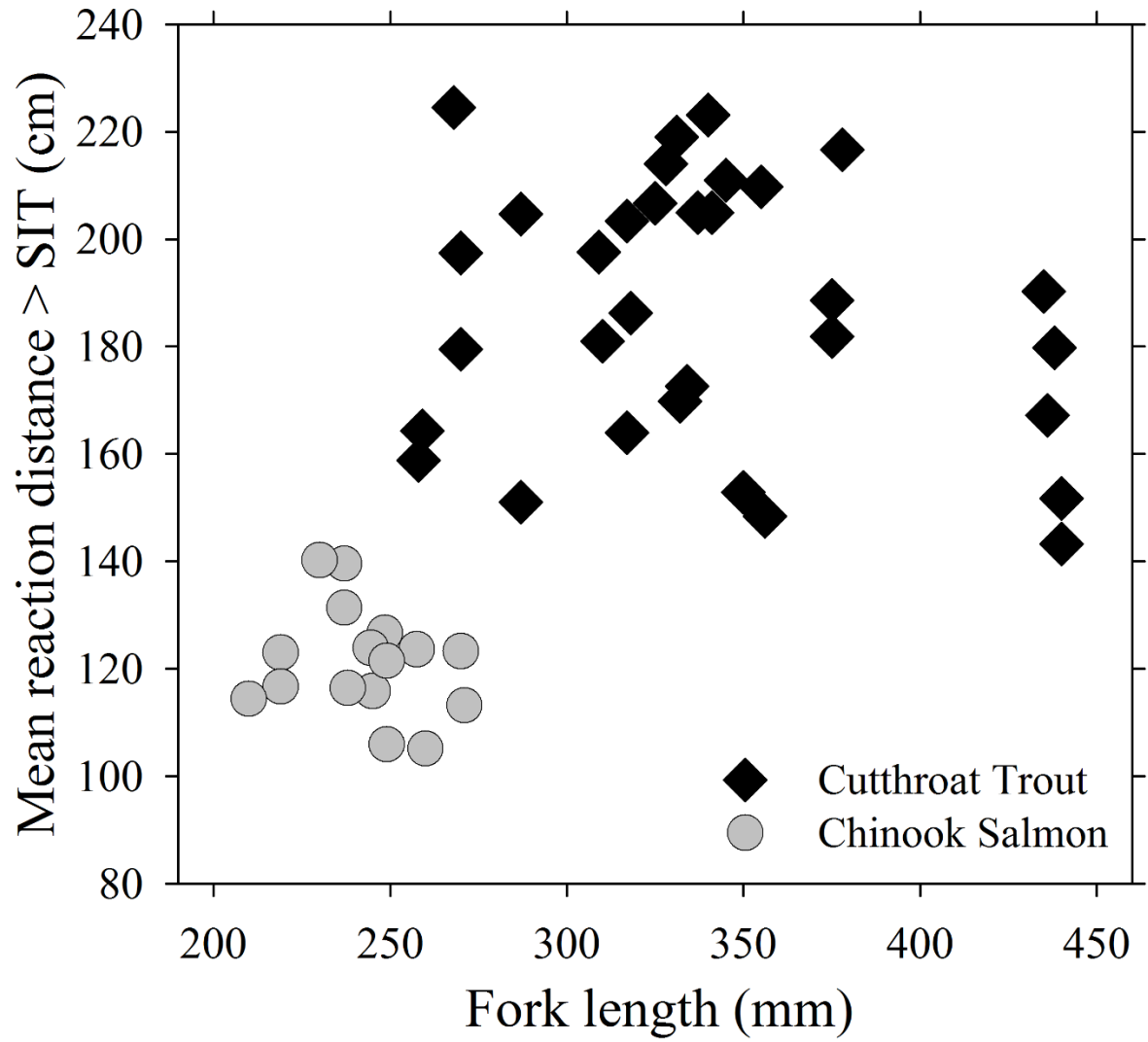


Figure 2.3. Mean reaction distances measured for pairs of Chinook Salmon ($N = 16$) and individual Coastal Cutthroat Trout ($N = 32$) to 47-52 mm fork length Rainbow Trout at light levels above the saturation intensity threshold (SIT) as a function of predator fork length.

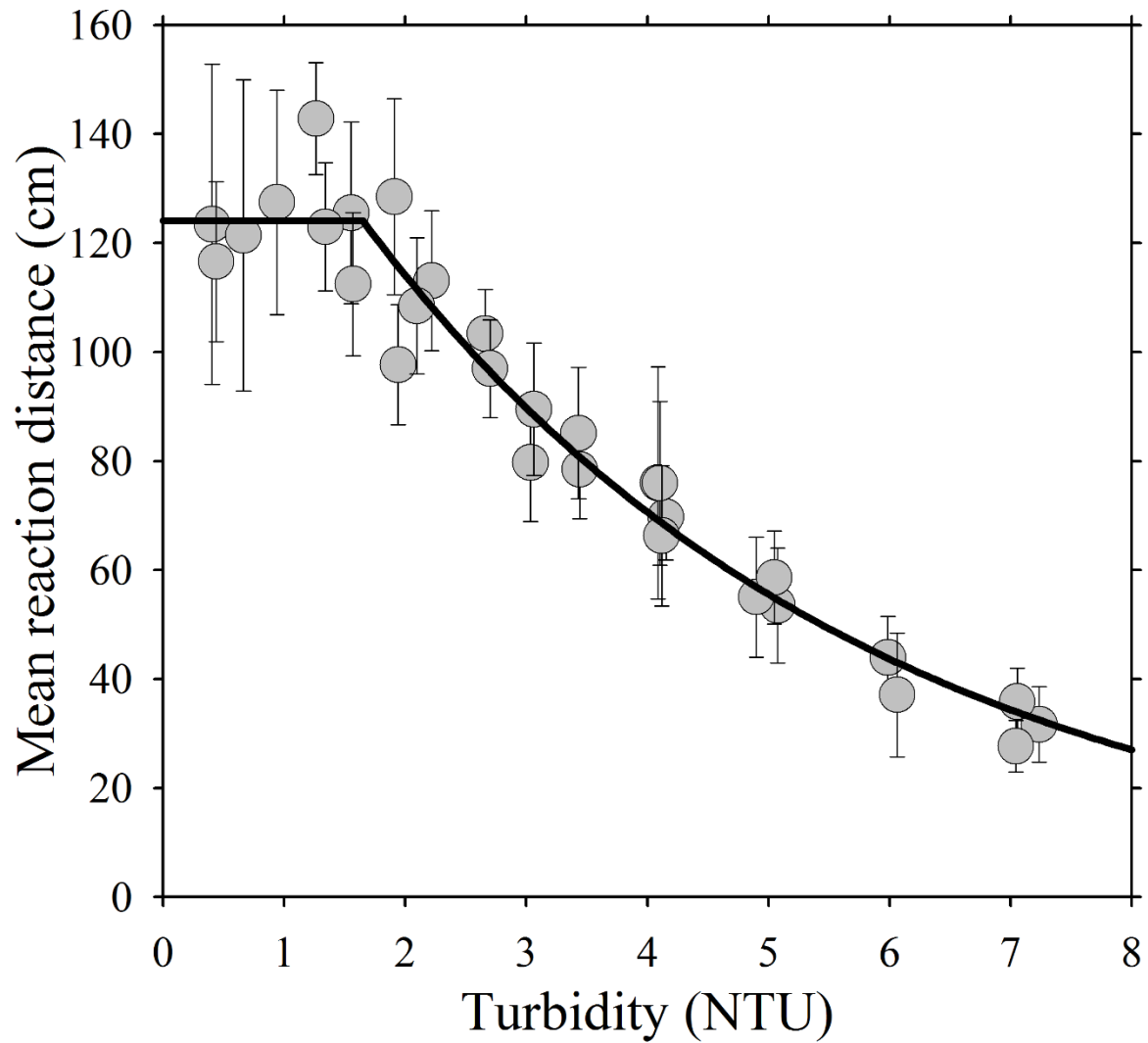


Figure 2.4. Reaction distance as a function of turbidity for Chinook Salmon ($N = 30$) to 48-54 mm fork length Rainbow Trout. Data points represent the mean reaction distance $\pm 2 SE$ pooled across predators from each individual trial. The solid line represents the fitted piecewise model.

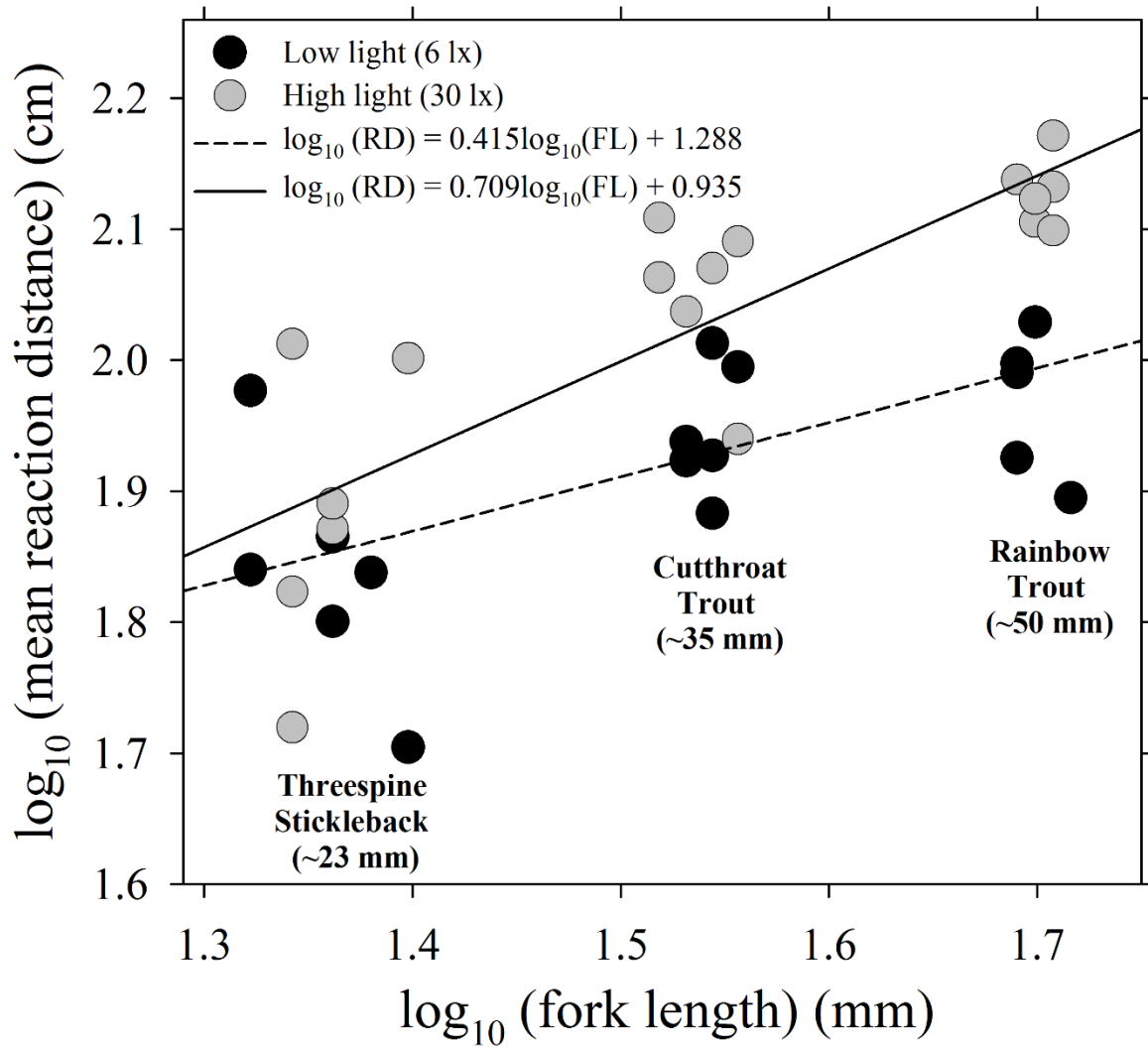


Figure 2.5. Reaction distances (RD) measured for Chinook Salmon at different light and prey size (fork length; FL) combinations. Points represent the mean reaction distances observed from replicate trials ($N = 6$) at each combination. Lines represent the best fit linear model. Note that both reaction distance and fork length are on \log_{10} scales.

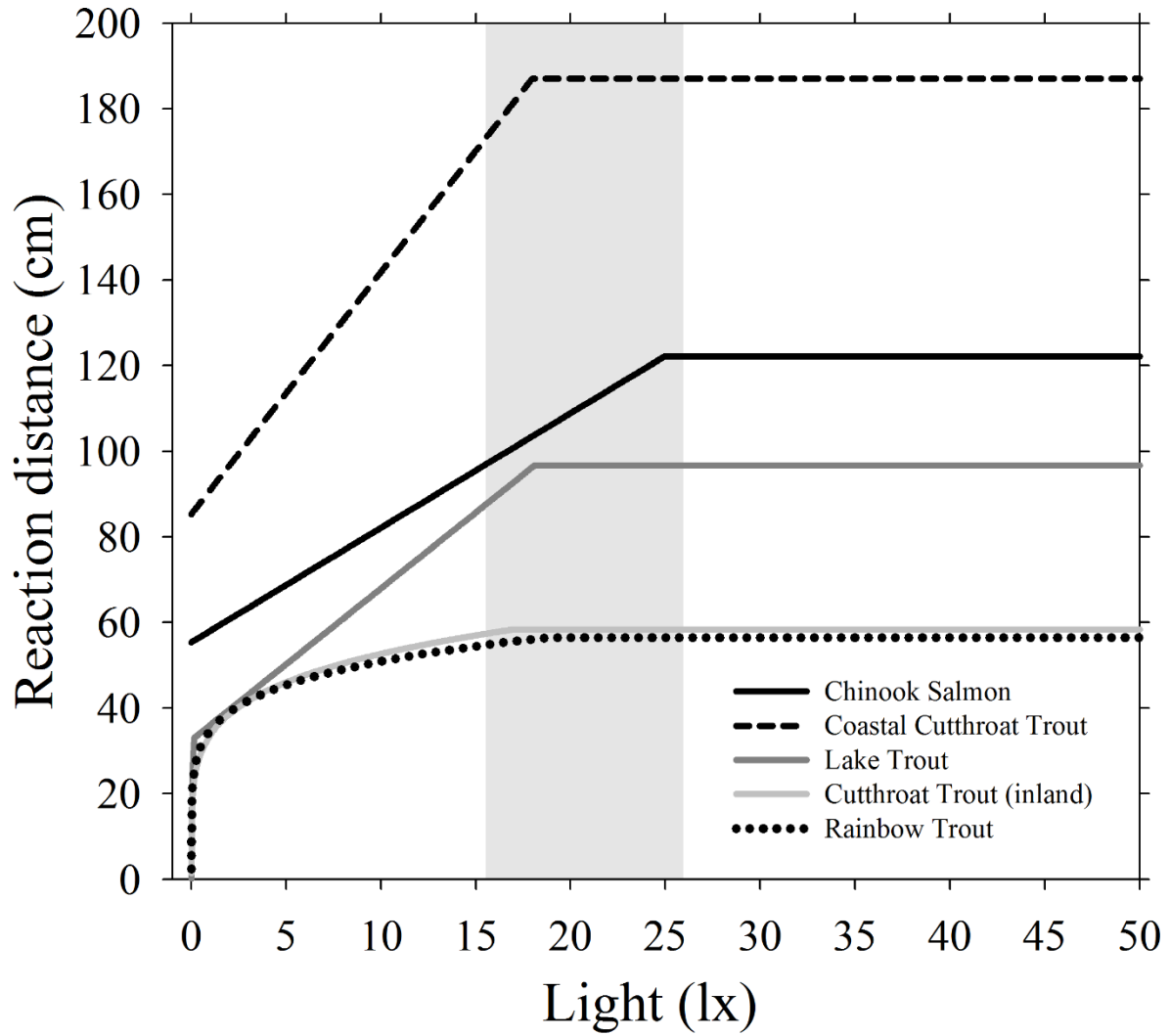


Figure 2.6. Clear water, light-dependent reaction distance functions for all piscivorous salmonids evaluated to date. Lines for Chinook Salmon and Coastal Cutthroat Trout are from the present study. All other species are from Mazur and Beauchamp (2006). The gray shaded region brackets the range of estimated saturation intensity threshold values.

Chapter 3.—Latitudinal and photic effects on diel foraging and predation risk in pelagic ecosystems

Abstract.—Clark and Levy (1988) described an antipredation window for smaller planktivorous fishes during crepuscular periods when light permits feeding on zooplankton, but limits visual detection by piscivores. Yet, it remains unclear how pelagic predator-prey interactions change with latitude in response to shifts in the diel light environment or water clarity. We evaluated how latitudinal and seasonal shifts in diel light regimes alter the foraging-risk environment for visually-feeding planktivores and piscivores across a natural range of turbidities. Using a model of aquatic visual feeding, paired with a model of sun and moon illuminance, we estimated foraging rates of an idealized planktivore and piscivore over depth and time across factorial combinations of latitude (0-70°) and turbidity (0-5 NTU) during the summer solstice and fall equinox. We evaluated the foraging-risk environment based on changes in the magnitude, duration, and peak timing of the antipredation window. The model scenarios generated up to 10-fold shifts in magnitude, 24-fold shifts in duration, and 6 hr shifts in timing of the peak antipredation window. In general, the size of the window increased with increasing latitude. This pattern was strongest during the solstice. In clear water (≤ 1.5 NTU), sharp peaks in the magnitude and duration of the window formed at 58-62° latitude, before falling near zero as the environment became saturated with light under a midnight sun at latitudes approaching 70°. Conversely, at turbidities > 1.5 NTU, steeper reductions in the visual range of piscivores than planktivores created an antipredation window for much longer periods at these higher latitudes. Latitudinal dependencies were essentially lost during the equinox, indicating a progressive compression of the antipredation window in magnitude and duration from early summer into fall. These model results suggest that the foraging-risk environment for visually-feeding planktivores

and piscivores changes in systematic ways along a broad latitudinal gradient and with increasing turbidity. These changes have different implications for the structure of pelagic predator-prey interactions and the behavioral strategy needed to effectively cope with the fundamental tradeoff between feeding and avoiding predators at different latitudes.

Introduction

Most consumers are confronted with spatial and temporal trade-offs between foraging opportunities and predation risk (Lima and Dill 1990). The challenge is to balance this tradeoff such that sufficient energy intake and a corresponding level of fitness is achieved (Mangel and Clark 1986; Hughie and Dill 1994). This is no easy task considering the dynamic nature of generally limited foraging opportunities (Armstrong and Schindler 2011) and mortality risk over time and space (Clark and Levy 1988; Jensen et al. 2006). Dynamics in feeding profitability and predation risk are driven largely by asymmetric responses of predators and prey to varying environmental conditions (Hansen et al. 2013a) and heterogeneity in the physical habitat where predator-prey interactions occur (Crowder and Cooper 1982; Ellner et al. 2001; Kauffman et al. 2007; Rilov et al. 2007). Achieving certain energetic states often requires adaptive behavioral strategies that exploit habitat complexity in a manner that attempts to minimize the ratio of mortality risk to foraging gain on a sustainable basis (Werner and Gilliam 1984; Mangel and Clark 1986; Clark and Levy 1988; Lima and Dill 1990).

Behavioral strategies come in diverse forms for different taxa (Lima and Dill 1990; Damsgard and Dill 1998; Lima 1998). Perhaps the most well-known strategy is diel vertical migration by fishes and invertebrates in pelagic marine and freshwater habitats (Neilson and Perry 1990; Hays 2003; Mehner 2012). The model of Clark and Levy (1988) was the first to integrate foraging gain and predation risk as constraints on habitat use for fishes at intermediate

trophic levels. This model predicted that visually-feeding planktivores should use diel vertical migration to forage near the surface (where prey densities are greatest) during crepuscular periods when light intensities are sufficient for detecting zooplankton prey, yet low enough to reduce mortality risk from visually-feeding piscivores; termed the “antipredation window” (Clark and Levy 1988) (Figure 3.1). Empirical support exists for the antipredation window hypothesis, but seasonal dynamics in biotic (e.g., body size, prey density and distribution) and abiotic (e.g., light, turbidity, and temperature) factors can generate variation in movement patterns within and among systems and individuals (Stockwell and Johnson 1999; Scheuerell and Schindler 2003; Hardiman et al. 2004; Jensen et al. 2006; Gjelland et al. 2009; Kahilainen et al. 2009; Busch et al. 2011). Despite rigorous evaluation, the general suggestion that planktivores move and feed within the antipredation window still remains (Mehner 2012). However, research on this topic consists primarily of system-specific case studies. A broader conceptual understanding of this phenomenon is lacking. How different characteristics of the antipredation window (Figure 3.1) change with shifts in the diel light environment over a broad latitudinal gradient, and whether turbidity, the scatter of light from suspended particles (Davie-Colley and Smith 2001), modifies these patterns remains unexplored.

The latitudinal dependency in seasonal and diel light regimes, and differences in the visual systems of planktivores versus piscivores provide reason to expect meaningful changes to the antipredation window across these dimensions of time and space. Peak solar elevation and solar irradiance decrease with increasing latitude (Figure 3.2A, B) (Janiczek and DeYoung 1987). Daily insolation follows accordingly, except around the summer solstice when increasing day-length counteracts the effect of reduced solar elevation; most notably above the polar circle ($66^{\circ} 33' 44''$ N or S) where the sun remains above the horizon 24 h a day (Kirk 2011). More

ecologically relevant is the transition between daylight and night (i.e., twilight) along this gradient. Twilight may only last 20-25 min near the equator, but extend for hours at high latitudes (Figure 3.2C, D).

Planktivores employ an acuity-based visual system for feeding on small prey like zooplankton, whereas piscivores employ a contrast-based system for pursuing larger, more conspicuous fish (Breck 1993; De Robertis et al. 2003). As a result, the scale at which prey are detected and the sensitivity to changes in light intensity and turbidity differ considerably between planktivores and piscivores. For both groups, reaction distance (a behavioral proxy for prey detection) responds asymptotically with light, but the magnitude of the response saturates at a higher light level and is approximately five-fold greater for contrast-based piscivores (Howick and O'Brien 1983; Vogel and Beauchamp 1999; Mazur and Beauchamp 2003; Hansen et al. 2013b) than for acuity-based planktivores (Vinyard and O'Brien 1976; O'Brien 1987; Link and Edsall 1996). These asymmetries in the visual systems of planktivores versus piscivores have the potential to interact with the diel light regime at different latitudes to produce meaningful changes in the antipredation window.

Turbidity is an important component of pelagic ecosystems and influences visual predator-prey interactions (Abrahams and Kattenfeld 1997; De Robertis et al. 2003). Like shifts in diel illuminance over a broad latitudinal gradient, turbidity should also significantly and predictably modify the foraging-risk environment for pelagic consumers. Reaction distances for both planktivores and piscivores decline with increasing turbidity. This decline is steeper for piscivores (Vogel and Beauchamp 1999; Hansen et al. 2013b) than for planktivores (Vinyard and O'Brien 1976; Gregory and Northcote 1993), because piscivores detect prey at greater distances and the degree of contrast degradation (by backscatter from suspended particles) increases

exponentially with distance between predator and prey (Utne-Palm 2002; De Robertis et al. 2003). Therefore, increases in turbidity should reduce predation risk for planktivores across all times of day.

In this study, we integrate a sun and moon illuminance model, the foraging rate model of Clark and Levy (1988), and empirical relationships describing the light- and turbidity-dependent visual prey detection responses of an idealized planktivore and piscivore to ask: how does natural variation in photic conditions shape the foraging-risk environment for visually-feeding planktivores and piscivores in pelagic ecosystems? To address this question, we use the antipredation window as an integrative representation of the foraging-risk environment. Our specific objective was to determine whether the magnitude, duration, and timing of the antipredation window changes in systematic ways in response to latitudinal, seasonal (summer and fall), and diel shifts in light regime, and to coincident increases in water turbidity. We evaluate changes in these factors across the full gradient of latitude and turbidity that characterize freshwater systems supporting visually-feeding, pelagic planktivores and piscivores.

Methods

Generalized pelagic setting

Diel-seasonal variation in vertical light gradients, turbidity, and thermal stratification provide the predominant habitat structure in pelagic predator-prey systems (Beauchamp et al. 1999; Hansen et al. 2013a). How planktivores, their zooplankton prey, and piscivores distribute in response to shifts in these factors determines how foraging opportunities and predation risk vary over time and space. For this analysis, we considered a common pelagic predator-prey scenario in which (1) zooplankton are concentrated within and above the thermocline at all times (Edmondson and Litt 1982; Hardiman et al. 2004; Baldwin et al. 2000), thus creating a distinct

contrast in the potential foraging gain of planktivores inhabiting deeper darker waters versus brighter surface waters (Eggers 1978; Clark and Levy 1988), and (2) piscivores track the vertical distribution of planktivores (Hrabik et al. 2006; Jensen et al. 2006). The latter assumed that predator-prey movements were not limited by physiological constraints (e.g., temperature tolerances or hypoxia: Hansen et al. 2013a). Above 70° latitude, lakes are amictic (ice covered year-round) or cold monomictic (ice free, but not warming above 4°C during summer), and 70° is considered the upper extent at which lakes can thermally stratify during the growing season (Lewis 1983; Lewis 2011). Therefore, we defined 70° as the upper extent at which predator-prey interactions of this nature are likely to occur (Jensen et al. 2008; Gjelland et al. 2009).

We used information collected from a large sample of temperate lakes to provide an empirical summary for (1) the depths containing zooplankton prey, and therefore, the depths over which foraging rates were modeled under this scenario, and (2) the range of turbidities that characterize pelagic ecosystems. To define the maximum depth containing zooplankton, we used the frequency of meta-limnetic depths (i.e., bottom of the thermocline) generated from temperature profiles ($N = 315$ records) measured during summer and fall in 285 thermally stratified lakes (U.S. Environmental Protection Agency 2009). We restricted our evaluation to lakes ≥ 10 m deep, as shallower lakes were generally not consistently stratified when sampled. Lakes of these depths are prone to periodic mixing during the growing season (Lewis 1983). The frequency distribution for the bottom of the thermocline was slightly skewed to the right, but centered on 10 m (Figure 3.3A). Therefore, foraging rates were modeled over 0-10 m. The efficacy of pelagic piscivory declines with increasing eutrophication (Colby et al. 1972; Persson et al. 1991; Beauchamp et al. 1999). So, turbidities were selected based on measurements from oligotrophic and mesotrophic lakes only. Turbidities in these lakes ($N = 596$) were mostly ≤ 5

NTU (92nd percentile of 670 records; U.S. Environmental Protection Agency 2009; Figure 3.3B). This distribution corresponded well with those in north-temperate and sub-arctic lakes (Ruhland and Smol 1998; LaPerriere et al. 2003a; Ogbebo et al. 2009).

Diel light regimes

The light regimes under which this predator-prey scenario was evaluated were generated using the illuminance model of Janiczek and DeYoung (1987) assuming average cloud cover. Mean incident light levels (lux) were modeled for every 5-min interval and 1° of latitude (longitude = 120° W) in the northern hemisphere during the summer solstice (20 June 2012; solar declination = 23°27') and fall equinox (23 Sept. 2014; solar declination = 0°) (Figure 3.2A, B). Dates were selected such that each period exhibited an identical moon phase (waning or waxing), and were within one day of a new moon. Some solar radiation reflects back into the atmosphere from the surface of the water. The amount of reflection depends on the solar zenith angle (90° — solar elevation). Although solar rays are most concentrated at the zenith angle, the angular distribution of skylight is still quite complex, particularly under cloud cover and during twilight when the sun is below the horizon and light continues reflecting off the upper atmosphere. Thus, total reflectance is difficult to determine accurately (Kirk 2011). Assuming radiance is the same from all directions, a reflectance of 6.6% is obtained under clear skies, and 5.2% under an overcast sky for a flat water surface (Bukata et al. 1995). We used the average of these two values (5.9%) to adjust the incident light levels modeled for each season, latitude, and 5-min interval to what was available for the aquatic consumers. Lastly, we used the Beer Lambert equation:

$$L_z = L_0 e^{-kz} \quad (3.1),$$

where light at depth z (L_z) depends on incident light penetrating the air-water interface L_0 and the

extinction coefficient k , to estimate light attenuation and model light availability within 1-m depth strata from 0-10 m.

Turbidity and light extinction

Suspended and dissolved substances (inorganic and organic) impair vision underwater in two ways: first, through reduced light penetration, and second, by degrading the apparent contrast or brightness of an object from its background through the scattering of image-forming light (Loew and McFarland 1990). Turbidity samples from natural systems can contain both inorganic and organic material, but determining the relative contribution of each is difficult (Kirk 2011). The effect of suspended organic matter on the visual prey detection responses of planktivores and piscivores has received little attention (Utne-Palm 2002). Thus, for the purposes of this study, we were forced to assume that both forms of turbidity influence visual prey detection equally. To link the visual responses of consumers (see below) to an appropriate rate of light extinction caused in part by sediment or other organic material at a particular turbidity level (in NTU), we back-calculated light extinction coefficients of photosynthetically active radiation (400-700 nm waveband; k in equation 3.1) from an empirical model relating the compensation depth $Z_{0.01}$ (depth in m at which 1% of surface light remains) to turbidity in a suite of clear water to glacially-dominated systems in Alaska (from Lloyd et al. 1987) (Figure 3.3B):

$$\log(Z_{0.01}) = 1.147 - 0.603(\log(NTU)) \quad (3.2).$$

Substituting $Z_{0.01}$ for z and solving for k by setting L_z/L_0 equal 0.01 in equation (3.1) leaves:

$$k = -\frac{\ln(0.01)}{Z_{0.01}} \quad (3.3).$$

Model of aquatic visual feeding

To explore how natural variation in photic conditions shapes the foraging-risk environment for visually-feeding planktivores and piscivores, we estimated foraging rates for

both groups across the full range of latitude (0-70° N) and turbidity (0-5 NTU). The foraging rates of the piscivores were considered a proxy for predation risk (μ). These responses were then used to formulate the corresponding antipredation windows. We implemented the model and model parameters of Clark and Levy (1988), as modified by Scheuerell and Schindler (2003):

$$f \text{ or } \mu = \frac{\pi(r+b)^2 v \rho}{1+h\pi(r+b)^2 v \rho} \quad (3.4),$$

where r is the light- and turbidity-dependent reaction distance of the consumer to either zooplankton for planktivores or fish prey for piscivores, b is the radius of an individual zooplankter (5×10^{-4} m) or school of planktivores (0.5 m), v is the mean cruising speed of a planktivore (0.05 m/s) or piscivore (0.3 m/s), ρ is the density of zooplankton (10,000 per m³) or schools of planktivores (0.001 per m³), and h is the attack and handling time for a planktivore feeding on zooplankton (1.8 s), or a piscivore hunting planktivores (5 s). Foraging rates were estimated for every 5-min interval over a 24-h period and for every 1-m strata from 0-10 m. All parameter values, except reaction distance, were held constant across the suite of photic conditions examined. The purpose of this study was to explore how the generalized predator-prey scenario plays out under different patterns of diel illuminance over a broad latitudinal gradient and increases in turbidity, all else being equal. Keeping environmental conditions and model parameters constant across simulations isolated the effects of changes in photic conditions on the foraging-risk environment for pelagic consumers at different latitudes. Therefore, this analysis represents a foundation upon which additional layers of complexity can be constructed.

Planktivore and piscivore reaction distance

We created generalized relationships describing the reaction distance of planktivores and piscivores as a function of light intensity L (lx; Figure 3.4A) by averaging reaction distances r (cm) predicted from empirical models developed from experimental studies for pelagically-

oriented fish species. The following saturating relationship was generated for planktivores (Link and Edsall 1996; Holbrook et al. 2013):

$$r = \frac{11.46(L)}{0.23 + L} \quad (3.5),$$

and for piscivores (Mazur and Beauchamp 2003; Hansen et al. 2013b):

$$r = \begin{cases} 44.56(L)^{0.266} & \text{if } L \leq 24.19 \text{ lx} \\ 104.13 & \text{if } L > 24.19 \text{ lx} \end{cases} \quad (3.6).$$

Reaction distance declines exponentially with turbidity T for both planktivores (Gregory and Northcote 1993) and piscivores (Beauchamp et al. 1999), but only after exceeding a low turbidity threshold (1.65 NTU) for piscivores (Hansen et al. 2013b). Experiments with planktivores have not been conducted at the resolution necessary to detect a parallel threshold response (Gregory and Northcote 1993), so we applied the same threshold to both groups. Experimentally derived relationships were adjusted to represent the proportion of the maximum reaction distance measured in clear water ($P[r_{max}]$; Figure 3.4B). The following relationship was used for planktivores (Gregory and Northcote 1993):

$$P(r_{max}) = \begin{cases} 1.0 & \text{if } T \leq 1.65 \text{ NTU} \\ 0.89 - 0.37\log(T) & \text{if } T > 1.65 \text{ NTU} \end{cases} \quad (3.7),$$

and for piscivores (Hansen et al. 2013b):

$$P(r_{max}) = \begin{cases} 1.0 & \text{if } T \leq 1.65 \text{ NTU} \\ 1.49e^{(-0.240*T)} & \text{if } T > 1.65 \text{ NTU} \end{cases} \quad (3.8).$$

Illumination threshold for feeding

It is suggested that planktivores move and feed within the antipredation window based on a minimum light intensity threshold that allows for the efficient uptake of zooplankton (reviewed by Mehner 2012), not just the visual detection of prey, as originally proposed by Clark and Levy (1988). For example, feeding experiments and field observations of depth-distributions for coregonids suggest that this threshold falls between 0.01-0.03 lx (Ohlberger et al. 2008; Gjelland

et al. 2009). Juvenile sockeye salmon (*Oncorhynchus nerka*) occupy depths with light levels below 0.001 lx at times (Levy 1990; Hardiman et al. 2004), even though 0.001 lx represents the minimum intensity required for scotopic vision and feeding in this species (Ali 1959). Light intensities near 1 lx are needed for photopic vision, and therefore, more efficient uptake of zooplankton (Ali 1959). Koski and Johnson (2002) indicated a switch in feeding mode for kokanee at 0.1 lx. Here, kokanee fed randomly by striking prey only as it drifted in front of their snouts, but actively pursued larger prey at higher light levels reminiscent of crepuscular periods in surface waters. A similar threshold could also exist for piscivores (Mehner 2012). Lake trout (*Salvelinus namaycush*) captured prey at 0.01-0.4 lx, but at very low rates when compared to 0.5-0.75 lx where spikes in both feeding rate and swimming speed were also observed (Mazur and Beauchamp 2003). Conversely, predation rates for northern pikeminnow (*Ptychocheilus oregonensis*) were relatively high between 0.01-0.03 lx (Petersen and Gadomski 1994). We wanted to characterize the antipredation window under conditions where pelagic predators and prey forage most effectively or actively, and therefore, present the greatest risk to prey. So, we applied a minimum light intensity threshold (below which feeding did not occur) for both planktivores and piscivores. We selected 0.02 lx, as this value was a conservative representation for both groups (Mehner 2012).

Characterizing the antipredation window

The antipredation window concept provides an integrative approach for describing the foraging-risk environment for pelagic consumers. Foraging rates were used to compute several dimensions of the antipredation window: (1) the magnitude—total difference between the foraging gain of the planktivore integrated over depth and time and that of the piscivore (i.e., predation risk), (2) duration—total time when predation risk was less than foraging gain, and (3)

peak timing—the time during morning and evening when the ratio of risk to gain (μ/f) was minimized (Figure 3.1). Values for magnitude were scaled to the maximum observed response to enable comparisons across seasons, latitudes, and turbidities.

Model sensitivity

Different dimensions of the antipredation window hinge most heavily on the relation between the generalized light-dependent reaction distance functions we developed for planktivores and piscivores. To estimate uncertainty surrounding our model results, we repeated simulations for the summer solstice using a set of species-specific reaction distance functions that bracketed the range of variability that we currently see for pelagic planktivores and piscivores. Parameter values describing reaction distance as a function of light for individual species in the laboratory are typically estimated with relatively little error (Holbrook et al. 2012; Hansen et al. 2013c). Therefore, using empirical relationships generated for specific species, as opposed to incorporating error into parameter values for our generalized reaction distance functions directly, should provide a better measure of uncertainty. The species-specific reaction distance functions that we selected tested four new scenarios: (1) reduced visual prey detection by planktivores, (2) improved prey detection by planktivores, (3) reduced prey detection by piscivores, and (4) improved prey detection by piscivores. Reductions or improvements in prey detection were relative to the responses developed for a generalized planktivore and piscivore, and were represented by parallel decreases or increases in the both the rate at which r_{\max} was achieved, and r_{\max} itself (Table A3.1).

Results

Latitudinal dependency in the magnitude, duration, and peak timing of the antipredation window varied considerably by season and with increases in turbidity. The greatest changes

occurred during the summer solstice. Under clear water (≤ 1.5 NTU) during the solstice, sharp peaks in the magnitude and duration of the window (summed across dawn and dusk) were observed along a narrow band of latitudes extending from 58-62°, before then dropping to zero or near zero when approaching 70° (Figure 3.5A, C). The magnitudes and durations of the antipredation windows were 2-6 fold greater at 58-62° than near the equator. This band of latitudes fell just below the polar circle. Here, solar elevations produced incident light levels ideal for extending the antipredation window over much longer periods (5-7.5 h) than at higher or lower latitudes (Figure 3.5C). Likewise, beginning at 58-59°, a single window spanning from dusk to dawn formed, and was centered on midnight (Figure 3.6). As distinct dusk and dawn windows merged into a single window centered on midnight, so did the timing, but only at latitudes (59-70°) above where the greatest magnitude and duration were observed. Overall, timing of the peak of the antipredation window at dawn shifted by 6 h across latitudes, starting just after midnight near 60° compared to 0600 hours near the equator; and dusk: starting at 1800 hours near the equator to just before midnight near 60° (Figure 3.5E). At latitudes below 58-62° where distinct dawn and dusk peaks in the timing of the window occurred, the corresponding incident light levels ranged from 0.1 to 4.57 lx and averaged 0.88 lx ($2 SE = 0.04$ lx). At higher latitudes where the peak timing occurred at midnight, incident light ranged from 0.18 lx below the Arctic or Antarctic Circle to 947.16 lx above the circle. However, under clear water and a midnight sun, the foraging environment became saturated with light, eliminating the possibility of a biologically meaningful antipredation window at latitudes near 70° (Figure 3.5A, C; Figure 3.6).

Latitudinal patterns in magnitude and duration of the antipredation window during the summer solstice changed dramatically at higher turbidities (2-5 NTU). With increasing turbidity,

the duration of the antipredation window increased with latitude up to 24 h per day beginning at 59-60° where light conditions were sufficient to form the window at night (Figure 3.5C; Figure 3.6). This extension of the antipredation window was driven by the greater effect of turbidity on the reaction distance for piscivores than planktivores (Figure 3.4B). These differences in visual range generated up to 10-fold shifts in magnitude across latitudes and turbidities during the solstice (Figure 3.5A). Despite these large shifts, the timing of the window remained relatively insensitive to increases in turbidity, but tended to converge at midnight at slightly higher latitudes under higher turbidities (Figure 3.5E). Incident light levels corresponding with these shifts in timing (before convergence at midnight) were higher and more variable under turbid conditions (range: 0.51-91.70 lx; mean = 3.80 lx; 2 *SE* = 0.4 lx). This greater variability stemmed largely from dynamics at low to intermediate latitudes (0-40°) where deviations in timing were seemingly negligible (Figure 3.5E). Across this space, incident light levels changed more rapidly per unit time than at higher latitudes (Figure 3.2A, C). Consequently, small deviations in timing (5-10 min) produced larger deviations in the corresponding incident light levels at these latitudes.

When the sun was centered on the equator during the fall equinox, latitudinal dependencies of the antipredation window were minimal. The magnitude, duration, and timing of the window were nearly continuous across all, but the highest latitudes at each turbidity level examined (Figure 3.5B, D, and F). In clear water (≤ 1.5 NTU), the window expanded by several orders of magnitude (Figure 3.5B) for up to 5 h at latitudes near and above the polar circle where the midnight sun had restricted its formation closer to the summer solstice (Figure 3.5D). Conversely, the magnitude and duration of the windows were greatly reduced at latitudes where strong peaks in these variables were previously observed during the solstice (58-62°). At these

latitudes, the magnitude dropped by 104-231% from the solstice to the equinox, and the duration dropped by 152-211% (Figure 3.5B, D). Similar solstice-to-equinox reductions in these variables were observed at higher turbidities (> 2 NTU). The greatest reductions occurred at high latitudes and ranged from 0.7% near the equator to 85% near and above the polar circle for magnitude, and 0.63-69% for duration (Figure 3.5B, D). Similarly, the timing of the window was condensed from a 6 h range during the solstice to a 2 h range (0400-0600 hours for dawn and 1800-2000 hours for dusk) during the equinox (Figure 3.5F). Yet, incident light levels corresponding with these times in clear water (range: 0.09-3.07 lx; mean = 0.88 lx; $2 SE = 0.04$ lx) and in turbid water (range: 0.50-21.36 lx; mean = 3.13 lx; $2 SE = 0.16$ lx) were conserved between seasons.

Model sensitivity

Broad patterns in different dimensions of the antipredation window across latitudes and turbidities during the summer solstice were not sensitive to reductions or improvements in the light-dependent visual prey detection responses of the planktivores and piscivores. Changes in the magnitude, duration, and peak timing of the window were quite minor across all prey detection scenarios examined, especially in turbid water (Table A3.2), despite relatively large percentage changes in the parameter values used to describe reaction distance as a function of light for the different consumer groups (Table A3.1). The greatest mean percent changes in magnitude (reductions by 52.8-70.1%) and duration (reductions by 30.4-38.5%) were observed under clear water for the scenario where prey detection by planktivores was reduced (Table A3.2). Interestingly, the scenario where prey detection by piscivores was reduced also produced reductions in magnitude (35.3-37.6%) and duration (20.1-20.3%). Here, r_{\max} was reduced, but the rate at which r_{\max} was achieved was still quite high. Consequently, the piscivores were still

achieving relatively high feeding rates at low light levels in this scenario. This highlights the important distinction between relative and absolute predation risk.

Discussion

Our results show that the foraging-risk environment for visually-feeding planktivores and piscivores can look very different when considering diel and seasonal patterns in illuminance and changes in water turbidity over a broad latitudinal gradient. We observed up to 10-fold shifts in the magnitude, 24-fold shifts in the duration, and 6-h shifts in the peak timing of the window across seasons, latitudes, and turbidities. These changes in diel feeding and risk have different implications for the structure of pelagic predator-prey interactions and the behavioral strategy needed to effectively cope with the fundamental tradeoff between feeding and avoiding predators at different latitudes. The antipredation window was most dynamic during the summer solstice, when solar declination and latitudinal variability in solar elevation and the diel light environment were greatest. The highest magnitudes and longest durations were observed at high latitudes during this period. During the fall equinox, the effect of latitude was minimal, and turbidity drove most of the change in magnitude and duration of the window. Localized variation in the physical environment (e.g., topography, cloud cover, depth, and thermal stratification) and ecological conditions (e.g., density and depth-distribution of zooplankton, planktivores, and piscivores) can lead to myriad pelagic predator-prey scenarios that were not explored in this analysis. Even though these complexities may alter the shape, profitability, and riskiness of the antipredation window among systems at a given latitude, this study is the first to demonstrate the strong, systematic effects of diel illuminance and turbidity on the foraging-risk environment for pelagic consumers over a broad latitudinal gradient.

With broad-scale diversity in the form of the antipredation window should come variation

in behavioral strategies tailored to cope with the tradeoff between feeding and avoiding predators under different conditions. According to the model results, planktivores inhabiting clear water lakes at latitudes approaching the polar circle (beginning at 58-60°) have the added benefit of experiencing a continuous window available through the night during early summer. A continuous window provides more time for migrating to and actively feeding within surface waters. Empirical observations revealed a continuous window forming for up to 6 h for juvenile sockeye salmon inhabiting clear water lakes positioned at 59° N in Alaska (Scheuerell and Schindler 2003). Here, sockeye salmon remained near the surface through the night after ascending around 2200 hours and then descending around 0330 hours. The peak timing of the window predicted by our model corresponded well with these movements by juvenile sockeye salmon during early summer at this latitude. The window for sockeye salmon split into two discrete periods later in the summer as expected. The peak timing of these periods predicted by our model differed slightly from those reported for sockeye salmon at 59° N, but corresponded well with a study on coregonids at mid-latitudes (Jensen et al. 2006). These discrepancies highlight the importance of localized variability in environmental and ecological conditions in driving pelagic predator-prey interactions. Therefore, results from this study are best suited as a general construct for predicting directional changes in the diel feeding and risk environment for pelagic consumers when other system-specific information is unavailable.

As the environment becomes more risky, planktivores are expected to adapt their feeding behavior to balance individual foraging gain (or growth potential) with predation risk (Biro et al. 2003). Above the polar circle and under clear water during early summer, a midnight sun restricted the formation of an antipredation window by saturating surface waters with light. In the absence of a thermal refuge in the epilimnion (Martinez et al. 1995; Hansen et al. 2013a),

schooling becomes the only known option for reducing predation risk while achieving adequate feeding rates. Schooling reduces per-capita mortality risk, but may also increase intraspecific competition and reduce per-capita foraging gain (Pitcher and Parrish 2003). However, increases in per-capita foraging gain from schooling have been observed (Milne et al. 2005). At 69° N where antipredation windows should be absent, whitefish (*Coregonus lavaretus*) and vendace (*Coregonus albula*) exhibited strong shoaling patterns at intermediate depths with light levels ranging between 0.1-100 lx during day and night in Lake Skrukkebukta, Norway (Gjelland et al. 2009). Likewise, schooling extended feeding opportunities for *O. nerka* during daylight in lakes at intermediate latitudes (44-47° N) where two distinct, but relatively short antipredation windows persisted throughout the growing season (Eggers 1978; Beauchamp et al. 1997). This indicated that feeding only during the antipredation window may not always be sufficient given the risk environment, thermal conditions, food supply, or other density dependent factors operating in some lakes.

Late in the growing season, we observed a strong expansion in the antipredation window at latitudes above the polar circle as day length declined. Under these conditions, we would expect planktivores to shift from shoaling to diel vertical migration. In fact, diel vertical migration was observed by whitefish and vendace during August in Lake Skrukkebukta (Gjelland et al. 2009), and during September by conspecifics in nearby Lake Muddusjarvi (Kahilainen et al. 2009). During September, Lake Skrukkebukta was nearly isothermal and zooplankton densities in surface waters dropped to levels that were 20-50% of those present in August (Gjelland et al. 2009). During this time, whitefish and vendace were dispersed throughout the water column at night instead of congregated near the surface. This indicated that a portion of the population became more risk-averse as the growing season progressed and

feeding opportunity declined, supporting the notion that the tradeoff between feeding and avoiding predators is state-dependent (Mangel and Clark 1986; Lima and Dill 1990; Lima 1998; Mehner 2012). Some individuals may need to accept more risk toward the end of the growing season, particularly if a certain size or energetic state is required to survive the winter (Schindler et al. 1999; Biro et al. 2005). At latitudes above the polar circle, the potential need for increased risk-taking by planktivores in a reduced energetic state during fall could be ameliorated by the coincident expansion of the antipredation window (Damsgard and Dill 1998). In contrast, photic conditions earlier in the summer above the polar circle dictated that schooling with conspecifics was the only recourse in clear water. Whether anticipated movement and distribution patterns manifest near the end of the growth period not only depends on how bio-physical processes in lakes at different latitudes respond to shifts in seasons, but also on the condition of the individual; determined by environmental and ecological conditions experienced over summer.

The magnitude and duration of the antipredation window expanded as turbidity increased, which leveled the playing field for planktivores across seasons and latitudes. Under these conditions, planktivores could conceivably feed until satiated in well-lit surface waters throughout daylight, then find depths offering more efficient temperatures for digestion if such tradeoffs existed, as predicted by the bioenergetic efficiency hypothesis (Clark and Levy 1988). Most studies that evaluate the bioenergetic efficiency hypothesis as the key driver of diel vertical migration concluded that factors related to both energetics and predator avoidance are at play; however, all of these studies were conducted in clear water lakes (Scheuerell and Schindler 2003; Jensen et al. 2006; Busch et al. 2011). The game changes in even mildly turbid water, and the bioenergetic efficiency hypothesis may become most parsimonious under these conditions. However, whether visually-feeding planktivores perceive a reduced risk of predation across the

0-5 NTU range, and adjust their feeding strategies by reducing antipredator behavior in natural lakes, is still an open question (Gregory 1993; Abrahams and Kattenfeld 1997). Under laboratory conditions, planktivores can maintain adequate feeding rates at turbidity levels (e.g., 40 NTU) well beyond those examined here (Gregory and Northcote 1993), whereas feeding rates of piscivores decline quickly from 0-5 NTU (De Robertis et al. 2003). Given the strong decline in the efficacy of pelagic piscivory with increasing turbidity, we might expect pelagic piscivores to revert to a benthic feeding strategy during transient periods of high turbidity. The strong effect of turbidity could also help explain the general loss of pelagic piscivory in productive or eutrophic systems that are chronically turbid (Colby et al. 1972; Persson et al. 1991).

Water clarity and the vertical light environment in lakes are inherently linked to productivity and other watershed processes (Lathrop et al. 1996; Stasko et al. 2012). The absorption and scattering properties of dissolved organic carbon (DOC), algae, and inanimate particulate matter all differ (Kirk 2011). Consequently, the foraging environment for visual consumers can look very different depending on which substances predominate (Koenings and Edmundson 1991; Kirk 2011; Jonsson et al. *in press*). We used turbidities measured in oligotrophic to mesotrophic temperate lakes to bracket the natural range of water clarities observed in systems that typically contain visually-feeding predators and prey (Colby et al. 1972; Persson et al. 1991). We excluded glacially dominated lakes as food supplies can be severely reduced (Lloyd et al. 1987). However, the contribution of organic versus inorganic material to these turbidity measurements were unknown, and the visual responses of consumers under organic versus inorganic turbidity may not be equivalent. Understanding how the different components of lake ecosystems most closely linked to productivity (algae) and other watershed processes (DOC) can influence the visual responses of consumers should offer new insights into

how the foraging-risk environment changes across different classes lakes. Such analyses may reveal greater diversity in the configuration of the antipredation window for different consumers.

The magnitude and duration of the antipredation window for visually-feeding planktivores and piscivores were minimal at latitudes near the equator, and did not begin to expand until approximately 40° latitude. Interestingly, 40° latitude corresponded well with the lower bound of freshwater systems (38-39°) from all studies evaluating the adaptive significance of diel vertical migration by pelagic planktivores considered in this study and others (Mehner 2012). Although this may reflect an inherent bias in the types of systems that are of interest to scientists, the lack of related studies in tropical to sub-tropical regions could also reflect a fundamental change in the nature of predator-prey interactions, the physical structure of freshwater ecosystems, fish communities, or the feeding tactics of both planktivores and piscivores along this broad latitudinal gradient. Lastly, given that the effect of latitude on the foraging-risk environment for pelagic consumers was so large, the relationships observed in this study may extend to pelagic marine ecosystems (Eiane et al. 1999; Asknes et al. 2004). Critical reviews of these topics are needed.

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Figures

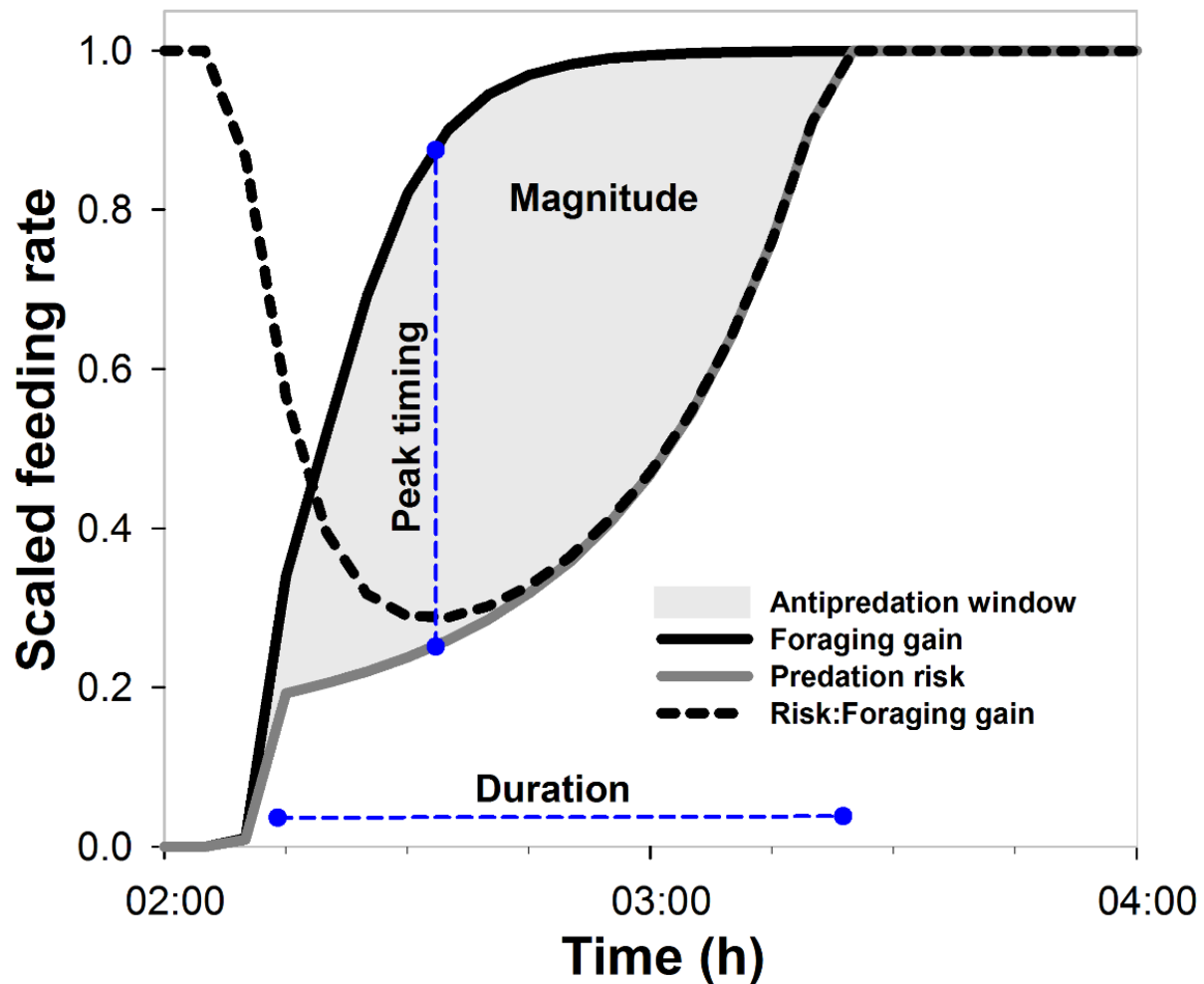


Figure 3.1. Scaled foraging responses of an idealized planktivore (foraging gain) and piscivore (predation risk) feeding during twilight before sunrise in clear water at 52° latitude on the summer solstice. Responses for the planktivores and piscivores are scaled to the maximum observed foraging rate estimated for each group separately. The magnitude of the antipredation window is the total area between the scaled foraging gain and predation risk curves. Timing of the peak of the antipredation window occurs when the ratio of risk to gain is minimized. The duration of the window is the total time risk is less than gain.

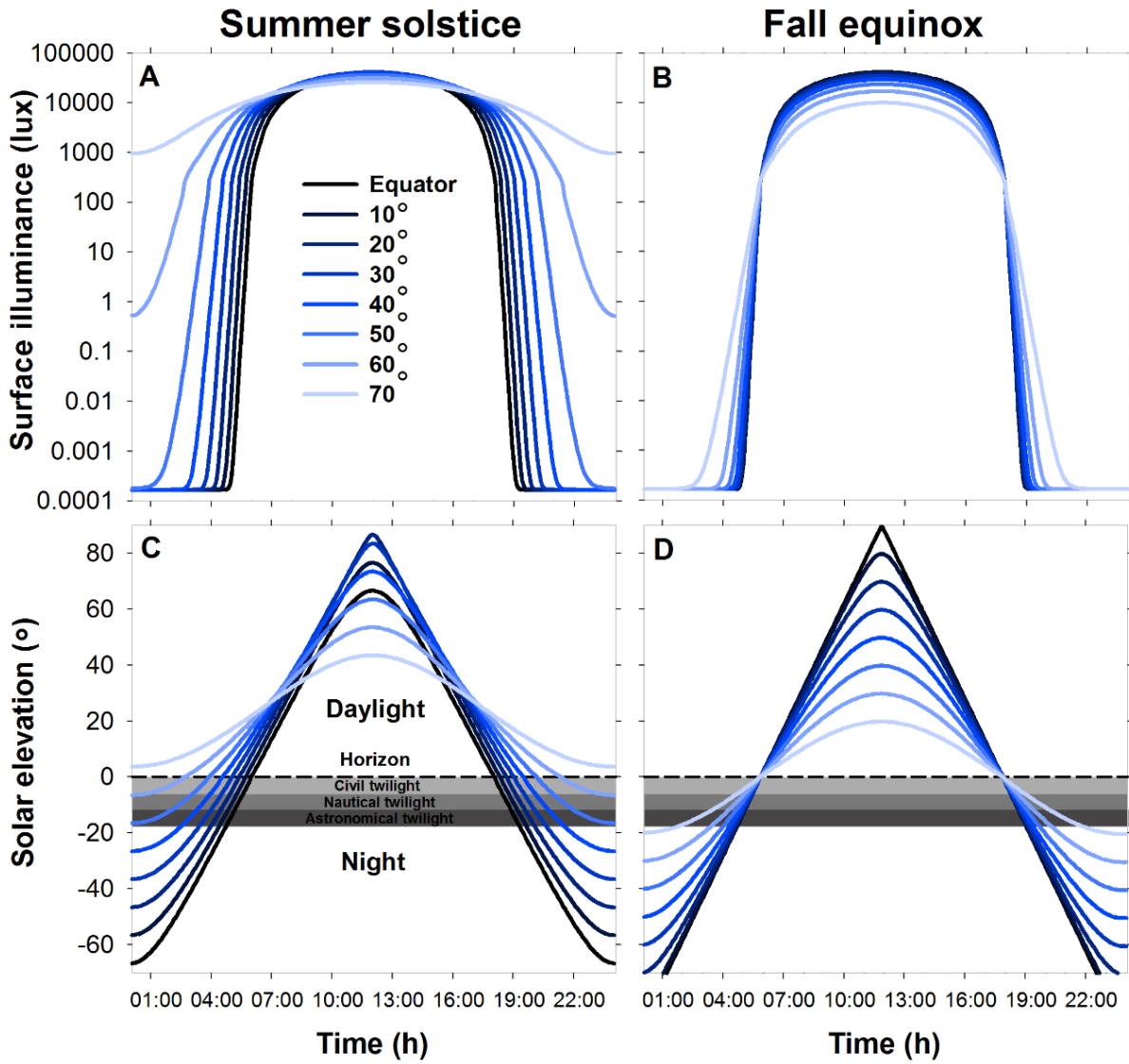


Figure 3.2. (A and B) Diel light regimes as a function of latitude generated from the sun and moon illuminance model of Janiczek and DeYoung (1987) and (C and D) corresponding diurnal solar elevations (corrected for atmospheric refraction) generated from the solar position calculator from the National Oceanic and Atmospheric Administration (accessed 23 July 2013 at: <http://www.esrl.noaa.gov/gmd/grad/solcalc/calcdetails.html>). Solar elevations of 0-6° below the horizon define civil twilight, 6-12° for nautical twilight, and 12-18° for astronomical twilight.

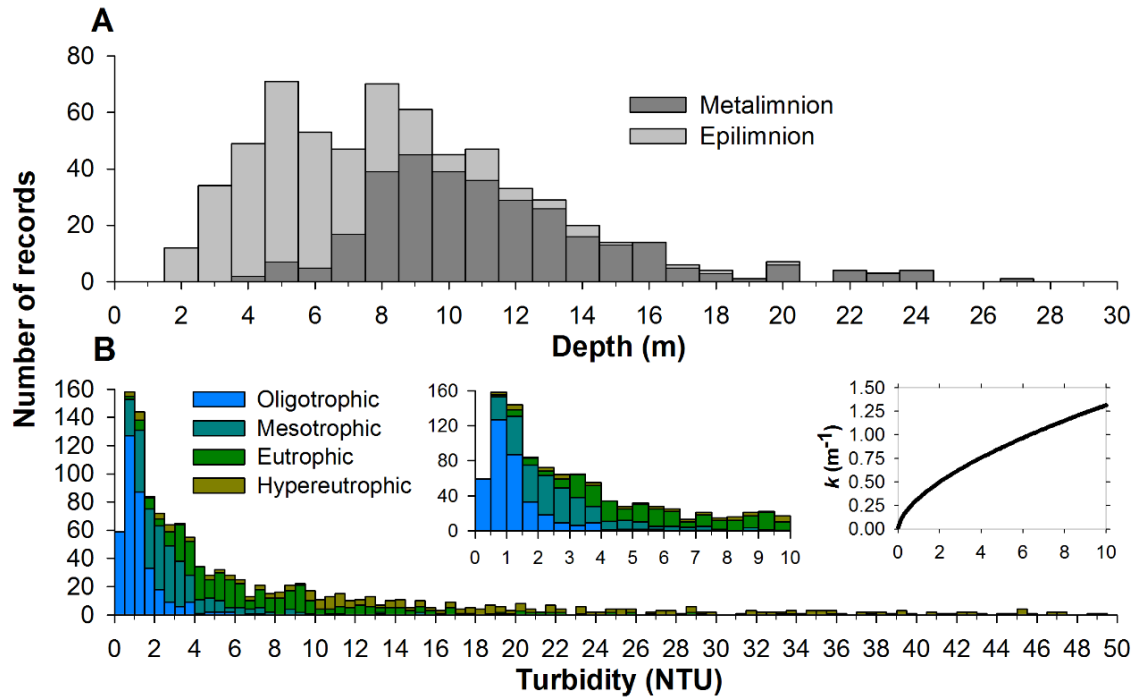


Figure 3.3. (A) Frequency and of epi- and meta-limnetic depths measured in stratified temperate lakes ≥ 10 m deep ($N = 315$ records from 285 lakes). (B) Frequency of turbidity measurements ($N = 1,326$ records) taken in 909 temperate lakes of varying trophic states. Trophic state designations were based on total phosphorus concentration. Data are from the 2007 National Lakes Assessment conducted by the United States Environmental Protection Agency (U.S. Environmental Protection Agency 2009). The insets in panel B show the magnified frequency distribution of turbidities, and the relationship between light extinction (k) and turbidity over 0-10 NTU.

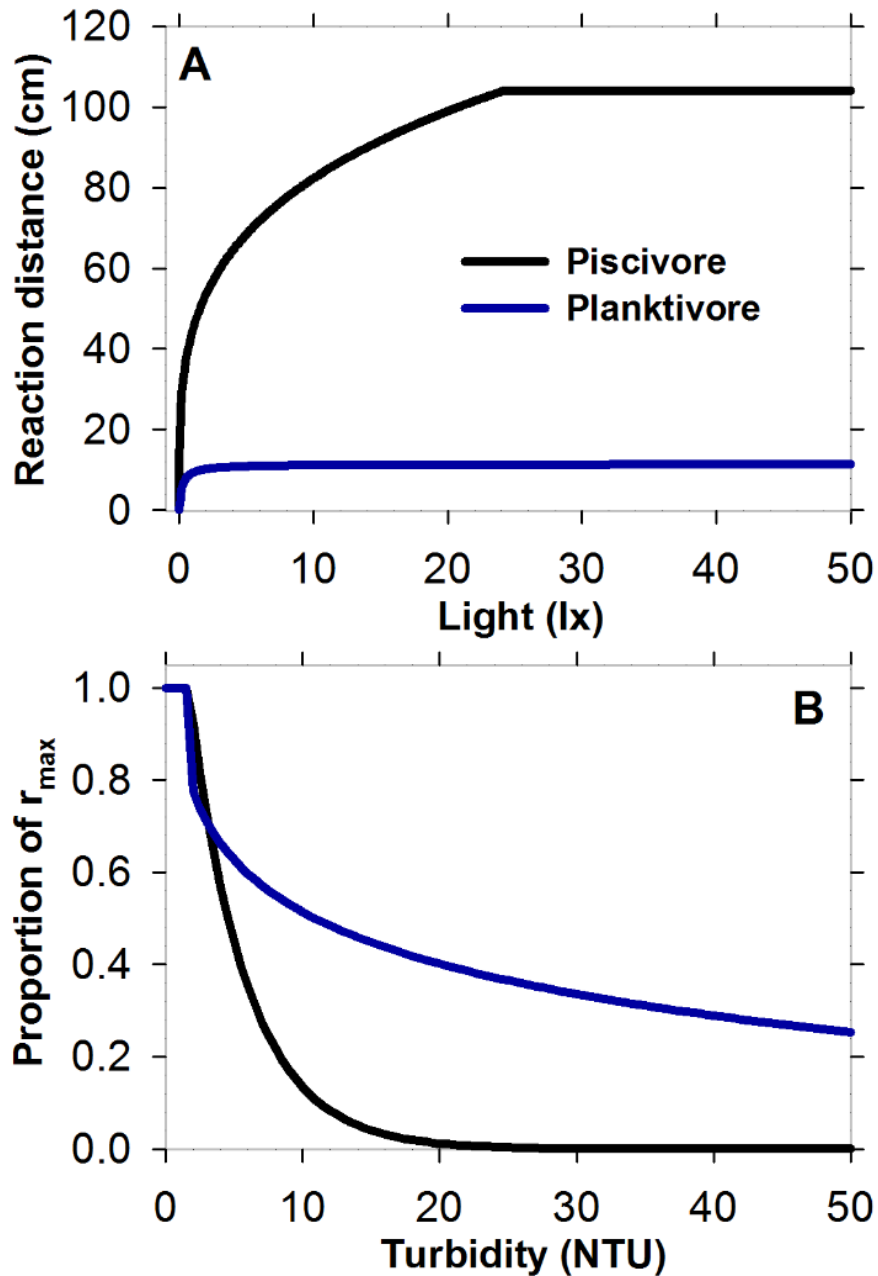


Figure 3.4. Reaction distance as a function of (A) light and (B) turbidity for an idealized planktivore and piscivore. Reaction distance as a function of turbidity is represented by the proportion of the maximum observed reaction distance (r_{max}) under clear water.

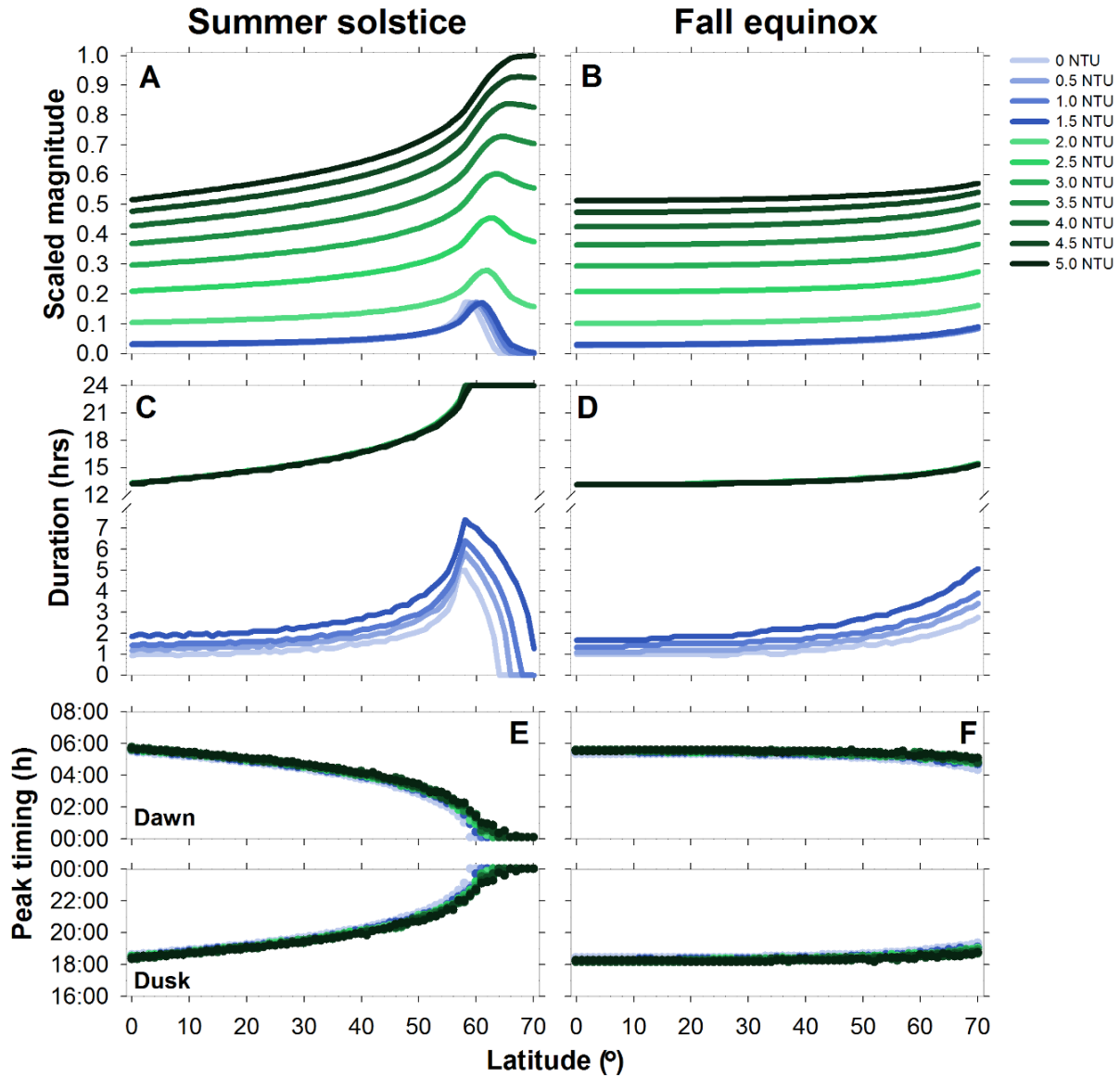


Figure 3.5. (A and B) Magnitude, (C and D) duration, and (E and F) timing of the peak of the antipredation window at low turbidities across latitudes during the summer solstice and fall equinox. For magnitude and duration, values from both dawn and dusk windows were summed together. Values for magnitude are scaled to the maximum value observed across seasons.

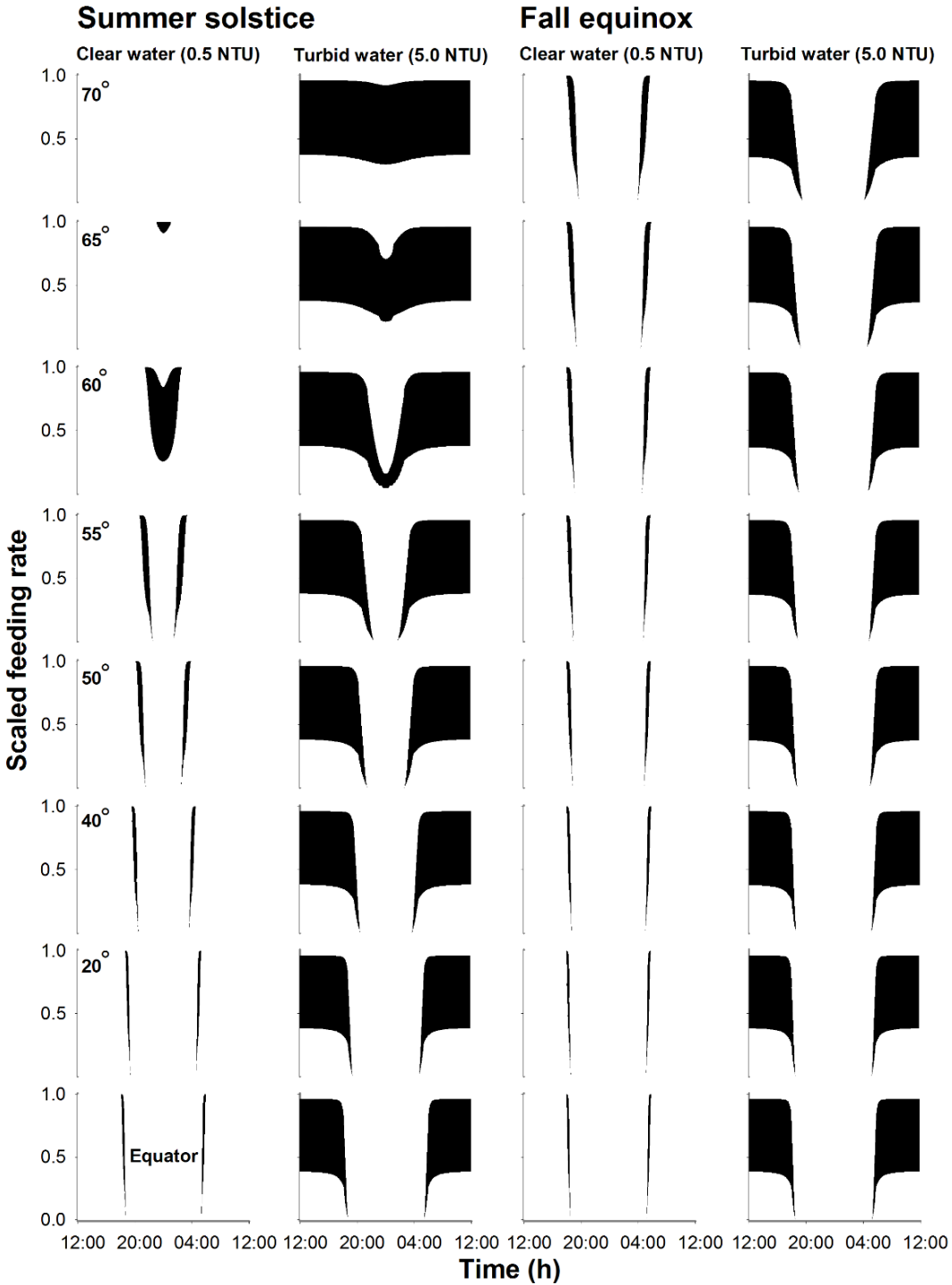


Figure 3.6. Form of the antipredation window at different latitudes and turbidities during the summer solstice and fall equinox. The shaded regions represent the area (i.e., the change in instantaneous magnitude) between the scaled foraging gain and predation risk curves estimated for the planktivores and piscivores over a continuous 24-h period. Panels are centered on midnight.

Appendix A

Table A3.1. Parameter values for the species-specific light-dependent (L and l in lux) reaction distance (r and r_{max} in cm) functions used to evaluate uncertainty surrounding estimates of different dimensions of the antipredation window. Differences (in percent) between parameter values for individual species and those for a generalized planktivore and piscivore are shown.

Functional form	Consumer group	Parameter values				Percent change			
		α	β	l	r_{max}	α	β	l	r_{max}
$r = \frac{\alpha L}{\beta + L}$	Generalized planktivore	11.46	0.23	-	-	-	-	-	-
	Reduced detection ^a	8.28	2.06	-	-	-27.7	795.7	-	-
	Improved detection ^b	15.00	0.004	-	-	30.9	-98.3	-	-
$r = \begin{cases} \alpha L^\beta & \text{if } L \leq l \\ r_{max} & \text{if } L > l \end{cases}$	Generalized piscivore	44.56	0.266	24.19	104.13	-	-	-	-
	Reduced detection ^c	34.80	0.165	18.75	56.45	-21.9	-37.9	-22.5	-45.8
	Improved detection ^d	109.93	0.154	36.44	191.01	146.7	-42.2	50.7	83.4

^aLake herring (*Coregonus artedii*) from Link and Edsall (1996).

^bJuvenile lake trout (*Salvelinus namaycush*) from Holbrook et al. (2012).

^cRainbow trout (*Oncorhynchus mykiss*) from Mazur and Beauchamp (2003).

^dCoastal cutthroat trout (*O. clarkii clarkii*) from Hansen et al. (2012c).

Table A3.2. Sensitivity of different dimensions of the antipredation window during the summer solstice to reductions or improvements in the visual prey detection responses of planktivores and piscivores relative to those of a generalized planktivore and piscivore. Positive and negative values for magnitude and duration reflect the general direction of change at different latitudes and under different turbidity levels.

Turbidity	Latitude (°)	Change in magnitude (%)		Change in duration (%)		Change in peak timing (hours)	
		Mean	2 SE	Mean	2 SE	Mean	2 SE
Reduced detection by planktivores							
Clear water (0-1.5 NTU)	0-40	-70.1	0.295	-38.5	0.677	0.194	0.006
	41-70	-52.8	4.257	-30.4	3.797	0.362	0.044
Turbid water (> 1.5 NTU)	0-40	-1.4	1.057	-4.4	0.062	0.824	0.042
	41-70	-5.7	1.551	-5.7	0.626	1.758	0.124
Improved detection by planktivores							
Clear water (0-1.5 NTU)	0-40	22.7	0.393	0.1	0.089	0.195	0.007
	41-70	16.5	1.802	0.1	0.124	0.359	0.048
Turbid water (> 1.5 NTU)	0-40	2.9	0.419	0.3	0.039	0.275	0.006
	41-70	4.1	0.693	0.3	0.064	0.538	0.044
Reduced detection by piscivores							
Clear water (0-1.5 NTU)	0-40	-37.6	0.144	-20.1	0.849	0.057	0.007
	41-70	-35.3	1.891	-20.3	3.323	0.198	0.138
Turbid water (> 1.5 NTU)	0-40	-4.8	0.603	-1.2	0.047	0.266	0.018
	41-70	-6.2	0.829	-1.4	0.230	0.470	0.052
Improved detection by piscivores							
Clear water (0-1.5 NTU)	0-40	-16.7	0.121	5.1	0.678	0.004	0.002
	41-70	-10.3	2.060	6.9	2.850	0.152	0.168
Turbid water (> 1.5 NTU)	0-40	1.4	0.092	0.1	0.034	0.005	0.002
	41-70	0.6	0.229	0.1	0.059	0.019	0.007

Chapter 4.—Environmental constraints on piscivory: insights from linking ultrasonic telemetry to a visual foraging model for cutthroat trout

Abstract.—Managing pelagic food webs under a shifting climate requires an understanding of how behavior, physiological tolerance, and the environment interact to mediate the foraging rates of consumers. However, analyses that treat each of these factors explicitly in a framework that captures interdependencies are lacking. We linked a visual foraging model and bioenergetics simulations with ultrasonic telemetry to mechanistically evaluate how stressful abiotic conditions (high temperature and low dissolved oxygen) influenced the foraging success of piscivorous cutthroat trout *Oncorhynchus clarki* feeding on juvenile salmonids in Strawberry Reservoir, Utah. Our primary objectives were to 1) determine whether the foraging success of apex predators changes during periods of environmental stress and 2) identify the behavioral mechanisms that either lead to or buffer against shifts in foraging success. During a temperature-oxygen squeeze in early and mid-August, high temperatures and low oxygen levels generated divergent diel vertical distributions between predators and prey. Consequently, encounters with prey were restricted to crepuscular or early morning periods, and the potential foraging success of the piscivores was reduced by 53-98%. Conversely, predator-prey overlap increased considerably when the reservoir was destratified during October, allowing the piscivores to achieve up to 98% of their maximum predation rate. Comparing encounter and predation rate estimates from the visual foraging model to estimates of fish consumption from a bioenergetics model indicated that prey capture success was higher for piscivores during low light periods. Therefore, as periods of stress impose constraints on the distribution of pelagic fishes, the magnitude of piscivory will depend on the resulting temporal-spatial overlap of predators and prey in complex ways. This study demonstrates how dynamic environmental conditions can mediate foraging success of piscivores and predation risk for prey.

Introduction

A host of biological and physical factors govern the ability of predators to exploit prey resources over time and space. Habitat heterogeneity in particular influences predation in terrestrial (Kauffman et al. 2007) and aquatic communities (Crowder and Cooper 1982; Rilov et al. 2007). In co-evolved predator-prey systems, habitat complexity is theorized to boost persistence by reducing the ability of predators to locate and capture prey and by creating refugia (Ellner et al. 2001; Kauffman et al. 2007). Refuge habitats influence predation differently in pelagic versus terrestrial systems. Pelagic habitats lack structural features (e.g., coarse vegetation or complex terrain) that physically inhibit access or searching efficiency of predators. Instead, vertical gradients (temperature, oxygen, and light) form the predominant physical structure. This vertical structure can create refugia if interspecific or ontogenetic asymmetries in environmental tolerance or foraging constraints exist between prey and predators (Hardiman et al. 2004; Mackenzie-Grieve and Post 2006). The intensity of vertical gradients changes across diel periods and seasons, and could differentially influence the movement and distribution of prey fishes versus piscivores. Therefore, dynamic environmental conditions likely alter the spatial dimensions and profitability of foraging habitat for piscivores and refugia for prey.

Adaptive shifts in movement or other mechanisms may allow piscivores to capitalize on fish prey even when environmental conditions are limiting. For example, pelagic refuges are permeable. This enables forays of varying duration into profitable foraging regions that are either physiologically-demanding due to hypoxia (Luecke and Teuscher 1994; Rahel and Nutzman 1994), warm temperature (Coutant 1990), or visually challenging for sight-feeding piscivores (Beauchamp et al. 1999). Although degraded visual conditions reduce search volume and prey encounters for piscivores, experimental evidence suggests that capture success, given

an encounter, is significantly higher under these conditions (Howick and O'Brien 1983; Petersen and Gadomski 1994; Mazur and Beauchamp 2003). Therefore, environmentally-mediated segregation or overlap of predators and prey can include a combination of limiting and compensatory processes that determine the ultimate foraging success of piscivores and temporal-spatial dimensions of prey refugia.

Generating data on movement and distribution of apex predators with sufficient temporal-spatial resolution to identify these sorts of mechanisms has been a continual challenge for fisheries ecologists. Acoustic telemetry generates high resolution data on fine-scale vertical and horizontal movements by piscivores. It provides insight into how predators experience and respond to changes in environmental stressors, ambient visual conditions, and the associated prey field. Telemetry data for piscivores can be linked with visual foraging models that account for time- and depth-dependent changes in search volume as functions of light and water clarity. These dynamic search volumes can then be overlaid on the diel distribution and density of prey fishes to quantify how observed movements translate into prey encounters at ecologically relevant scales. We can also explore how capture success might vary among prey encountered under different visual conditions. Collectively, these relationships should further our understanding of how predation risk for prey and foraging success of piscivores are mediated by the structure and dynamics of environmental conditions.

To explore how environmental conditions affect piscivory, we applied a visual foraging model to the diel and seasonal distribution of prey fish and telemetry data for piscivorous cutthroat trout *Oncorhynchus clarki* in Strawberry Reservoir, Utah (Figure 4.1). Telemetry data (Baldwin et al. 2002) and consumption data (Baldwin et al. 2000) were collected during summer and autumn 1997. Baldwin et al. (2002) concluded that vertical movements of cutthroat trout

tracked in early August were constrained to the lower half of the metalimnion (11-13 m deep) between high epilimnetic temperatures (18-20 °C) and a hypoxic hypolimnion (1.7 ± 0.7 mg/L dissolved oxygen) across all diel periods. During mid-August, hypoxia encroached into the lower metalimnion (< 3.0 mg/L), and tagged cutthroat trout moved up into the warmer epilimnion where they initiated diel vertical migration. Destratification in October released the thermal (8-14 °C in epilimnion) and oxygen constraints (> 5.0 mg/L throughout all depths), and cutthroat trout became more surface-oriented (Figure 4.2). Prey fishes were thought to exhibit diel horizontal and vertical migrations during summer: they were surface-oriented or occupied the littoral zone during daylight (0-5 m depth), then shifted offshore and to deeper epilimnetic depths during crepuscular and night periods (Baldwin et al. 2000). Vertical movement patterns by the piscivores allowed varying degrees of overlap with salmonid prey during these three limnological periods (i.e., early August, mid-August, and October; Baldwin et al. 2002).

Management of pelagic food webs would benefit from a greater mechanistic understanding of how the interplay among behavior, physiological tolerance, and environmental conditions influences the foraging success of apex predators and predation risk for prey. Given potential future anthropogenic and climate impacts, it is particularly important to understand how interactions change when pelagic communities are subject to stressful environmental conditions (Ficke et al. 2007). Our objectives were to determine whether the foraging success of apex predators changes during periods of environmental stress and identify the behavioral mechanisms that either lead to or buffer against shifts in foraging success. We used visual foraging and bioenergetics models to ask: 1) do periods of stress restrict encounters with prey in time and space?, 2) do these shifts change foraging success for piscivores?, 3) does capture success vary as a function of visibility?, and 4) when environmental stressors restrict piscivore

movements, do the visual conditions that coincide with periods of prey overlap improve or diminish foraging success? For cutthroat trout in Strawberry Reservoir, we predicted that:

- Encounters with prey should be more restricted in time and space during periods of stress in August compared to the non-limiting conditions during October.
- Restricted encounters with prey in August would reduce the foraging success of piscivores compared to non-limiting conditions during October.
- Capture success [P(capture|encounter)] would be higher under low light conditions thus increasing the profitability of low-light encounters.
- Declines in foraging success would be buffered during the periods of restricted prey overlap in August if prey encounters coincided with low-light periods, because improved capture success could compensate somewhat for the reduction in total daily prey encounters. Conversely, declines in foraging success would be exacerbated if prey overlap was restricted to high-light periods, because the reduction in total daily prey encounters would coincide with lower capture success.

Methods

Study system

Strawberry Reservoir is located in Utah's central mountains (Uinta National Forest) at 2,300 m elevation, and is a major water supply for Wasatch County, Utah. The reservoir is meso-eutrophic, dimictic, and contains 0.83 km³ of water over a surface area of 61 km². Maximum depth rarely exceeds 28 m. Epilimnetic depths ranged from 7-15 m with up to 21 °C temperatures during summer stratification. Secchi depths varied from 9 m in spring to 2.5 m in midsummer and 3.5 m in October. Ice cover typically forms in December and thaws in May (Baldwin et al. 2000).

Strawberry Reservoir is considered Utah's most important coldwater fishery (Ward et al. 2008). Cutthroat trout dominate the salmonid sport fish community. Heavy hatchery supplementation supports high angler catch and harvest. For example, 1.08 million juvenile cutthroat trout (39,000 kg), 680,000 rainbow trout *O. mykiss* (22,000 kg), and 750,000 kokanee *O. nerka* (1,000 kg) were stocked into Strawberry and its tributaries in 2006 (Ward et al. 2008). In summer and autumn 1997, *Daphnia* sp. and invertebrates dominated diets of adult cutthroat trout, but juvenile salmonids episodically represented 11-44 % of the diet (Baldwin et al. 2000). Utah chub *Gila atraria*, Utah sucker *Catostomus ardens*, and redbelt shiner *Richardsonius balteatus* represent the nongame fishes, which comprised negligible fractions of the diet for adult cutthroat trout during the study period (< 1.1 % of the diet; Baldwin et al. 2000).

Ultrasonic tracking

See Baldwin et al. (2002) for detailed methods concerning cutthroat trout capture and tagging, ultrasonic tracking, and limnological sampling. Briefly, depths and horizontal locations of five cutthroat trout (total length = 475-502 mm; 906-1,127 g) were recorded every 10 s continuously over seven tracking episodes with each including one or more diel cycles. Cutthroat trout were captured via hook-and-line and surgically implanted with pressure-sensitive transmitters. The tracking episodes and corresponding limnological conditions included: early August (fish A6 and A2a; August 2nd-8th) when hypolimnetic hypoxia and warm epilimnetic temperatures "squeezed" the piscivores in the lower metalimnion; mid-August (fish A1 and A2b; August 13th-18th), when the lower metalimnion also became hypoxic and the piscivores moved into the upper metalimnion and warmer epilimnion; and October (fish O6, O9, and O3; October 8th-19th), when destratification reduced temperatures and increased oxygen concentrations throughout the water column (Baldwin et al. 2002; Table 4.1). Fish A2 was tracked during early

August and again in mid-August, hence A2a and A2b designations. Similarly, fish A6 was tracked in early August and again in October, receiving the designation O6. Minimum swimming speeds of the piscivores were computed from average movements of the tracking boat each diel period. Tracking took place in Strawberry Basin (Figure 4.1).

Temperature, dissolved oxygen, light, Secchi depth, and turbidity were recorded monthly to describe limnological conditions associated with the different tracking episodes (Baldwin et al. 2000). Diel-vertical movements were linked with these limnological data to estimate abiotic conditions at each recorded location for tagged cutthroat trout. Vertical profiles of light, temperature, and oxygen were recorded every meter (0-28 m) on the first and fifteenth of each month. Light ($\mu\text{Einst}/[\text{cm}^2 \cdot \text{sec}]$) at the surface and underwater was measured with a LI-COR spherical sensor. These light profiles were used to calculate extinction coefficients (Horne and Goldman 1994). For each tracking episode, corresponding vertical temperature and oxygen profiles were linearly-interpolated between adjacent limnological sampling dates. Corresponding vertical light profiles were estimated by generating continuous surface light levels from a computer program by Janiczek and DeYoung (1987). Light extinction coefficients computed above were interpolated from the two nearest limnological sampling dates and used to model light availability at depth:

$$I_{z,t} = I_{0,t}e^{-zk} \quad (4.1),$$

where the light level ($I_{z,t}$; lx) at depth z (m) and time t was the product of surface light ($I_{0,t}$) and the exponential reduction of light at depth z based on the light extinction coefficient k .

Reconstruction of prey fields

Seasonal stocking of hatchery-raised juvenile cutthroat trout and kokanee in 1997 provided the majority of fish prey available to piscivores (Table 4.2; Baldwin et al. 2000). We

integrated stocking records with estimates of growth, survival, and variability in length to estimate the abundance and size distribution of prey available on dates centered between piscivore tracking episodes during each limnological period (Figure 4.3). Demographic rates were specific to stocked and naturally recruiting juvenile cutthroat trout in Strawberry Reservoir (Table 4.2; Orme 1999). Prey stocked in August 1997 were excluded from the analysis because fish were only released in the more isolated Indian Basin (Baldwin et al. 2000, 2002; Figure 4.1). However, we assumed 100,000 cutthroat trout recruited (25 mm long) naturally to the reservoir from tributaries on 15 August (Table 4.2; Knight 1997; Baldwin et al. 2000). To account for variability in size at stocking, the coefficient of variation for total length ($N = 392$) from spring-stocked prey in 1996 (Baldwin et al. 2000) was applied to the mean total length of each cohort (Table 4.2). The resulting length frequency distributions were adjusted for growth through time and used to assign the surviving numbers of prey from each cohort into appropriate size classes. For modeling, we only considered prey 40-169 mm long vulnerable to piscivory to match what was observed in the diet of adult cutthroat during, before, or after stocking events (Baldwin et al. 2000). A separate prey field was generated for predator O3 to account for additional hatchery supplementation (post-stocked October) that occurred after tracking episodes for O6 and O9 (pre-stocked October).

Hydroacoustics data from surveys conducted 26-28 June 1996 (Beauchamp et al. 1999) were used to reconstruct the estimated abundance of prey (40-169 mm) available during each limnological period into densities (prey fish per 1,000 m³) proportioned among 5-m depth strata and diel periods (Figure 4.4A-C). Estimated abundances of prey in 1997 were normalized against the number of prey available during the hydroacoustic survey (counted fish targets 50-120 mm) to produce scaling factors that were applied to diel depth-specific densities measured in

June 1996 (Figure 4.4D-O). The reservoir was stratified in June 1996; therefore, we assumed salmonid prey exhibited the same distribution pattern during the more intense stratification periods in August 1997. This assumption was supported by catch data from 24-h offshore vertical gill net sets (June 1996, June 1997, and August 1997; Baldwin et al. 2000) and diel onshore-offshore gill net catches of larger prey-sized salmonids (100-280 mm) from 21-22 July 1997 (D. A. Beauchamp, unpublished data), when the intensity of stratification resembled that of August. To account for redistribution of prey during destratification in October, we utilized hydroacoustics data from 20-21 October 1995 (D. A. Beauchamp, unpublished data). We used the proportional allocation of targets 40-169 mm (-53 to -41 dB; 420 kHz; Love 1971) by depth and among diel periods from this survey to redistribute the corrected diel-specific densities from June 1996 into appropriate depth strata (Figure 4.4J-O).

Visual foraging model

Raw tracking data (at 10-s recording intervals) for each cutthroat trout were examined for fine-scale temporal variability before determining that data could be averaged over 20-min intervals without losing critical information on depth-specific exposure to temperature, oxygen, and light. Prey encounters during each interval were modeled using a modified version of equation 1 from Beauchamp et al. (1999) for each tracked cutthroat trout during each limnological and unique prey stocking period (early August, mid-August, pre-stocked October, or post-stocked October):

$$ER_{z,i} = SV_{z,i} \cdot PD_{z,d} \quad (4.2),$$

where encounter rate ($ER_{z,i}$) at mean fish depth z (m), during the i th tracking interval was equal to the product of the search volume ($SV_{z,i}$; m³) and prey density ($PD_{z,d}$; prey fish/m³) at depth z during diel period d . Search volume was modeled as a cylinder with the equation:

$$SV_{z,i} = \pi R_{z,i}^2 \cdot SS_d \cdot T \quad (4.3),$$

where interval-specific $R_{z,i}$ represents the reaction distance of cutthroat trout to prey fish at depth z , SS_d was the mean swimming speed (m/s) estimated specifically for each tagged cutthroat trout during diel period d (Table 4.1), and T was the interval duration. Under clear water (nephelometric turbidity units < 1.0; NTU), reaction distance (cm) was defined by a saturating function specific to Bear Lake strain cutthroat trout (Mazur and Beauchamp 2003):

$$R_{z,i} = \begin{cases} 33.7 \cdot I_{z,i}^{0.194} & \text{for } I_{z,i} \leq 17 \\ 58.3 & \text{for } I_{z,i} > 17 \end{cases} \quad (4.4),$$

where $I_{z,i}$ was the mean interval light level (lx) experienced by each cutthroat trout at depth z . Over the range of prey lengths (55-139 mm long rainbow trout), prey fish size did not affect reaction distances for piscivorous lake trout *Salvelinus namaycush* (Vogel and Beauchamp 1999), so a similar relationship was assumed for the reaction distance of cutthroat trout. We refer readers to Beauchamp et al. (1999) and Mazur and Beauchamp (2006) for more in depth presentation of basic assumptions and sensitivities associated with this modeling approach.

Turbidity varied significantly between the August and October tracking periods. Therefore, we included the effects of turbidity on reaction distance in the model explicitly. Turbidity was 3.5 NTU during August and 1.5 NTU in October, and was considered constant throughout the water column (C. M. Baldwin, unpublished data). We modeled this turbidity effect as a proportional reduction (P_{NTU}) in reaction distance by fitting a declining power function ($r^2 = 0.93$) through experimental data generated above the saturation intensity threshold (SIT; Henderson and Northcote 1985) for lake trout by Vogel and Beauchamp (1999) and Mazur and Beauchamp (2003), yielding:

$$P_{NTU} = 0.921 \cdot NTU^{-0.320} \quad (4.5).$$

Prey encounters per 20-min interval were scaled to 1 h (prey/h) and averaged within each

diel period. To standardize across tracking episodes, surface light thresholds designated transitions among diel periods (500 lx for dawn-to-day and day-to-dusk; 0.005 lx for dusk-to-night and night-to-dawn). Following Mazur and Beauchamp (2006), a light-dependent prey capture probability P_c :

$$P_c = \begin{cases} 0.49 & \text{for } I_{z,i} > 0.75 \\ 1.0 & \text{for } I_{z,i} \leq 0.75 \end{cases} \quad (4.6),$$

was applied to each of these rates to compute light-adjusted predation rates (prey consumed/h). These capture probabilities accounted for the shift in relative advantage toward piscivores under low light (Howick and O'Brien 1983; Petersen and Gadomski 1994; Mazur and Beauchamp 2003). Daily prey encounters and light-adjusted predation rates were computed by multiplying the mean encounter rates by the corresponding duration (h) for each diel period (Table 4.1), then summing across all diel periods within 24-h periods during August and October. To allow comparison with bioenergetics results, daily numerical rates were converted to biomasses (g/d) using associated size frequency distributions of vulnerable prey and a length-weight regression developed for cutthroat trout in Strawberry Reservoir (N = 481; $r^2 = 0.99$; Orme 1999):

$$W = 0.0000067 \cdot TL^{3.038} \quad (4.7).$$

Within each limnological period, we estimated the relative foraging success of each cutthroat trout by comparing daily light-adjusted predation rates to hypothetical rates for piscivores continuously foraging, without environmental restrictions, at depths yielding the maximum predation rate. Maximum predation rates were based on the suite of available diel depth-specific prey densities and light. This comparison was aimed at calculating the possible reduction in foraging success created by hypoxia or high temperatures.

Bioenergetics modeling

Bioenergetics simulations provided independent estimates of fish consumption by

cutthroat trout for comparison to encounter and predation rates generated by the visual foraging model for each limnological period. These comparisons allowed us to evaluate the extent to which capture success might vary between different diel periods. The daily biomass of fish and invertebrate prey consumed (g/d) by each tracked individual was estimated using the Wisconsin bioenergetics model (Hanson et al. 1997) parameterized for cutthroat trout (Beauchamp et al. 1995). Seasonal diet proportions for large cutthroat trout (age-4 and older; 351-600 mm) modified from Baldwin et al. (2000) were interpolated to the dates corresponding with each tracking episode (Table 4.3). Prey energy densities followed Baldwin et al. (2000) (Table 4.3). We assumed 3% indigestibility for fish and 17% for invertebrates (Beauchamp et al. 2007). Estimates of fish consumption were averaged for the simulation days corresponding with the tracking dates for each piscivore.

The duration of each bioenergetic simulation was determined by the closest dates before and after a tracking episode wherein a growth interval (14-31 d) was recorded for the size class representing the tracked fish (Table 4.3; Baldwin et al. 2000). Bioenergetic simulations for cutthroat trout tracked in early (30 July – 12 August) and mid-August (10-23 August) each lasted 14 d. Simulations for cutthroat tracked in October lasted 31 d (Table 4.3). Since no growth was observed in age-4 cutthroat trout during summer (Baldwin et al. 2000), initial and final weights for piscivores in August were held constant, so simulation results represented the requirements needed to maintain body weight, given the different thermal experiences observed during the early and mid-August periods. Large cutthroat trout increased body mass by 2.5% in autumn, but this growth increment was considered most concentrated during the 31 d simulation period for fish in October, based on the rapid decline in water temperature and prey supply during subsequent months (Baldwin et al. 2000). Thermal experience for fish in August was computed

as the time- and depth-averaged daily temperature associated with their observed vertical movements. Conversely, since destratification in October allowed unrestricted movement, thermal experience followed the interpolation by Baldwin et al. (2000) (Table 4.3). We assumed no change in predator energy density during simulation periods for both August and October.

We investigated the net effect of diel period on prey encounters and capture success by regressing the bioenergetic estimates of daily prey fish consumption against: a) visual prey encounters, and b) the light-adjusted predation rates. The regressions were performed both separately for each diel period and for totals over the 24-h periods. Higher correlations and slopes approaching values of 1.0 would suggest greater importance of certain diel periods for piscivory. Since we did not know how bioenergetics estimates of fish consumption were partitioned among diel periods, these correlations were intended only as an initial examination of light-dependent capture success in a natural population.

Results

Temporal-spatial patterns in prey encounter rates

In early August, when piscivores remained within the thermocline (11-13 m) between high epilimnetic temperatures and a hypoxic hypolimnion, the visual foraging model predicted peak prey encounter rates during brief periods at dusk and dawn (range: 0.00073-0.53 prey/h). These were the only periods when limnetic prey fish densities extended down to overlapping depths while light levels were sufficient for measurable reaction distance (Figure 4.4E). Ambient light levels at the depth of the piscivores during daylight always exceeded SIT (17 lx) and maximized reaction distance; however, surface-oriented (0-5 m) and littoral juvenile salmonids did not overlap with the depths of the piscivores (Figure 4.4D), thus precluding any visual encounters (all < 0.01 prey/h) during daylight. At night, low light greatly reduced reaction

distance, search volume, and encounters (all < 0.002 prey/h), even though juvenile salmonids were available within the restricted depth strata (10-15 m) containing the piscivores (Figure 4.4F). Prey encounter rates peaked sharply during dusk and dawn as light changed rapidly at the depths occupied by the piscivores (A6: 0.065-0.53 prey/h and A2a: 0.032-0.047 prey/h; Figure 4.5A, B). The combination of relatively high crepuscular (i.e., dusk and dawn and characterized by twilight) swimming speeds (Table 4.1), increased limnetic prey density at 10-15 m (Figure 4.4E), and sufficient light for moderate reaction distances produced these peak prey encounter rates.

In mid-August, hypoxia encroached into the thermocline, dramatically altering the diel depth distributions of piscivores and the timing and magnitude of prey encounters. The highest encounter rates occurred during short periods at dusk and dawn (range: 0.00025-0.47 prey/h), primarily less than 10 m as the piscivores migrated to shallower depths with greater prey fish densities and higher light-dependent reaction distance (Figure 4.4H). Daylight encounters were common, particularly during early morning (i.e., 0600-0800 hours; averaged 0.25 prey/h for A1 and 0.086 prey/h for A2b). The crepuscular peaks in prey encounters were prolonged (Figure 4.5C, D) as short term forays in surface waters (0-5 m) after dawn increased overlap with prey (Figure 4.4G). Subsequent descent into the upper metalimnion reduced encounters for the remainder of the daylight period (Figure 4.5C, D).

In October, destratification removed hypoxic and thermal constraints on vertical movement for both piscivores and prey, and prey encounter rates increased. For piscivores, diel encounter rate patterns were similar to mid-August, except that fish O9 and O3 sustained higher rates during daylight by remaining longer near the surface after dawn (Figure 4.4J, M and 4.6B, C). Strong surface orientation by fish O3 resulted in much higher daylight encounter rates

(averaged 5.80 prey/h) than for all other tracked piscivores. Encounter rates were considerably greater for piscivores tracked in October compared to August and ranged 0.0039-5.59 prey/h (Figure 4.6A-C). These differences were driven by the large numbers of prey stocked in September and October (Table 4.2), and by greater surface orientation by the piscivores, which increased their overlap with higher prey densities and reaction distances across all diel periods (Figure 4.4J-O).

Relative foraging success

The predicted daily prey encounter rates were lowest in early August (0.07-0.23 prey/d) during the temperature-oxygen squeeze, intermediate during mid-August (1.6-3.7 prey/d), and highest during destratification in October (26.9-70.4 prey/d). Similar patterns emerged when numerical encounters were converted to biomass (to account for temporal changes in prey size), and when prey encounters were converted to light-adjusted predation rates. Daily encounter rates of prey fish biomass ranged 0.7-2.3 g/d in early August, 20.1-47.3 g/d in mid-August, and 303.1-693.3 g/d during October. Corresponding estimates of light-adjusted predation rates were 0.4-1.2 g/d in early August, 11.0-23.3 g/d during mid-August, and 152.5-344.2 g/d in October. The light-adjusted predation rates were 37-50% lower than the daily encounter rates.

For early August, bioenergetics simulations indicated that the piscivores were feeding at 45-47% of the maximum theoretical rate (C_{\max}) on fish and invertebrates just to maintain body weight. Visual prey encounters (0.7-2.3 g/d) and light-adjusted predation rates (0.4-1.2 g/d) were too low to satisfy daily maintenance rations based on a diet of fish alone (9.1-10.3 g/d), thus highlighting the need for invertebrate prey to supplement the energy budget during the temperature-oxygen squeeze. After accounting for the energy contributed by invertebrates in the diet, fish A6 required an additional 1.3 g/d of prey fish to maintain body weight, which just

exceeded the predicted light-adjusted predation rate of 1.2 g/d. Fish A2a required 1.4 g/d of fish prey in addition to invertebrates; however, the light-adjusted predation rate was only 0.4 g/d.

During mid-August conditions, warmer epilimnetic thermal experience and higher metabolic demands required higher feeding rates of 73% C_{\max} for A1 and 96% C_{\max} for A2b on fish and invertebrates to maintain the observed body mass (Baldwin et al. 2000). The light-adjusted predation rate estimated for A1 (23.3 g/d) was sufficient to satisfy daily maintenance rations (19.2 g/d) with just fish prey. In contrast, the light-adjusted predation rate for A2b (11.0 g/d) provided only half the ration required to maintain body weight (21.7 g/d). After accounting for the energy contributed by invertebrates in the diet, A1 required an additional 3.6 g/d of prey fish, and A2a required 4.4 g/d. Corresponding light-adjusted predation rates provided 2.5-6.5 times more fish consumption than was required for maintenance rations after accounting for invertebrate diet contributions.

During destratification in October, the cooler thermal experience enabled the observed 2.5% increase in body mass (Baldwin et al. 2000) to be satisfied by lower feeding rates of 51-52% C_{\max} over the 31 d simulation interval. Unlike the August periods, light-adjusted predation rates on fish exceeded the daily consumption required to achieve observed growth for all piscivores if their diet had been composed entirely of fish (11.1-12.4 g/d). After accounting for the energy contributed by invertebrates in the diet, O6 required 2.5 g/d of fish prey, O9 required 2.5 g/d, and O3 required 7.1 g/d. The predicted light-adjusted predation rates of 152.5 g/d for O6, 193.1 g/d for O9, and 344.2 g/d for O3 indicated a large surplus of prey during this period, because these potential predation rates were 48.5-77.2 fold higher than the food required, based on the bioenergetics estimates of fish consumption during October.

The visual foraging model indicated that the foraging performance of piscivores were

similar for individuals tracked within the same limnological period, but differed greatly among limnological periods. Piscivores realized only 2-6% of the maximum potential predation rate during the temperature-oxygen squeeze in early August (these values corresponded to 1.1-3.0% of C_{\max} on fish prey alone), 35-47% in mid-August after hypoxic encroachment into the thermocline forced piscivores into warmer epilimnetic waters (26.3-48.1% of C_{\max}), and 41-98% after destratification in October (all values exceeded C_{\max}). During early August, piscivores remained in the lower metalimnion (11-13 m) and were largely segregated from concentrations of prey fishes at 0-5 m during daylight and 5-10 m during crepuscular and night periods (Figure 4.4D, E and 4.7A, B). In mid-August, piscivores realized much more of the potential maximum predation rate by increased foraging during crepuscular and night periods in 5-10 m and in 0-5 m where predation opportunities were nearly as high (Figure 4.7C, D). Predation rates were reduced by descent into the upper metalimnion from mid-morning through the afternoon, which segregated them from prey. Predation rates were higher at 5-10 m than 0-5 m during crepuscular periods because reduced light below 5 m improved piscivore capture success ($P_c = 1.0$ for $I_{z,i} \leq 0.75$ lx), whereas both depth intervals contained similar prey availability (Figure 4.4H). In October, piscivores more consistently overlapped with high prey concentrations in the 0-5 m depth strata where higher predation rates could be realized (41% of maximum by O6, 88% by O9, 98% by O3) across all diel periods (Figure 4.7E-G). For O6, a foray into 10-20 m depths during daylight where prey densities were much lower (Figure 4.4J) reduced its relative predation rate considerably (Figure 4.7E) when compared to conspecifics in October (Figure 4.7F, G). Slight deviations out of 0-5 m and into 5-10 m depths by O9 (Figure 4.7F) had little impact on its relative foraging success. Prey densities were high across all diel periods in 5-10 m (Figure 4.4J-L), while light was sufficient for either maximized (daylight) or only moderately-

reduced (crepuscular periods) search volumes.

Correlations between bioenergetics and foraging predictions

Daily consumption estimates of prey fish from bioenergetics simulations were generally more strongly correlated to encounter and light-adjusted predation rates from the daylight period and summed across a 24-h period ($r^2 = 0.46-0.47$; slopes = 0.005-0.011; Figure 4.8A-D) than from crepuscular periods, but the slopes of these relationships were negligible and not significantly different from zero. The slopes of the relationships only considering crepuscular periods were higher (slopes = 0.079-0.16; $P = 0.33-0.38$; $r^2 = 0.16-0.19$), but also not significantly different from zero (Figure 4.8E, F). However, six of the seven crepuscular points fell much closer to the one-to-one consumption line in these relationships when compared to those including the daylight period. The visual foraging model estimated a high prey encounter rate coupled with only a moderate prey consumption rate for fish O6 during crepuscular periods. For purposes of exploration only, removing this point produced a significant linear relationship with a much higher slope and coefficient of determination ($r^2 = 0.72$; slope = 0.26; $P = 0.03$), which improved further after testing the light-adjusted predation rates ($r^2 = 0.75$; slope = 0.47; $P = 0.03$).

Discussion

Integrating the visual foraging model with bioenergetics simulations and known vertical movement patterns from telemetry provided a novel approach for mechanistically evaluating the influence of abiotic forcing on temporal-spatial overlap of pelagic piscivores with prey and the consequent foraging success of piscivores. Periods of stress redistributed the timing and magnitude of prey encounters. Collectively, this reduced the foraging success of the piscivores and increased refugia for prey. However, these patterns are likely dependent on both the

duration and severity of stress. Asymmetries in environmental tolerances that allow for the creation of temporally dynamic refuge space for prey may be weakened if environmental conditions become too severe. Our results also suggested that ambient visual conditions affected capture success, but correlations were not definitive enough to infer the importance of particular diel periods over others. However, there was some indication that encounters during crepuscular periods were more profitable, which parallels empirical and experimental evidence in the literature (see below). Therefore, as environmental stressors impose constraints on diel movement and distribution of prey or predators, the resulting spatial-temporal redistribution of prey encounters can affect the magnitude of piscivory in complex ways that will require a mechanistic understanding of key factors and responses.

There are some important limitations to our study that should be considered when interpreting model outcomes and associated conclusions. Small sample size is a common criticism of telemetry studies, and we were limited to data from five cutthroat trout, two of which were tracked during two limnological periods. However, individuals tracked within the same limnological periods exhibited strikingly similar diel-vertical movement patterns, increasing confidence in the generalization of our results. Additionally, cutthroat trout that were tracked during two limnological periods (A6 and A2a) exhibited highly divergent diel-vertical movement patterns between the two periods, strengthening our assertion that environmental conditions were driving fish distributions.

Estimates of encounter rates from foraging models are highly dependent on the manner in which prey fields are derived (Mazur and Beauchamp 2006), which could limit interpretations in some cases. We reconstructed prey fields using hydroacoustics and gill netting data that were disconnected temporally and spatially from the tracking periods for cutthroat trout. The

reconstructed prey fields also did not account for prey patchiness (e.g., schooling), particularly at depth and in surface waters during daylight, as this is challenging to characterize with combined down-looking hydroacoustics and netting surveys (Yule 2000; Mazur and Beauchamp 2006). Similarly, we used population level diet proportions and growth estimated over a longer temporal window to model consumption for each cutthroat trout. These simulations only provided an average daily consumption level as diet data for specific diel periods and tagged cutthroat trout were not available (Baldwin et al. 2000). All of these factors limited our ability to draw stronger conclusions regarding empirical versus predicted foraging performance at the individual organism level, and light-dependency in capture success. Despite these limitations, results provide useful insights into foraging tradeoffs confronting piscivores under a suite of environmental conditions that can be explored further with more targeted sampling efforts.

The temperature-oxygen squeeze during August was likely the primary factor limiting overlap between predators and prey, and consequently, altering the timing of prey encounters. The combined vertical movements of piscivores and prey during this period produced pulsed diel encounters which were primarily squeezed into short crepuscular or early daylight windows. In early August when vertical movements by the cutthroat trout were restricted to the lower metalimnion, the visual foraging model indicated that prey encounters were minimal, limited to brief periods during dusk and dawn as prey dispersed over greater depths. After hypoxia encroached into the lower metalimnion during mid-August, piscivores moved into the warmer epilimnion, which considerably increased crepuscular and morning encounter rates, but at a metabolic cost.

The temperature-dependent scope for growth for different sizes of salmonids (Beauchamp 2009) provides insight into processes contributing to vertical segregation of

piscivores and prey and the relative profitability of foraging among depths during stratified periods (Figure 4.9). These growth curves indicate that piscivorous cutthroat trout would lose weight if they remained in epilimnetic temperatures of 18-20°C, even if feeding at their maximum rate. In contrast, prey-sized juvenile cutthroat trout and kokanee could still achieve positive growth at epilimnetic temperatures if they could maintain a reasonably high feeding rate. Despite the potential for increased overlap with prey fish near the surface in early August, the piscivores remained within the metalimnion, thus reducing metabolic costs and the feeding rate required to maintain body weight by inhabiting cooler temperatures (Figure 4.9) and adequate oxygen levels (9.0-11.1 °C; 3.0-3.9 mg/L; Baldwin et al. 2002). During mid-August, piscivores needed to forage near C_{max} on prey fish and invertebrates in the warmer epilimnion just to maintain the observed body condition (Baldwin et al. 2000); even with minimizing exposure to higher surface temperatures by descending to greater daytime depths after being shallow during crepuscular, night, and early morning periods (13.0-16.3 °C and 3.1-6.2 mg/L during daylight versus 18.3 °C and 9.4 mg/L at night; Baldwin et al. 2002). The visual foraging model indicated that the piscivores achieved small fractions of the maximum daily light-adjusted predation rates during this period because limnological stressors regulated their vertical movements. Consequently, a larger contribution of invertebrates, as observed in the diet during periods of stress, was necessary for the piscivores to maintain body mass.

More factors limited foraging success of piscivores in August compared to October. Temperature and oxygen (8.9-12.5 °C and 9.7-11.8 mg/L at occupied depths) did not constrain vertical movements of piscivores during destratification in October (Baldwin et al. 2002). The visual foraging model indicated that the piscivores consistently maintained overlap with salmonid prey at temperatures more conducive for growth (Figure 4.9). This increased prey

encounters and nearly maximized their daily light-adjusted predation rates, which exceeded the theoretical rations for satiation. Unlike August, minor deviations from depths that maximized predation rates by the piscivores in October had little effect on their foraging success (with the exception of fish O6 during daylight). Thus, piscivory in October was not limited by either encounters with prey or environmental stressors. The fact that they still incorporated large fractions of invertebrates into their diet suggests that some other process related to capture success limited their intake of fish. Conversely, piscivory was limited by lower prey encounters, environmental conditions, and capture success during periods of stress.

When interpreting the predicted time- and depth-specific prey encounters, it is important to consider the underlying assumptions about the distribution of prey and the empirical support for those assumptions. We assumed that stocked juvenile cutthroat trout exhibited similar diel-vertical and horizontal distribution patterns (i.e., onshore-offshore migration) during August 1997 as was observed during a hydroacoustics survey after the reservoir was thermally stratified in June 1996 (Beauchamp et al. 1999). Catch rates of larger prey-sized cutthroat trout (100-280 mm) were generally higher in offshore floating and sinking horizontal gill nets during dusk and dawn compared to simultaneous efforts nearshore during late July 1997. Conversely, no prey-sized cutthroat trout were captured offshore during daylight when concurrent catch rates nearshore were high (D. A. Beauchamp, unpublished data). In addition, 100-225 mm cutthroat trout captured during 24-h integrated vertical gill net sets during August and October spanned the depths assumed for the visual foraging model during crepuscular and night periods (Baldwin et al. 2000). Diel horizontal migration by juvenile fish is common (Hall and Werner 1977; Wurtsbaugh and Li 1985; Comeau and Boisclair 1998), and has been reported for hatchery rainbow trout. Stocked rainbow trout use littoral zones extensively to minimize predation risk

(Tabor and Wurtsbaugh 1991; Post et al. 1998; Biro et al. 2003), but habitat use may shift to pelagic regions as they grow and become less vulnerable to gape-limited predators (Landry et al. 1999), or as growth and mortality trade-offs shift in response to changing environmental or ecological conditions (Biro et al. 2005, 2007).

Unlike juvenile trout, juvenile kokanee are predominately pelagic, making assumptions regarding their distribution and potential contribution to prey encounters less certain. In Strawberry Reservoir during August, juvenile kokanee likely remained in the pelagic zone during daylight while juvenile cutthroat trout migrated nearshore, but low catch rates of kokanee during onshore-offshore gill netting during late July 1997 precluded proper examination. Interestingly, the June 1996 acoustics data lacked a strong mode of pelagic targets at greater depths during daylight where we would expect kokanee to reside. Both near-surface and schooling fish are difficult to detect reliably with standard down-looking hydroacoustics (Beauchamp et al. 2009). Kokanee could have formed schools that were undetected by hydroacoustics, or remained more surface oriented. Hardiman et al. (2004) reported that age-0 kokanee in Blue Mesa Reservoir, Colorado remained closer to the surface by exhibiting dampened vertical oscillations as stratification intensified during August.

Crepuscular foraging periods are important for pelagic piscivores. Six of seven predicted crepuscular light-adjusted predation rates were in agreement with the independent bioenergetic estimates of daily fish consumption, whereas analogous relationships were much weaker for other diel periods. Although this relationship did not hold for one of the seven piscivores, these comparisons indicated that light-adjusted predation rates were superior to simple estimates of prey encounters and that predation rates during crepuscular periods provided a better predictor of piscivory than similar metrics from either the daylight or entire 24-h period. The slopes of the

latter two relationships suggested that only a small proportion of encounters (i.e., < 1%) during daylight or over a 24-h period would result in successful capture. In contrast, the slope of crepuscular prey encounters versus daily fish consumption for six of the seven piscivores suggested a capture success of approximately 25% if the majority of fish consumption occurred during crepuscular periods. These relationships highlight the need incorporate the capture success process into future formulations of these models (Beauchamp et al. 1999).

Because capture success appeared to be higher during crepuscular periods, more active foraging during these periods could reflect a strategy that exploits favorable conditions for piscivory while minimizing exposure to stressful environmental conditions. Piscivores tracked under stressful conditions in August experienced much higher fractions of encounters during crepuscular periods when capture success could have been higher (37-84 % for early August and 7-20 % in mid-August), and thus compensated to some extent for the more restricted overlap with prey. However, the lower absolute number of encounters during periods of stress still limited overall foraging success on prey fish. Lower prey fish abundance was one contributing factor, but piscivores in early August remained in the lower metalimnion and relied on prey migrating to overlapping depths during low light periods. Conversely, piscivores in mid-August moved into more profitable surface waters (i.e., further into thermal refuge habitat) during low light periods. Even though total prey encounters increased dramatically in October, most of this increase was attributed to greater predator-prey overlap during daylight (89-97 % of daily encounters) when capture success was likely much lower (Petersen and Gadomski 1994; Mazur and Beauchamp 2003).

Several factors likely affect how visual conditions influence prey encounters and capture success among diel periods. Empirical evidence for crepuscular peaks in piscivory has been

reported for pelagic predators (Beauchamp 1990; Beauchamp et al. 1992; Malmquist et al. 1993; Kahilainen et al. 2009). The underlying mechanisms have only partially been explored, but could largely be related to light-dependent behavior of both forage fishes (e.g., schooling and evasion) and piscivores (e.g., foraging activity; Helfman 1986). During daylight, schooling and diel vertical or horizontal migration effectively reduce encounters in shallower lighted habitats. Capture success is inhibited by schooling behavior and the enhanced evasion capabilities of prey under higher light (Howick and O'Brien 1983; Petersen and Gadomski 1994; Mazur and Beauchamp 2003). Crepuscular encounters increase as schools disperse or as prey fishes migrate into the upper pelagic zone (Mazur and Beauchamp 2006), while declining visibility may improve the probability of capture after prey are encountered. At night, prey densities are often highest in the upper pelagic zone, but low light levels reduce the effective search volume and encounter rates dramatically. However, full moonlight and urban light pollution can potentially increase the efficacy of nocturnal piscivory (Luecke and Wurtsbaugh 1993; Kitano et al. 2008).

Understanding how spatial variation in habitat interacts with feeding behavior and physiology to mediate the foraging rates of apex predators has important implications for how we manage systems prone to environmental stress. In our study, the periods of stress were relatively short in duration (2-4 weeks). Although the foraging success of the piscivores on fish prey was reduced during these times, adaptive shifts in movement behavior and the presence of invertebrate prey buffered them from severe losses in body weight. These short-term reductions in consumption and growth may not limit the overall quality of the fishery for larger predators (e.g., Mathews et al. 1985) until the frequency, duration, or severity of environmental stress trumps the buffering capacity of alternative prey and hinders recovery from resulting deficits in growth during other parts of the year (e.g., during the fall when growth conditions improve).

However, whether managers should be concerned about reductions in growth and consumption of top predators depends on the goal of the fishery. In some instances, heavy predation may be limiting recruitment of juvenile fishes (either natural or hatchery produced) to the fishery (Baldwin et al. 2000). The creation of temporally-dynamic refuge space during periods of stress could provide a growth and survival advantage to prey fish (and potentially targeted for stocking; Baldwin et al. 2002), giving them an opportunity to outgrow some gape limited predators (Martinez and Wiltzius 1995). This obviously depends on the fish community, severity, and duration of stress, as under some conditions, overlap of predators and prey can increase as pelagic habitat becomes more confined (Pientka and Parrish 2002; Ficke et al. 2007). Adaptively managing for stressful conditions and associated shifts in predator-prey interactions will require well designed and established monitoring programs (e.g., targeted netting and hydroacoustics).

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Tables

Table 4.1. General information and fish specific visual foraging model inputs for cutthroat trout ultrasonically tracked in Strawberry Reservoir, Utah during August and October 1997 (data from Baldwin et al. 2002). Tracking intervals were 20 min in duration.

Fish ID	Total length (mm)	Weight (g) ^a	Tracking dates	Total tracking intervals	Diel period	Duration of diel period (h)	Mean swimming speed (m/s)	Mean temperature (°C)
A6 ^b	483	1,004	2-4 Aug	93	Dawn	1.0	0.24	10.6
					Daylight	14.0	0.25	10.6
					Dusk	1.0	0.20	11.1
					Night	8.0	0.09	10.6
A2a ^c	481	991	7-8 Aug	99	Dawn	1.0	0.16	9.9
					Daylight	14.0	0.28	9.5
					Dusk	1.0	0.26	9.0
					Night	8.0	0.13	9.9
A1	502	1,127	13-16 Aug	51	Dawn	1.0	0.23	18.0
					Daylight	14.0	0.50	13.0
					Dusk	1.0	0.22	18.1
					Night	8.0	0.12	18.2
A2b	481	991	16-18 Aug	62	Dawn	1.0	0.27	18.1
					Daylight	14.0	0.27	16.3
					Dusk	1.0	0.51	18.4
					Night	8.0	0.19	18.4
O6	483	1,004	8-10 Oct	51	Dawn	1.0	0.28	12.4
					Daylight	11.7	0.32	9.3
					Dusk	1.0	0.33	12.5
					Night	10.3	0.25	12.5
O9	495	1,026	12-14 Oct	83	Dawn	1.0	0.02	11.2
					Daylight	11.7	0.20	11.2
					Dusk	1.0	0.14	11.2
					Night	10.3	0.12	11.2
O3	475	906	18-19 Oct	82	Dawn	1.0	0.22	8.9
					Daylight	11.7	0.29	8.9
					Dusk	1.0	0.10	8.9
					Night	10.3	0.08	8.9

^aEstimated using a weight-length regression (N = 481; $r^2 = 0.99$) for this population (Orme 1999).

^bFish A6 was tracked again in October (Fish ID O6).

^cFish A2a was tracked again in mid-August (Fish ID A2b).

Table 4.2. Summary of salmonid stocking and cohort specific demographic rates (Orme 1999) used for estimating the size distribution (TL = total length) and abundance of prey through the spring-summer-fall period during 1997 in Strawberry Reservoir. Only the cohort stocked during spring of 1996 is shown since they were the only fish available for the acoustics survey conducted 26-28 June by Beauchamp et al. (1999). The acronym CV stands for coefficient of variation. Nat-recruit represents cutthroat trout fry that recruited naturally from tributaries into the reservoir.

Stocked or natural cohort	Presumed stocking or arrival date	Cutthroat trout		Kokanee		Cohort demographics			
		Number released	Mean TL (mm)	Number released	Mean TL (mm)	Growth (mm/d)	1 st months survival (%)	Daily inst. mortality (Z)	Mean stocking length CV
1996									
May-Jun	1-Jun	341,268	182	683,536	77	0.67	95.3	-0.0016	0.823
1997									
May-Jun	1-Jun	342,912	153	389,750	65	0.67	95.3	-0.0016	0.823
Jul	1-Jul	169,309	29	0	-	0.67	74.5	-0.0095	0.823
Aug	1-Aug	851,651	59	0	-	Excluded from analysis			
Sep	1-Sep	1,581,963	67	0	-	0.67	78.8	-0.0077	0.823
Oct	17-Oct	517,833	77	0	-	0.67	78.8	-0.0077	0.823
Nat-recruit	15-Aug	100,000	25	0	-	0.67	74.5	-0.0095	-

Table 4.3. Fish specific model inputs for bioenergetics simulations. Diet proportions and temperature were taken or modified from Baldwin et al. (2000, 2002).

Fish ID	Final weight (g) ^a	Day of simulation	Date	Simulation temperature (°C)	Diet proportions	
					Fish ^b	Invertebrates ^c
A6	1,004	1	30-Jul	10.60	0.053	0.947
		14	12-Aug	10.60	0.094	0.906
A2a	991	1	30-Jul	9.60	0.053	0.947
		14	12-Aug	9.60	0.094	0.906
A1	1,127	1	10-Aug	15.20	0.087	0.913
		11	20-Aug	15.20	0.119	0.881
		14	23-Aug	15.20	0.119	0.881
A2b	991	1	10-Aug	17.20	0.087	0.913
		11	20-Aug	17.20	0.119	0.881
		14	23-Aug	17.20	0.119	0.881
O6	1,029	1	20-Sep	11.09	0.117	0.883
		27	16-Oct	10.75	0.115	0.885
		28	17-Oct	10.74	0.323	0.677
		29	18-Oct	10.73	0.444	0.556
		31	20-Oct	10.70	0.115	0.885
O9	1,052	1	20-Sep	11.09	0.117	0.883
		27	16-Oct	10.75	0.115	0.885
		28	17-Oct	10.74	0.323	0.677
		29	18-Oct	10.73	0.444	0.556
		31	20-Oct	10.70	0.115	0.885
O3	929	1	20-Sep	11.09	0.117	0.883
		27	16-Oct	10.75	0.115	0.885
		28	17-Oct	10.74	0.323	0.677
		29	18-Oct	10.73	0.444	0.556
		31	20-Oct	10.70	0.115	0.885

^aInitial weights from Table 4.1 corrected for observed growth and used as end points in bioenergetics simulations.

^bAn energy density of 5,778 J/g was used for fish prey in simulations (Hewett and Johnson 1992).

^cAn energy density of 3,455 J/g was used for invertebrate prey in simulations. This is the average of the values reported for *Daphnia* sp. (Luecke and Brandt 1993) and other invertebrates (Beauchamp et al. 1995).

Figures

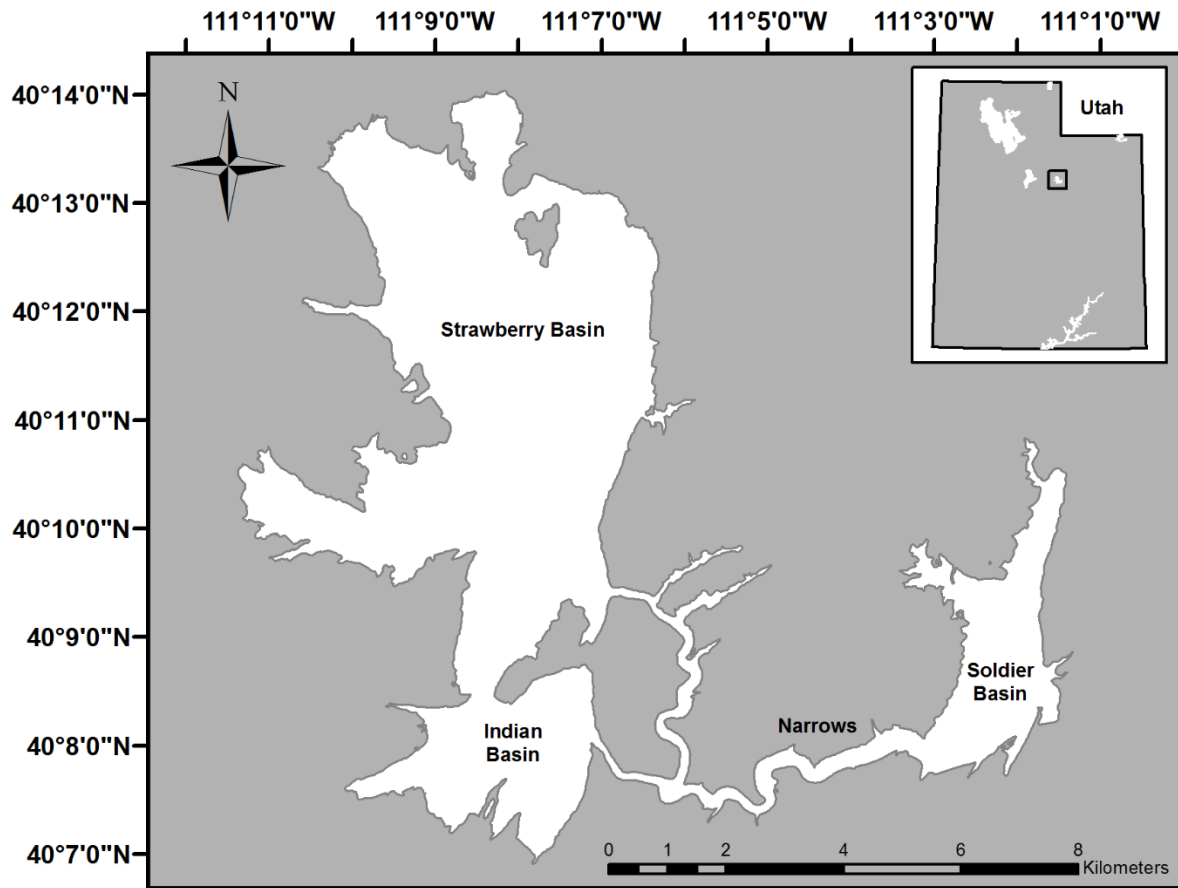


Figure 4.1. Map of Strawberry Reservoir, Utah where cutthroat trout were ultrasonically tracked throughout Strawberry Basin during August and October 1997.

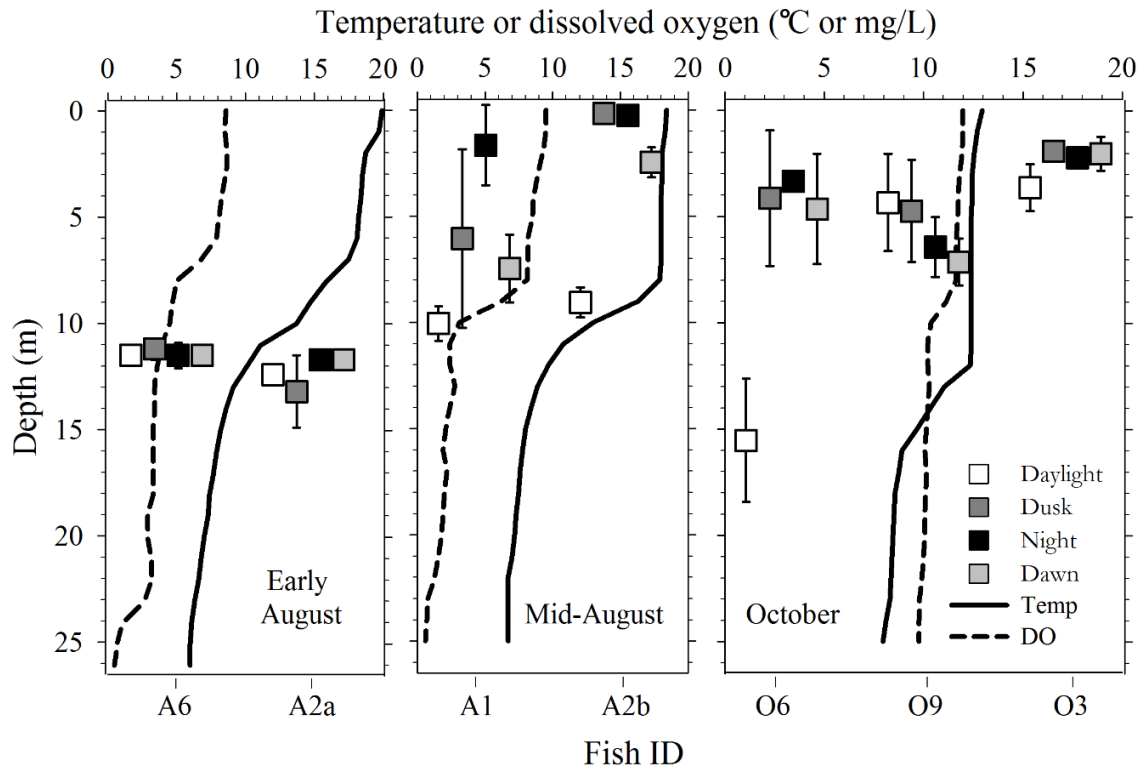


Figure 4.2. Diel mean depth distributions of cutthroat trout ultrasonically tracked in Strawberry Reservoir (shaded boxes) in relation to temperature and dissolved oxygen (DO) during three separate observation periods spanning summer and autumn 1997. Error bars represent one SD. Data were modified from Baldwin et al. (2002).

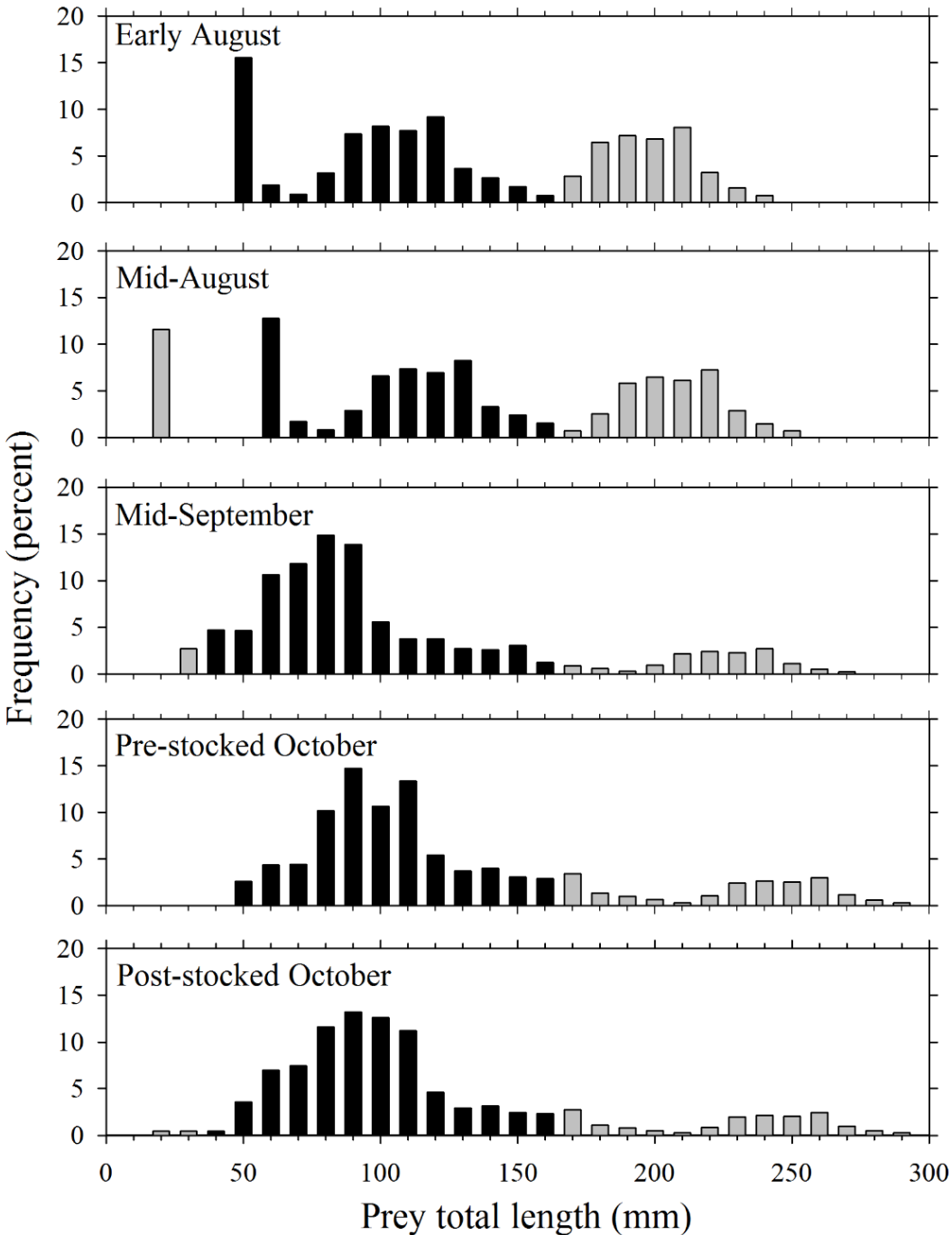


Figure 4.3. Estimated size distributions of the prey field during each limnological and unique prey stocking period in Strawberry Reservoir. Black bars represent the frequencies of 40-169 mm salmonids used for computing encounter rates with the visual foraging model and for converting rates into biomasses encountered. Gray bars represent the juveniles considered invulnerable to piscivory.

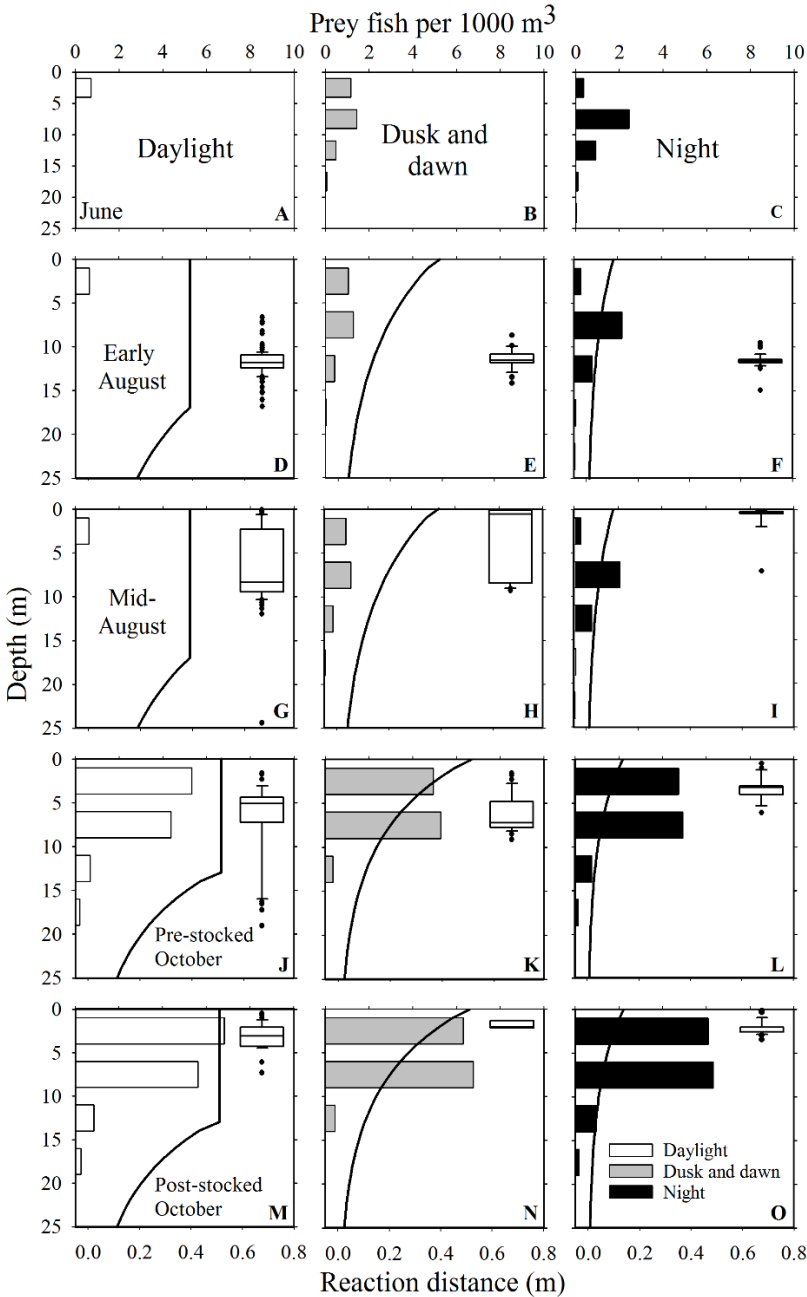


Figure 4.4. Diel-vertical prey density distributions (shaded bars) measured with hydroacoustics during (panels A,B,C) 26-28 June 1996 and reconstructed for (D,E,F) early August for fish A6 and A2a; (G,H,I) mid-August for fish A1 and A2b; (J,K,L) the pre-stocking period in October for fish O6 and O9; and (M,N,O) post-stocking period in October 1997 for fish O3. Solid lines represent corresponding estimates of reaction distance during each limnological and diel period. Box-and-whisker plots represent the average interval depth distributions of all cutthroat trout tracked during each limnological and diel period: horizontal line = median depth, box = 25th and 75th percentiles, error bars = 10th and 90th percentiles, and dots represent outliers.

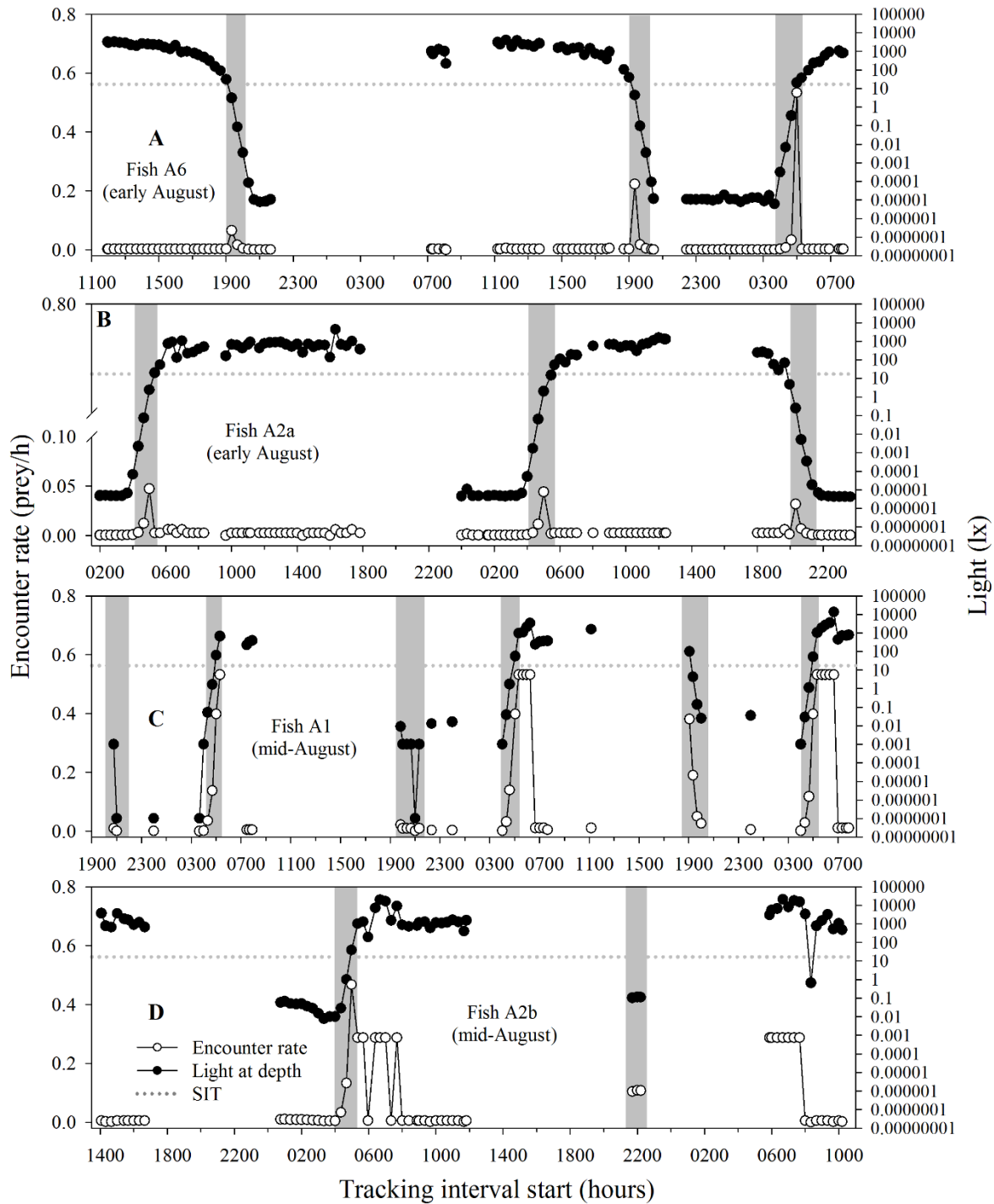


Figure 4.5. Prey encounter rates (prey/h) in relation to light at depth and the saturation intensity threshold (SIT) through time estimated with the visual foraging model for (A) fish A6 (tracked during early August); (B) fish A2a (early August); (C) fish A1 (mid-August); and (D) fish A2b (mid-August). Gray regions shade tracking intervals during crepuscular periods (dusk or dawn). Tracking episodes for each cutthroat trout spanned 2-3 d. Blank regions are times when no data were collected.

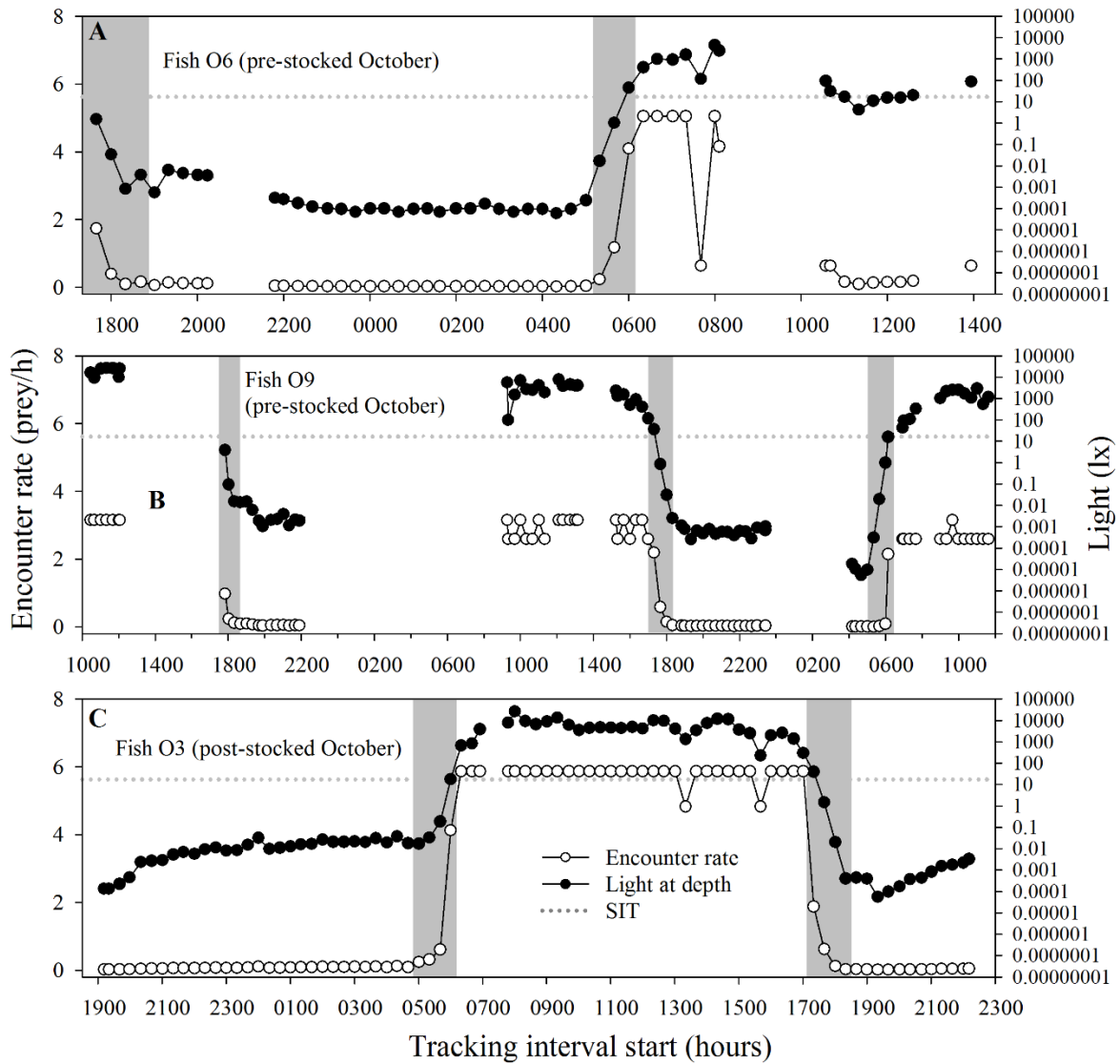


Figure 4.6. Prey encounter rates (prey/h) in relation to light at depth and the saturation intensity threshold (SIT) through time estimated with the visual foraging model for (A) fish O6 (tracked during pre-stocked October); (B) fish O9 (pre-stocked October); and (C) fish O3 (post-stocked October). Gray regions shade tracking intervals during crepuscular periods (dusk or dawn). Tracking episodes for each cutthroat trout spanned 2-3 d. Blank regions are times when no data were collected.

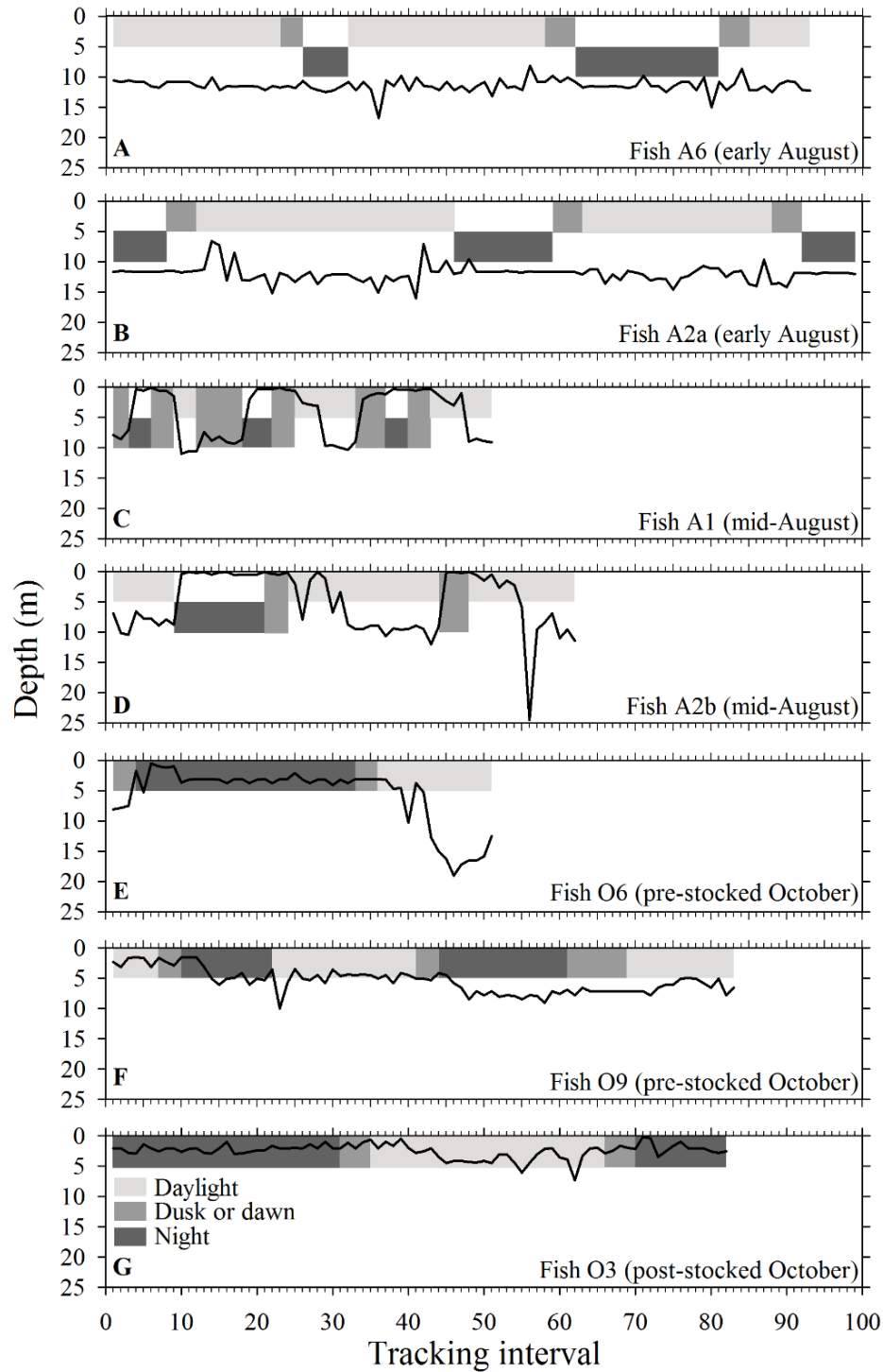


Figure 4.7. Mean diel-vertical movement trajectories (solid line) estimated with ultrasonic telemetry for (A) fish A6 (tracked during early August); (B) fish A2a (early August); (C) fish A1 (mid-August); (D) fish A2b (mid-August); (E) fish O6 (pre-stocked October); (F) fish O9 (pre-stocked October); and (G) fish O3 (post-stocked October). Observed movement trajectories are shown in relation to depth strata that would have maximized the light-adjusted predation rate during each consecutive tracking interval and associated diel period (shaded regions).

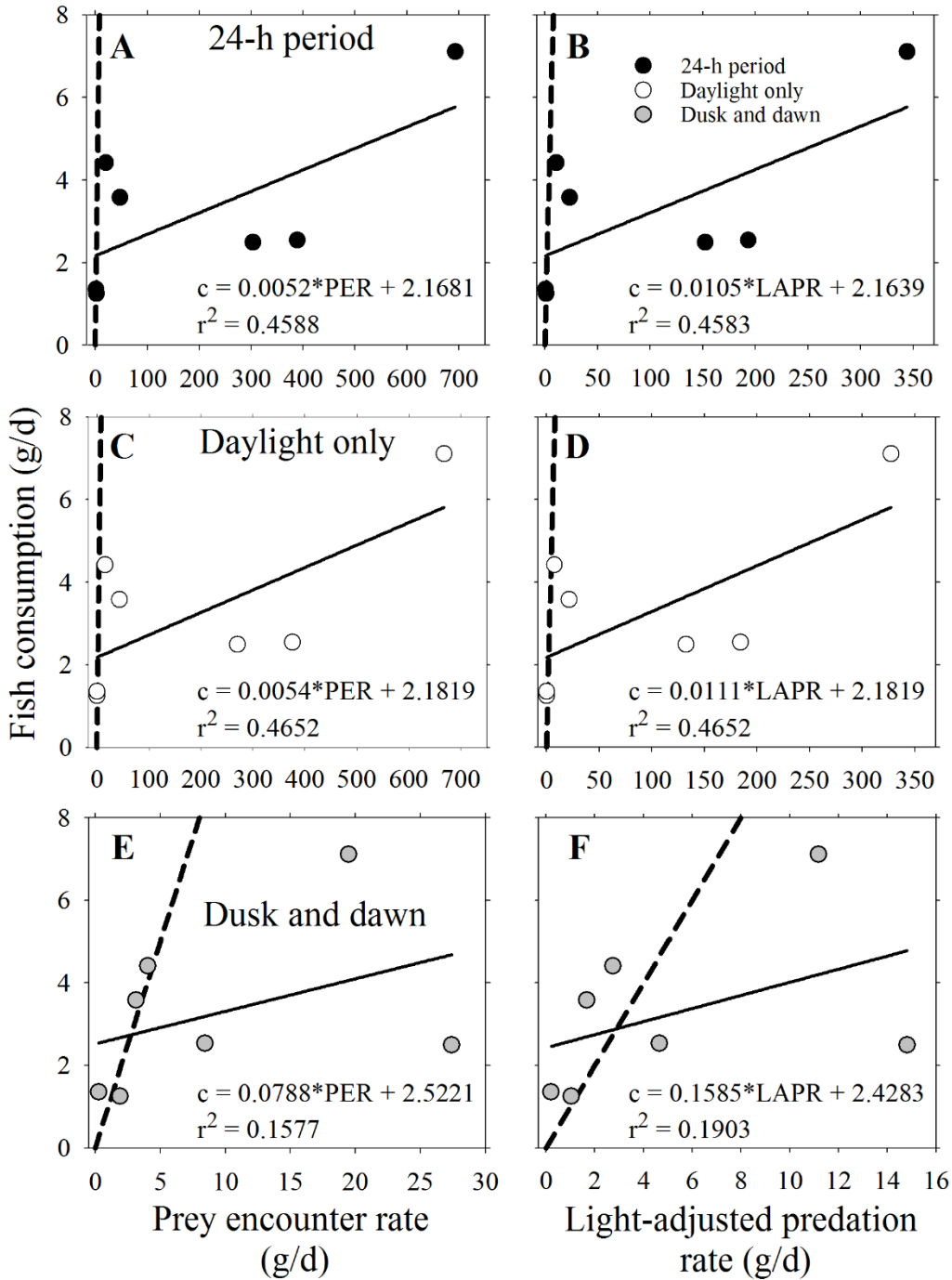


Figure 4.8. Fish consumption from bioenergetics simulations (c) as a function of (A,C,E; left panels) prey encounter rates (PER) and (B,D,F; right panels) light-adjusted predation rates (LAPR) incorporating a 24-h period (top), daylight only (center), and dusk and dawn only (bottom) as denoted by shaded circles. Dashed lines represent the one-to-one line where encounter rate or the light-adjusted predation rate matches consumption rate exactly. Solid lines represent the fitted linear regression models.

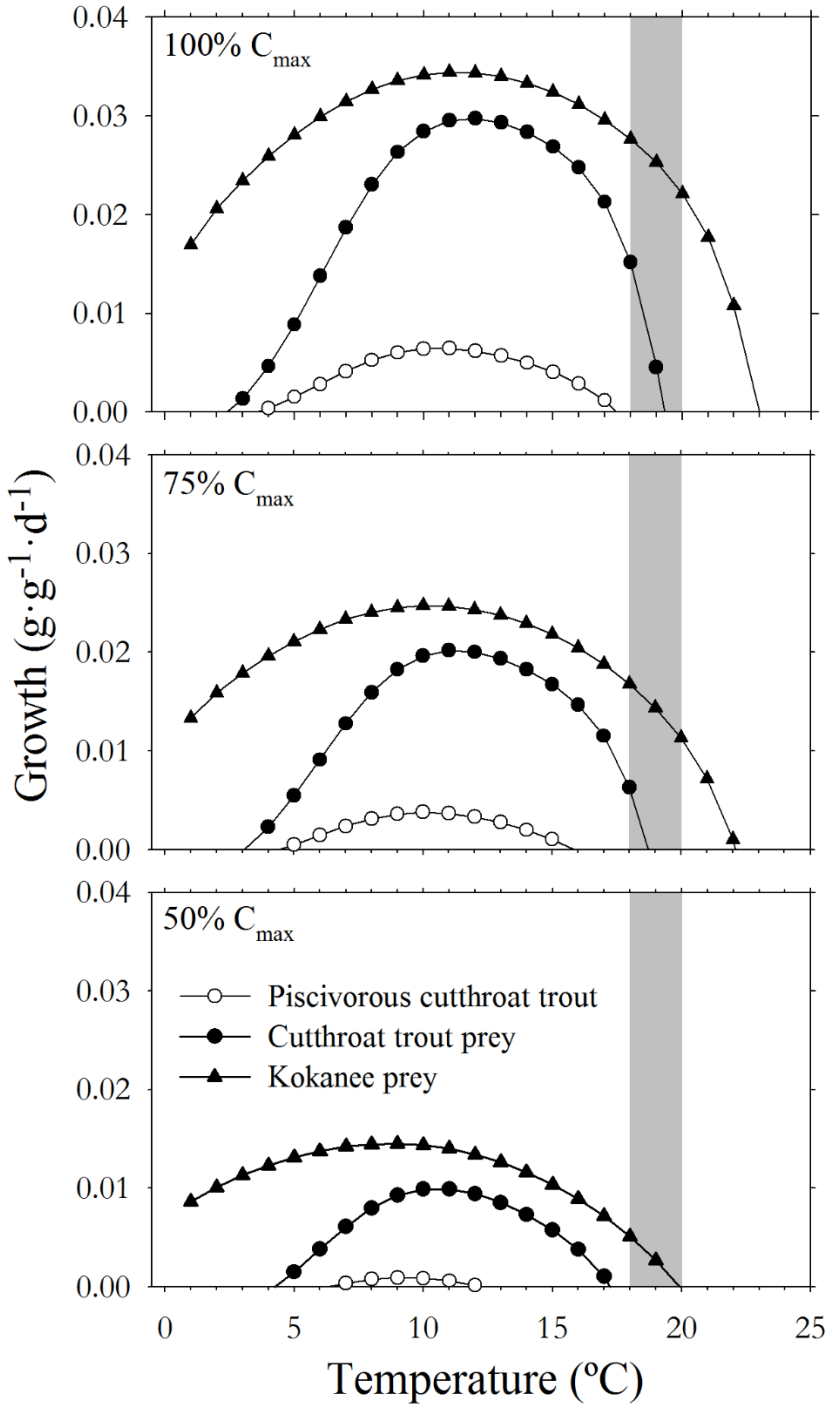


Figure 4.9. The relations between temperature and estimated growth for predators (cutthroat trout) and prey (juvenile cutthroat trout and kokanee) at different feeding rates (% of maximum theoretical consumption rate; C_{max}) in Strawberry Reservoir. Shaded regions bracket the range of daytime temperatures (18-20 $^{\circ}C$) measured in the 0-5 m depth strata during thermal stratification in August.

Chapter 5.—Effects of prey abundance, distribution, pigmentation, and morphology on apparent selection by a pelagic piscivore

Abstract.—The diets of most predators constitute only a subset of possible prey. However, most studies evaluating diet selection rarely measure prey availability in a manner that accounts for temporal-spatial overlap between predators and prey, how prey fields might be perceived by predators, the primary sensory mechanisms employed to detect prey, and constraints on prey capture given an encounter. We evaluated the diet selection of cutthroat trout *Oncorhynchus clarkii* feeding on a diverse planktivore community in Lake Washington to test the hypothesis that diet selection of piscivores would reflect random (opportunistic) as opposed to non-random (targeted) feeding after accounting for predator-prey overlap in time and space and constraints on the visual detection and capture of different prey groups. Diets were sampled in fall 2005 when the abundance of transparent, age-0 longfin smelt *Spirinchus thaleichthys* was low, and 2006 when their abundance was high. Diet selection was evaluated separately using regional depth-integrated and depth-specific prey densities and abundance. Abundances were then adjusted for constraints on visual detection and capture to see if factors related to prey susceptibility could explain the patterns of diet selection. In 2005, cutthroat trout fed non-randomly by selecting against the smaller, less conspicuous age-0 longfin smelt, but for the larger, more conspicuous age-1 longfin smelt. However, after adjusting prey abundances for visual detection and capture constraints, cutthroat trout fed randomly. In 2006, when the abundance of age-0 longfin smelt was 6-7 times higher than in 2005, regional and depth-specific abundances explained the diets of cutthroat trout well, indicating random feeding. However, feeding became non-random after adjusting for visual detection and capture: cutthroat trout selected for age-0 longfin smelt, but against similar sized threespine stickleback *Gasterosteus aculeatus* and larger age-1 longfin smelt. Spatial-temporal overlap between cutthroat trout and juvenile sockeye salmon *O. nerka*

was minimal during fall, and sockeye salmon were rare in the diet both years. The direction of the shift between random and non-random prey selection depended on the presence of a weak versus a strong year-class of age-0 longfin smelt. Age-0 longfin smelt 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 for cutthroat trout. Results show that the nature of the feeding selectivity of a visually-oriented predator can be highly dependent on fluctuations in the abundance and susceptibility of key prey to detection and capture.

Introduction

Most predators are considered selective feeders, consuming certain sizes or species of prey more than would be expected by their abundance (Stephen and Krebs 1986; Juanes 1994; Isaac et al. 2012). However, the realized diet of a predator could be influenced by multiple factors related to prey abundance (total abundance or abundance within overlapping depths in time and space), visual detectability (transparency or contrast of different prey), and vulnerability (behavior and morphology of different prey) to capture (Hambright 1991; Christensen 1996; Mazur and Beauchamp 2006). The apparent selectivity of a predator could range from random opportunistic feeding, reflecting the relative encounter rates of 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 evaluate whether selectivity depends on how prey abundance is measured (Hyvarinen and Huusko 2006; Jensen et al. 2008; Isaac et al. 2012; Jacobs et al. 2013). In systems containing diverse prey communities, potential asymmetries in detectability and vulnerability to capture

could either help explain the diet selection of predators, or reveal greater selection for or against certain prey groups after appropriately accounting for prey abundance.

The predation sequence (search-encounter-capture) provides a useful framework for considering how physical and biological processes regulate the diets of predators (Beauchamp et al. 2007). Predators must first overlap in time and space with prey in habitats suitable for detection and capture. In limnetic regions of lakes, vertical gradients of temperature, oxygen, light, and zooplankton density structure the foraging environment for planktivores and piscivores (Hardiman et al. 2004). These variables are dynamic over time and space and can differentially influence the distribution of predators and prey depending on species-specific or ontogenetic asymmetries in physiological tolerance and perception of the environment (Mackenzie-Grieve and Post 2006; Hansen et al. 2013a). For visually-feeding piscivores, ambient photic conditions, body-size, and pigmentation influence the detection of prey (an encounter) that are available within overlapping habitats (Denton 1970; Muntz 1990; Hansen et al. 2013c). Given an encounter, species-specific behavior (e.g., freeze, evade, or school) and morphological characteristics (e.g., body-size and spines) can then regulate the rate of capture and ingestion of prey when attacked (Einfalt and Wahl 1997; Christensen 1996; Scharf et al. 1998; Reimchen 2000). Therefore, the feeding selectivity of a predator may be sensitive to the behavioral and morphological constraints on prey encounter and capture that follow sequentially from the processes that determine the spatial-temporal dimensions of prey abundance.

Lake Washington, Washington, contains a diverse pelagic planktivore community and is well suited for evaluating the influence of different factors on the feeding selectivity of 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. clarki clarki* is regarded as the most important offshore piscivore (Nowak and 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 capture by visually-feeding piscivores. Juvenile sockeye salmon and longfin smelt achieve similar lengths over their lifespan in the lake (Hansen et al. 2013b), and are soft-rayed fishes which are generally captured with greater success than spiny-rayed fishes of a similar size (Savitz and Bardygula-Nonn 1997; Scharf et al. 1998). Threespine stickleback do not grow as large, but have spines and armor plating that may reduce their risk of predation (Scharf et al. 1998; Reimchen 2000; Kitano et al. 2008). Additionally, longfin smelt are semelparous, have a 2-year lifespan, and exhibit cyclic variations in abundance where recruitment during even years (strong year classes) is typically 5-15 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 fall (Chigbu and Sibley 1998), but individuals are highly transparent at this time, which could limit their detection by visual predators (Hansen et al. 2013c). Examining how different environmental, ecological, morphological, and life-history related factors affect the nature of diet selection (random or non-random) of top predators should offer important insight into the dynamic role predators play in regulating different prey groups in aquatic ecosystems.

The overall objectives of this study were to determine whether the diet selection of piscivores is sensitive to: (1) fluctuations in the abundance of key prey, (2) the total abundance of each prey species in the study region versus the density of prey that overlap in time and space with predators, (3) factors related to the visual detection and encounter with prey, and (4)

behavioral and other morphological factors related to the vulnerability of prey to capture after an encounter. We evaluated the offshore diet selection of piscivorous cutthroat trout in Lake Washington during the fall of an odd year (2005), when the abundance of age-0 longfin smelt was low, and an even year (2006), when abundance of age-0 longfin smelt was high from a strong year class. The abundance of different prey was represented one of two ways: (1) by the total abundance estimated for the study region of the lake where cutthroat trout were collected, and (2) by the total abundance estimated for just the depth intervals occupied by cutthroat trout. Prey abundances were then sequentially adjusted for potential differences in visual detection and capture by piscivores, and diet selection was reevaluated. With this approach, we were able to evaluate changes in diet selection across a range of “prey availability” that progressively scaled down to the perceptual field of the predator. We hypothesized that (1) cutthroat trout would exhibit non-random (targeted) patterns in diet selection when only considering prey abundance, as represented by a total abundance within the study region of Lake Washington, or by an abundance within the depth intervals occupied by cutthroat trout; (2) factors related to the visual detection and capture of different prey groups will help explain the diets of cutthroat trout for both years, and therefore, patterns in diet selection would shift from non-random to random (opportunistic) after adjusting prey abundance for these constraints; (3) the switch from non-random selection to random feeding would only emerge when considering prey abundance within the key depths occupied by cutthroat trout, as this should better account for predator-prey overlap in time and space; and (4) differences in the visual detectability of prey will have a stronger effect on the feeding selectivity of piscivores than morphological constraints on prey capture since visual detection is a key process that determines the pool of prey that are first encountered by predators.

Methods

Study system

Lake Washington is a large (32.2 km long by 2.5 km wide on average), glacially formed lake adjacent to Seattle in western Washington (Figure 5.1). Maximum depth of the lake is 66 m. Thermal stratification begins in May and persists through October. Epilimnetic temperatures approach 12°C during spring, 23°C during summer, and 16°C during fall. Dissolved oxygen concentrations typically remain above 5 mg/L throughout the water column year round (Beauchamp et al. 2004). The primary crustacean zooplankton are *Daphnia pulicaria*, *Cyclops bicuspidatus*, *Leptodiaptomus ashlandi*, and *Epischura nevadensis*. *Daphnia* predominate and achieve moderate to high densities (averaging 2-15 organisms/L) from mid-May through November, but are below detection limits during the winter and early spring. Copepod densities during winter and early spring vary among years (4-30 organisms/L) (Edmondson and Litt 1982; Beauchamp et al. 2004; Quinn et al. 2012).

The abundance of different size- or age-classes of planktivores in Lake Washington changes seasonally. Sockeye salmon enter the lake as 25-mm fry during the spring (February-May), rear offshore, then migrate to the ocean primarily during May of the following year. Longfin smelt mature after two years and spawn in tributaries between January and March, then die (Chigbu 2000). Threespine stickleback have a one year lifespan in the lake, spawn in nearshore habitats during late spring and die within days to several months later (Eggers et al. 1978). New cohorts of threespine stickleback are available offshore during summer and fall. During winter and spring when age-2 longfin smelt spawn in tributaries, a large and variable fraction of the age-1 cohort associate with surface, bottom, or slope zone habitats nearshore, but the population is mostly pelagic during summer and fall (Beauchamp 1987; Chigbu et al. 1998;

Overman et al. 2006). Longfin smelt exhibit strong density-dependent growth. Individuals from weak year classes are larger than those from strong year classes (Overman et al. 2006; Hansen et al. 2013b). During the fall, age-0 longfin smelt, age-1 longfin smelt, age-0 sockeye salmon parr, and age-0 threespine stickleback are present offshore (Quinn et al. 2012).

Abundance of prey

During 2001-2006 and 2012-2013, paired midwater trawl and hydroacoustics surveys were conducted at night in Lake Washington every spring (late March) and fall (late October). The purpose of these surveys was to monitor the distribution, abundance, growth, and survival of juvenile sockeye salmon, as well as their potential competitors (i.e., longfin smelt and threespine stickleback), during their first growing season and over-winter period in the lake (Hansen et al. 2013b). The benthic orientation of age-1 longfin smelt during spring make them difficult to detect with hydroacoustics and trawls. Consequently, their abundance is typically severely underestimated this time of year, but reliable estimates are obtained during the fall (Beauchamp 1987; Quinn et al. 2012). We used information from surveys conducted in fall (October 19-22, 2005 and October 16-20, 2006) (Overman and Beauchamp 2006; Overman et al. 2006) to obtain regional and depth-specific estimates of total abundance for each species and age-class of planktivore.

Each spring and fall survey was stratified by depth and region of the lake. Midwater trawls were conducted through 3-5 discrete depth intervals in 5 predetermined regions of the main lake basin. Parallel hydroacoustics transects ($N = 3-4$) were completed in each area prior to trawling (Figure 5.1). During fall 2005 and 2006, hydroacoustics surveys utilized a side-looking transducer in addition to a down-looking transducer so that single targets and schools of fish in close proximity to the surface could be detected (Yule 2000; Beauchamp et al. 2009). In these

years, size- and depth-specific fish densities were estimated using echo-counting procedures for single targets, supplemented with echo-integration for schooling fish (Simmonds and MacLennan 2005). Size- and depth-specific densities were partitioned into different species and age-classes based on the sizes and proportions of each prey group captured in midwater trawls (Love 1977; Overman and Beauchamp 2006; Overman et al. 2006). Densities were expanded to an abundance using region- and depth-specific (0-10, 11-20, 21-30, 31-40, and 41+ m) water volume estimates developed for Lake Washington (Dawson 1972).

Cutthroat trout diet

Cutthroat trout in Lake Washington move offshore once reaching approximately 250 mm fork length (Nowak et al. 2004). Individuals greater than 250 mm also comprise the most piscivorous fraction of the population. The percentage of fish in the diet by weight 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, cutthroat trout were captured offshore with a purse seine primarily in area 2 of Lake Washington (Figure 5.1) on 9-10 November 2005 ($N = 7$ sets; 2 sets were in area 3) and 8-9 November 2006 ($N = 10$ sets; 3 sets were in area 3). The purse seine fished down to 25 m and was deployed from the 17.7 m *FV Chasina* during dusk and night from 1625-0025 hours during both years. Fish found in stomach samples from cutthroat trout greater than 250 mm ($N = 19$ in 2005 and 27 in 2006) were counted and identified to species. Longfin smelt were assigned to an age-class by comparing standard lengths or lengths of intact vertebral columns measured in the diets and converted to fork lengths to mean fork lengths (mm) estimated from catches in midwater trawls. In 2005 and 2006, the lake was thermally stratified during October and early November. In 2005, epilimnetic temperatures averaged 15.3°C in October when the pelagic fish

assessments were conducted and 13.6°C in November when diets were collected. Corresponding values for 2006 were 16.0°C in October and 12.8 °C in November (D. A. Beauchamp, *unpublished data*). Given the similarity in thermocline depths and these temperatures, we did not expect the prey community to redistribute markedly between the periods when prey abundances were estimated and when cutthroat trout diets were collected.

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 within different diel periods during the fall (Nowak and Quinn 2002). The nocturnal distribution was most important, since this was when the majority of cutthroat trout were captured with fish in their stomachs ($N = 17$ or 89% in 2005 and $N = 25$ or 93% in 2006) and when prey abundances were estimated. This evaluation identified the most appropriate depth interval(s) for adjusting the regional prey abundances to densities that would better account for predator-prey overlap in time and space. Raw telemetry detections were assigned to a diel period (day, dusk, night, or dawn) based on the start and end of twilight in relation to sunrise and sunset on the specific dates during October and November when cutthroat trout were tracked (Nowak and Quinn 2002). Cutthroat trout occupied depths above and below the thermocline during day and night, but were mostly in the upper 5 m of the water column during dusk and dawn (Figure 5.2). Because (1) cutthroat trout occupied depths down to 25 m during the night, (2) could be effectively captured by the purse seine at those depths, and (3) the nocturnal light environment in Lake Washington allows for sufficient encounters with prey down to 20 m during fall (Mazur and Beauchamp 2006), we used abundances within 0-20 m for evaluating diet selection. We pooled estimates from areas 2 and 3, because nearly equal numbers of piscivorous cutthroat trout were captured in each location, despite fewer purse seine

sets in area 3 in 2005 and 2006. Lastly, gut fullness and percent frequency of fish in the diets of cutthroat trout were higher at night than at dusk for fall 2005 and 2006 (Figure 5.2), suggesting that the predators increased feeding activity during this period. Therefore, nocturnal abundances should provide an adequate representation of prey availability (Mazur and Beauchamp 2006).

Constraints on prey detection and capture

Prey abundance was adjusted for constraints on visual detection and capture by piscivores to test whether other components of the predation sequence explain patterns in apparent diet selection. Although certain sizes of prey influence visual detection by cutthroat trout, the mean fork length (FL) of each prey group in this study (see below) fell outside this range (Vogel and Beauchamp 1999; Hansen et al. 2013c). Comparable work evaluating prey of different transparencies is lacking. To adjust for the potential influence of transparency in age-0 longfin smelt on visual encounter, we generated standard measures of “relative contrast” for each prey group using digital photography (Stevens et al. 2007).

To adjust for possible differences in capture success by cutthroat trout due to prey morphology, we applied capture success rates of piscivorous bluefish *Pomatomus saltatrix* feeding on different sizes of Atlantic silverside *Menidia menidia* and striped bass *Morone saxatilis* (Scharf et al. 1998). Capture rates of soft-rayed Atlantic silverside were used for longfin smelt and sockeye salmon. Capture rates of spiny-rayed striped bass were used for threespine stickleback. These experiments accounted for the key morphological factors (body size, soft rays, and spines) simultaneously. The capture success rates of bluefish corresponded well with those from similar sized walleye *Sander vitreus* feeding on spiny-rayed versus soft-rayed fishes (Einfalt and Wahl 1997). Equivalent work using salmonid predators was limited (Savitz and Bardygula-Nonn 1997; Reimchen 2000). These processes were integrated into a

visual foraging model to adjust prey abundance. Visual foraging models link variability in feeding rate to changes in environmental conditions and prey density, based on the visual prey detection and behavioral responses of fishes in pelagic habitats (Beauchamp et al. 1999). We modified the general form of these models (Beauchamp et al. 1999) by substituting the parameter related to visual prey detection with our measures of relative contrast (R), and then applying the capture rates of the different prey groups (c):

$$\text{Adjusted availability} = \pi R^2 \cdot SS \cdot T \cdot PD \cdot c \quad (5.1),$$

where SS is the swimming speed (m/s), T is time spent foraging (s), and PD is prey density (fish per m³). Values for the constants SS and T had no bearing on the results of this study given the relative nature of this analysis, but are important parameters in other studies utilizing this approach (Beauchamp et al. 1999; Hansen et al. 2013a).

Samples of fish captured in midwater trawls during fall 2012 (Hansen et al. 2012b) were used for generating the relative measures of contrast. Raw, digital images of age-0 longfin smelt ($N = 15$; mean FL = 41 mm), age-1 longfin smelt ($N = 10$; 120 mm), sockeye salmon parr ($N = 14$; 94 mm) and threespine stickleback ($N = 10$; 51 mm) were taken with a Canon EOS Rebel XS camera (ISO = 400; F-stop = 7.1) immediately after capture. Fish were placed on a standard 18% gray card under indirect fluorescent lighting. Using the gray card as a reference (Stevens et al. 2007), image exposure was standardized in Adobe Photoshop CS5.1. Images were then converted to 8-bit gray scale (TIFF). Using ImageJ 1.45s, we compared the gray values (range: 0-255) of pixels sampled from the fish body to the mean gray value of the background (Figure 5.3A), and a total difference between the two was calculated. Differences were averaged for each prey group and normalized to the maximum. Whether differences in relative contrast observed using this method would reflect those perceived by cutthroat trout is uncertain.

However, transparency has been repeatedly flagged as a potentially important factor affecting visual detection by piscivores (Denton 1970; Muntz 1990; Hansen et al. 2013c). Given the absence of experimental data, this analysis was meant only as a preliminary evaluation.

Diet selection and random versus non-random feeding

Numerous indices exist for evaluating diet selection (Lechowicz 1982). We used the Jacobs index as it minimizes some of the problems (e.g., non-linearity and lack of symmetry) that have been identified with other metrics (Jacobs 1974):

$$D = \frac{r-p}{r+p-2rp} \quad (5.2),$$

where r is the numerical proportion of a prey group found in the diet and p is the numerical proportion of that prey group available in the environment. The index is centered on zero (neutral selection), and ranges from -1.0 (perfect selection against) to 1.0 (perfect selection for). To compute r , we pooled counts of each prey group across diets of cutthroat trout. Numerical diet proportions computed in this way described the diet of a population of piscivores better than other individually-weighted methods in model simulations. These simulations assumed that the predators were feeding and evacuating digested prey continuously (Ahlbeck et al. 2012). While the Jacobs index can indicate which prey might be selected for or against, using it for statistical inference regarding the randomness of feeding is cumbersome. For this, we relied on the χ^2 test for goodness of fit ($\alpha = 0.05$) by comparing the total number of each prey group found in the diets of cutthroat trout to the expected number based on the different prey availabilities as defined by each of our hypotheses (Lechowicz 1982).

Model robustness

Given potential uncertainty in our measures of relative contrast and the estimates of piscivore capture success for the different prey groups used in the visual foraging model, we

tested whether changes in these parameters could alter the outcome of random versus non-random feeding after adjusting prey abundance for both of these constraints. Individual parameter values for each prey group, in each year, and under each abundance scenario (total versus depth-specific) were increased (to a maximum of 1.0) and decreased by 20% (Jensen et al. 2006), and the model was rerun with the new parameter value. The χ^2 test for goodness of fit was then repeated to determine whether resulting patterns in the feeding selectivity of cutthroat trout still reflected random or non-random feeding.

Results

Visual detection and capture of prey

Relative contrast and vulnerability to capture differed among the size- and age-classes of planktivores. For relative contrast, age-1 longfin smelt (mean normalized relative contrast = 0.93; 2 *SE* = 0.03), sockeye salmon parr (0.76; 0.06), and threespine stickleback (0.88; 0.03) contrasted significantly more (by factors of 2.6-3.2) from the standard gray 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 from each other (Tukey test, $P = 0.50$). Additionally, relative contrast for age-0 longfin smelt increased significantly with FL ($r^2 = 0.74$, $N = 15$, $P < 0.001$):

$$\text{Normalized relative contrast} = 0.0055(\text{FL}) + 0.0624 \quad (5.3).$$

A similar length-dependent relationship with contrast was not observed for the other prey groups over the range of FL's examined (all $P > 0.06$) (Figure 5.3B).

The mean FL of piscivorous cutthroat trout captured in purse seines was 347 mm (2 *SE* = 29) in 2005 and 365 mm (28) in 2006. The mean FL of prey fishes captured in midwater trawls in 2005 was 55 mm (15.7) for age-0 longfin smelt, 101 mm (0.7) for age-1 longfin smelt, 110

mm (1.7) for sockeye salmon parr, and 64 mm (1.1) for threespine stickleback (Overman et al. 2006). Corresponding values for 2006 were 45 mm (0.5) for age-0 longfin smelt, 123 mm (2.7) for age-1 longfin smelt, 107 mm (7.5) for sockeye salmon parr, and 60 mm (0.7) for threespine stickleback (Overman and Beauchamp 2006). Based on the ratio of prey length to predator length between the planktivores and cutthroat trout, capture success rates estimated using the predictive equations from Scharf et al. (1998) for the different prey groups varied, but were all high (77-100%), given the large size of cutthroat trout in both years. Given the relatively small size of the spiny-rayed threespine stickleback, capture success rates estimated for this group were comparable to the larger, soft-rayed prey groups (Table 5.1).

Diet selection and random versus non-random feeding

The total number and age/species composition of prey fish found in the diets of cutthroat trout differed between years ($N = 50$ for 2005 and 154 for 2006). Most fish in 2005 were age-1 longfin smelt ($N = 35$; 70%), but age-0 longfin smelt ($N = 104$; 68%) in 2006. Sockeye salmon parr were nearly absent in 2005 ($N = 1$; 2%) and 2006 ($N = 2$; 1.3%). Conversely, threespine stickleback represented intermediate fractions of the diet in 2005 ($N = 11$; 22%) and 2006 ($N = 38$; 25%). Based on these observations, cutthroat trout exhibited contrasting patterns in diet selection and randomness of feeding between 2005, when age-0 longfin smelt from a weak year class represented 21-24% of the available prey, and 2006, when age-0 longfin smelt from a strong year class represented 71-72% of the available prey (Figure 5.4 and 5.5).

Patterns of diet selection within each year did not depend on how prey abundance was measured (total abundance versus depth-specific abundance), but were sensitive to the constraints imposed on visual detection and capture by piscivores (Figure 5.4 and 5.5). For cutthroat trout sampled in fall 2005, the Jacobs index indicated strong negative selection against

age-0 longfin smelt (-0.62 for regional and -0.66 for depth-specific abundances), but positive selection for their age-1 counterparts (0.46 and 0.48). This was before prey abundances were adjusted for visual detection and capture by piscivores (Figure 5.4A, B). At this stage, observed patterns in diet selection reflected non-random feeding ($\chi^2 = 13.14$ for regional and 15.50 for depth-specific abundances, $df = 3$, $P \leq 0.004$). After imposing constraints on visual detection and capture, the feeding selectivity of cutthroat trout switched from non-random to random ($\chi^2 = 3.45$ and $P = 0.327$ for both abundances). Similarly, the Jacobs index shifted toward neutral selection, and all values were between -0.3 and 0.35 (Figure 5.4C, D). Taken alone, differences in the relative contrast of each prey group drove the shift from non-random to random ($\chi^2 = 2.58$ and $P = 0.46$ for both abundances). Differences in the capture success rate of each prey group alone could not produce a similar shift to random feeding ($\chi^2 = 13.65-14.26$, $P \leq 0.003$). In general, differential capture success among prey groups had a minor influence on the feeding selectivity of cutthroat trout after applying the constraints on visual prey detection.

The opposite patterns in diet selection and randomness of feeding were observed in 2006 when the abundance of age-0 longfin smelt was 6-7 fold higher. Prior to adjusting prey abundances for constraints on visual detection and capture, the Jacobs index indicated nearly neutral selection for all prey groups (range: -0.11 to 0.11), except sockeye salmon, in which case the index indicated strong positive selection (0.55-0.80) (Figure 5.5A, B). However, like other metrics, the Jacobs index can be 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 could be misleading. Overall patterns in diet selection reflected random feeding by cutthroat trout when using both regional and depth-specific abundances ($\chi^2 = 2.31-2.69$, $P = 0.43-0.51$), despite the apparent selection for sockeye salmon. After applying constraints on

visual detection and capture, the feeding selectivity of cutthroat trout switched from random to highly non-random ($\chi^2 = 154.66-207.65$, $P \ll 0.001$). Resulting feeding patterns based on the Jacobs index indicated strong selection for age-0 longfin smelt (0.72-0.74) and sockeye salmon (0.29-0.65), but strong selection against age-1 longfin smelt (-0.46 to -0.57) and threespine stickleback (-0.58 to -0.63) (Figure 5.5C, D).

Model robustness

The observed outcome of random feeding by cutthroat trout in fall 2005 and non-random feeding by cutthroat trout in 2006, after adjusting prey abundance (both the total and depth-specific abundances) for constraints on visual detection and capture, was robust to the amount of uncertainty ($\pm 20\%$) we examined for the relative measures of contrast and piscivore capture success used in the visual foraging model. This amount of error paralleled or exceeded that observed in our measures of relative contrast and the estimates of piscivore capture success generated from the predictive equations of Scharf et al. (1997). For parameters re-examined in fall 2005, corresponding χ^2 statistics (0.58-7.17) and associated p-values (0.07-0.90) all reflected random feeding. In this year, 20% reductions in the relative contrast and capture success rate of threespine stickleback, but a 20% increase in the capture success rate of age-1 longfin smelt, greatly improved the description of the diet ($\chi^2 = 0.58-1.26$ and $P = 0.74-0.90$). Conversely, 20% reductions in the relative contrast of age-0 and age-1 longfin smelt worsened the description of the diet ($\chi^2 = 5.84-7.17$ and $P = 0.07-0.12$), but these perturbations were not enough to change the outcome to non-random feeding. For parameters re-examined in fall 2006, corresponding χ^2 statistics (92.89-284.7) and associated p-values (all $P \ll 0.001$) all reflected non-random feeding. In this year, a 20% reduction in the relative contrast of age-0 longfin smelt worsened the description of the diet ($\chi^2 = 268.88-284.7$), whereas a 20% increase in the relative contrast of

age-0 longfin improved the description of the diet ($\chi^2 = 92.89-97.66$).

Discussion

Different perceptions of prey availability can alter the interpretation of whether predators feed opportunistically or actively select certain prey. In this study, fluctuations in prey abundance interacted with differences in the visual detection and capture of prey to produce contrasting patterns in the nature of the feeding selectivity of piscivorous cutthroat trout. Whether cutthroat trout fed randomly or non-randomly before or after accounting for constraints on visual detection and capture hinged on the presence of a weak versus a strong year-class of the highly transparent age-0 longfin smelt. These outcomes were not sensitive to how prey abundance (regional versus depth-specific) was measured. The outcome of random versus non-random feeding was also robust to uncertainty in the measures of relative contrast and piscivore capture success. Prior to adjusting prey abundances for detection and capture, results suggested that cutthroat trout were feeding non-randomly in 2005, when the density of age-0 longfin smelt was low, but randomly in 2006, when their density was much higher. These patterns were reversed after accounting for differences in visual detection and capture. In 2005, poor detection and a reduced encounter rate relative to the other larger, more conspicuous planktivores could explain the rarity of age-0 longfin smelt in the diet of cutthroat trout. Conversely, poor visual detection of age-0 longfin smelt was of minor importance in 2006, given their high relative abundance. Results from 2006 ultimately suggested that cutthroat trout were targeting age-0 longfin smelt. Therefore, in systems containing diverse prey communities, the nature of the feeding selectivity of a predator can be a dynamic function of the interplay between fluctuations in prey abundance and the susceptibility of different prey to visual detection and capture.

In this study, we sequentially adjusted measures of total prey abundance (i.e., total prey

availability) for predator-prey overlap in time and space (i.e., spatial-temporal availability), the visual detectability of different prey groups (i.e., availability due to visible encounters), and for the vulnerability of different prey groups 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 primary hypothesis that the diet selection of cutthroat trout would reflect non-random feeding when representing prey availability by a regional or depth-specific abundance, but random feeding after adjusting the depth-specific abundances in particular for constraints on visual detection and capture was supported in 2005. Even though the opposite outcomes were observed in 2006 when the abundance of age-0 longfin smelt was 6-7 fold higher, accounting for processes throughout the predation sequence (search-encounter-capture) produced a shift from random to non-random feeding. Adjusting prey abundance for the relative contrast of different prey during the visual encounter phase of the predation sequence drove these shifts. Prey vulnerability during the successive capture phase of the predation sequence had very little influence on diet selection given the large size of the cutthroat trout. 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 community in Lake Washington suggests that pelagic piscivores are flexible predators. They can adapt their feeding behavior to take advantage of large influxes of highly catchable prey (i.e., develop a search image), as might be anticipated from optimal foraging theory (Steven and Krebs 1986; Sih and Christensen 2001; Jensen et al. 2008).

Whether predators feed randomly or non-randomly has important consequences for the relative degree of predation risk experienced by different prey groups. If predators feed randomly, we would expect them to pursue and attack different prey groups equally, or in

accordance with the rate at which each are encountered. In this situation, the diets of predators and the amount of direct predation mortality on different prey should reflect the extent and timing of predator-prey overlap (Mazur and Beauchamp 2006; Hansen et al. 2013a), differences in visual detectability, and innate predator-prey behavior or other morphological constraints on capture and ingestion once a predator encounters prey (Christensen 1996). If predators feed non-randomly, targeted groups should represent a disproportionate amount of the diet or total direct predation mortality after accounting for predator-prey overlap in time and space and other constraints on prey detection and capture. As observed in this study and others (Hyvarinen and Huusko 2006; Jensen et al. 2008), the process that governs the feeding selectivity of predators is largely dependent on fluctuations in the density and suitability of different prey. Some predators may continue selecting for certain prey types, despite continued reductions in their abundance. 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. However, selection for alewife by Chinook salmon has remained relatively inflexible to the ecological changes in the lake over the past 3 decades (Bunnell et al. 2006), which suggests that these predators are targeting alewife. Therefore, Chinook salmon are expected to severely depress alewife populations 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 very different consequences for the dynamics of different prey populations.

Apparent, strong selective feeding on a particular prey group could be driven by the

temporal-spatial structure of predator-prey interactions. If prey are highly aggregated, and predators can exploit these aggregations, then prey abundance could be depressed to low levels before a switch to alternative prey is needed to maintain growth. Consumption rates estimated for lake trout in Lake Superior, Michigan, and Ontario did not respond to 3-5 fold increases in prey density within the lakes, and were similar across a 100-fold difference in prey density among the lakes (Eby et al. 1995). These results demonstrated that piscivores can maintain adequate predation 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 dense patches of alewife form when at low total abundance, and if Chinook salmon are able to consistently find 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. Although most fishes are dispersed at night, light pollution can cause longfin smelt (particularly strong year-classes of age-0 fish) and threespine stickleback to form dense aggregations or schools near the surface where cutthroat trout actively feed (Mazur and Beauchamp 2006; Overman and Beauchamp 2006; Overman et al. 2006). Presumably, a dense school of prey is easier for visually-feeding piscivores to detect than an individual prey if a predator is lucky enough to run into one (Dunlop et al. 2010; Hansen et al. 2013c), even if the fish that are forming the school are highly transparent. The suggestion that cutthroat trout fed non-randomly by targeting the strong year-class of age-0 longfin smelt in 2006 could be misleading if cutthroat trout were able to readily detect and exploit schools or dense aggregations of age-0 longfin smelt near the surface. However, few prey 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 and Beauchamp 2006). Therefore, limited visual detection of individual age-0 longfin smelt, as represented by our measures of relative contrast, was likely an important factor influencing the diet selection of 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). Yet, the feeding selectivity of cutthroat trout was only evaluated during the fall when data on cutthroat trout diet, predator-prey distribution, and prey abundance were sufficiently comparable. The apparent feeding selectivity of a predator could change if seasonal 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 fall when the lake is still thermally stratified (Quinn et al. 2012). The spring is a highly dynamic period. Sockeye salmon fry (25-50 mm) are entering the lake and are present at high densities offshore at night. Contrary to fall, age-1 sockeye salmon are present at much higher densities near the surface at night during spring, where they are more accessible to cutthroat trout, whereas age-1 longfin smelt are oriented toward benthic habitats (Nowak and Quinn 2002; Overman et al. 2006; Quinn et al. 2010). Information on the distribution of pelagic prey fishes during peak thermal stratification in summer is sparse for Lake Washington (Beauchamp et al. 1992; Chigbu et al. 1998). Limited midwater trawling data suggest that threespine stickleback are the only planktivore that can tolerate the warm epilimnion, whereas piscivorous cutthroat trout (Nowak and Quinn 2002) and the other planktivores remain below the thermocline at all times of day (A. G. Hansen and D. A. Beauchamp, *unpublished data*). Results from this study show that the nature of the feeding

selectivity of a top pelagic piscivore can change with annual fluctuations in the abundance of key prey within a given season. There is a need to extend these types of analyses over a broader range environmental conditions and predator-prey communities.

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 predators play in regulating different prey groups in diverse aquatic communities. Such analyses can be particularly helpful if trying to identify when, where, and under what conditions species of conservation or management concern might be targeted 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 conditions that could trigger a shift to non-random feeding on the prey group of interest.

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Tables

Table 5.1. Mean length of piscivorous cutthroat trout and different planktivore groups captured offshore in purse seines and midwater trawls in Lake Washington during fall 2005 and 2006. The ratio between prey length and predator length, and associated values of piscivore capture success generated from the predictive equations of Scharf et al. (1997) are also shown.

Season and year	Predator-prey group	Fork length		Prey:predator size ratio	Piscivore capture success
		Mean (mm)	2 SE		
Fall 2005					
	Piscivorous cutthroat trout	347	29.0	-	-
	Age-0 longfin smelt	55	15.7	0.16	1.00
	Age-1 longfin smelt	101	0.7	0.29	0.83
	Threespine stickleback	64	1.1	0.18	0.81
	Sockeye salmon	110	1.7	0.32	0.79
Fall 2006					
	Piscivorous cutthroat trout	365	28.0	-	-
	Age-0 longfin smelt	45	0.5	0.12	1.00
	Age-1 longfin smelt	123	2.7	0.34	0.77
	Threespine stickleback	60	0.7	0.16	0.85
	Sockeye salmon	107	7.5	0.29	0.83

Figures

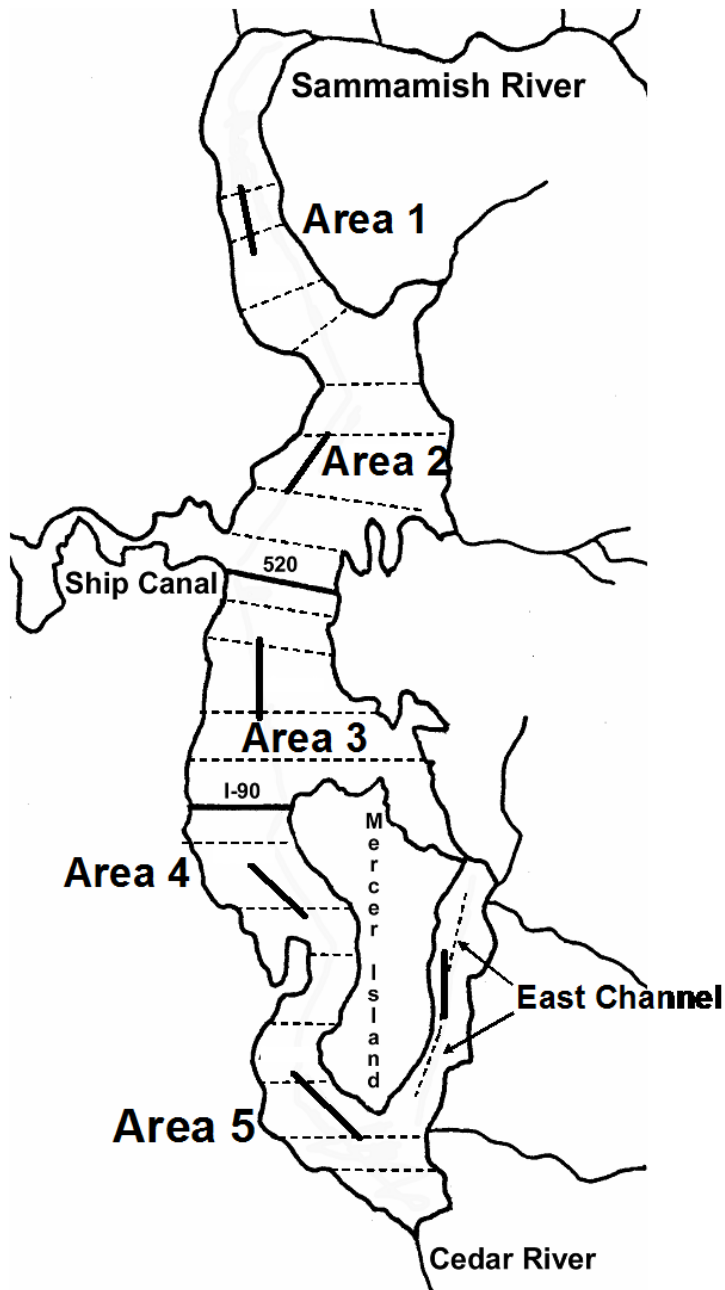


Figure 5.1. Map of Lake Washington showing the different stratified sampling regions (areas 1-5 and the East Channel), hydroacoustic transects (dashed lines), midwater trawling tracks (solid lines), and bridges (I-90 and 520).

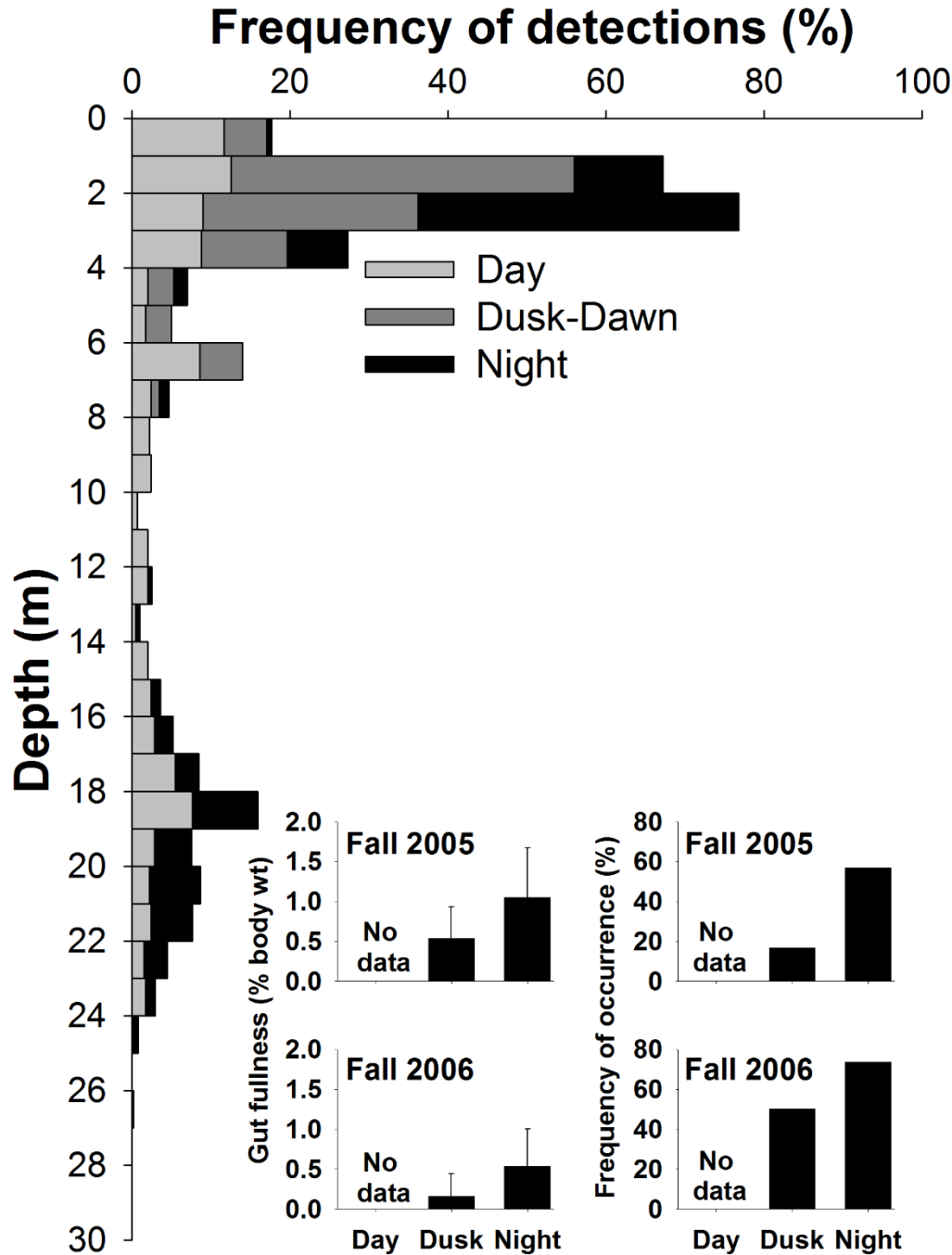


Figure 5.2. Fall (October and November) diel-depth distribution of piscivorous cutthroat trout in Lake Washington based on the frequency of ultrasonic telemetry detections at different depths and times of day. Data were modified from Nowak and Quinn (2002). The inset panels show the mean gut fullness and frequency of occurrence of fish in the diets of cutthroat trout captured offshore in the purse seine during fall 2005 and 2006. Error bars represent 2 SE's.

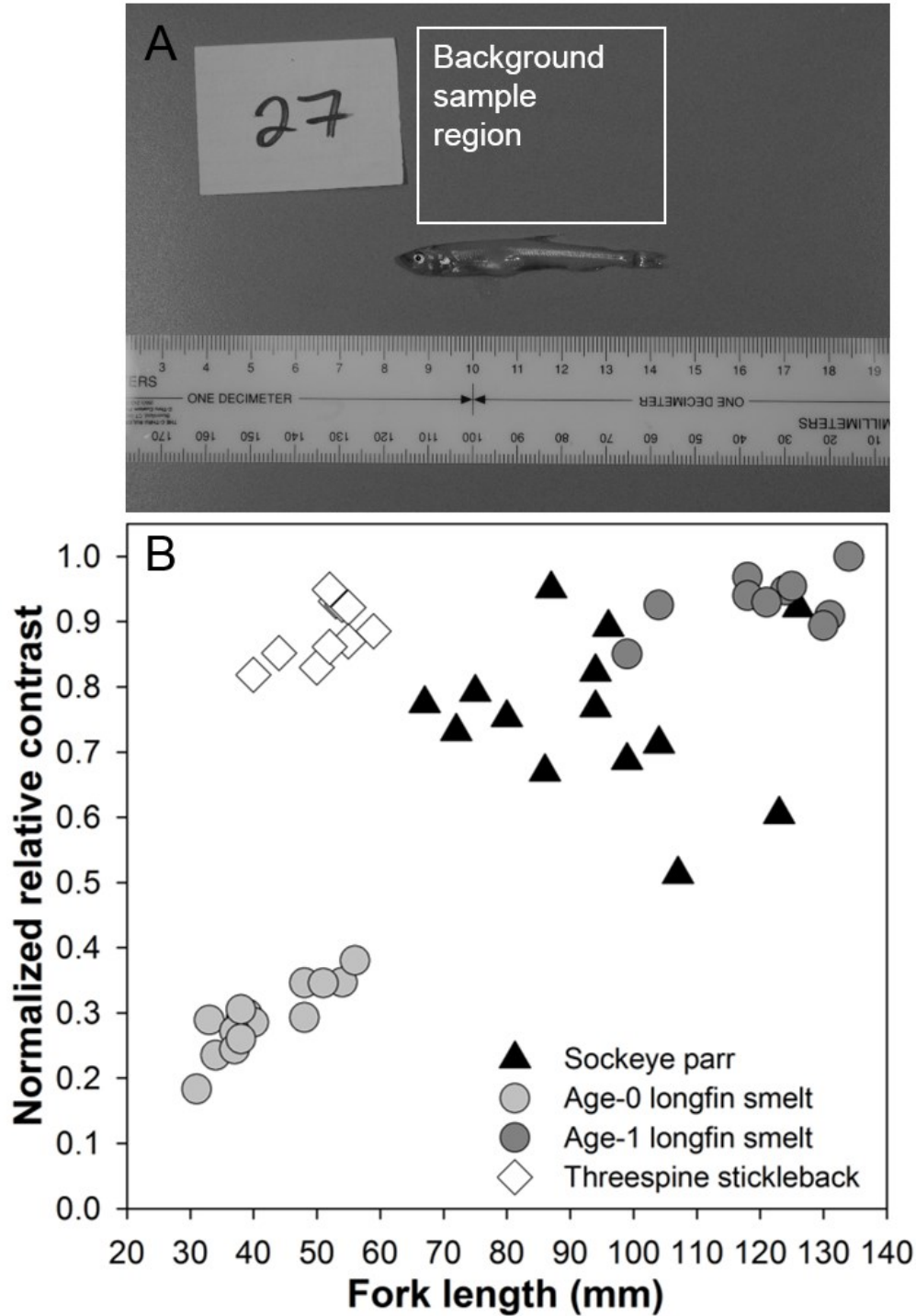


Figure 5.3. (A) Representative digital photograph taken of individuals from each age-class of planktivore present offshore in Lake Washington during October 2012. The white box shows where pixels were sampled to estimate the mean gray value of the background. (B) Normalized values of relative contrast generated for individuals from each age-class of planktivore. Individual observations instead of means are presented to show the relationship with fork length.

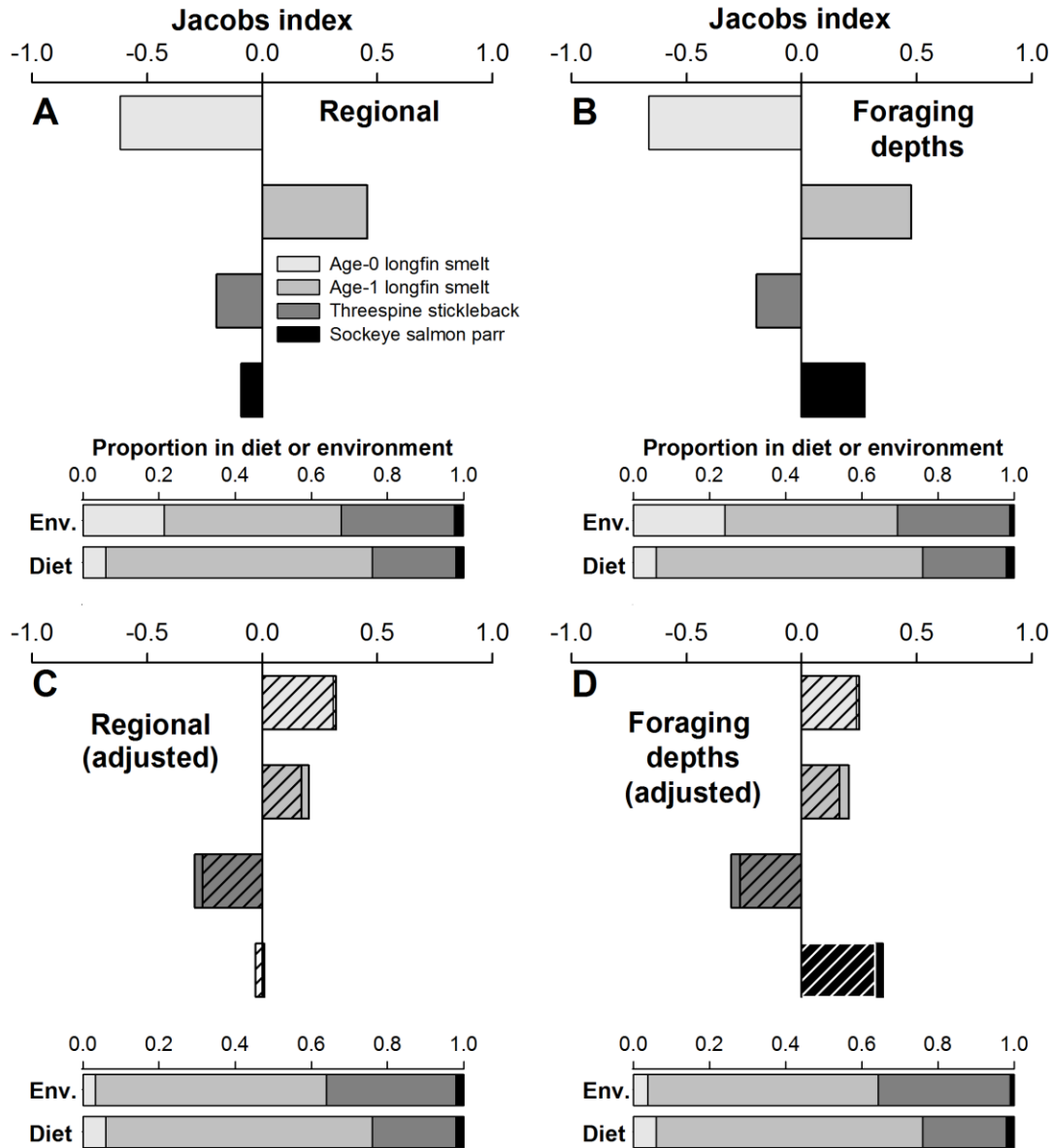


Figure 5.4. Diet selection indices (shaded bars) calculated for cutthroat trout feeding on the dominant planktivores in Lake Washington during fall 2005 using: (A) regional prey abundances summed over all depths, (B) prey abundances only within the key depths occupied by cutthroat trout, and (C and D) the same regional and depth-specific abundances, but adjusted for constraints on detection and capture by piscivores. For comparison, the hatched bars overlaid on the shaded bars in panels C and D denote diet selection indices calculated after applying constraints on visual prey detection only. The hatched bars are meant to show the minimal effect of prey morphology on piscivore capture success and resulting patterns in feeding selectivity. The corresponding stacked horizontal bars show the proportion of each prey group available in the environment versus what appeared in the diet.

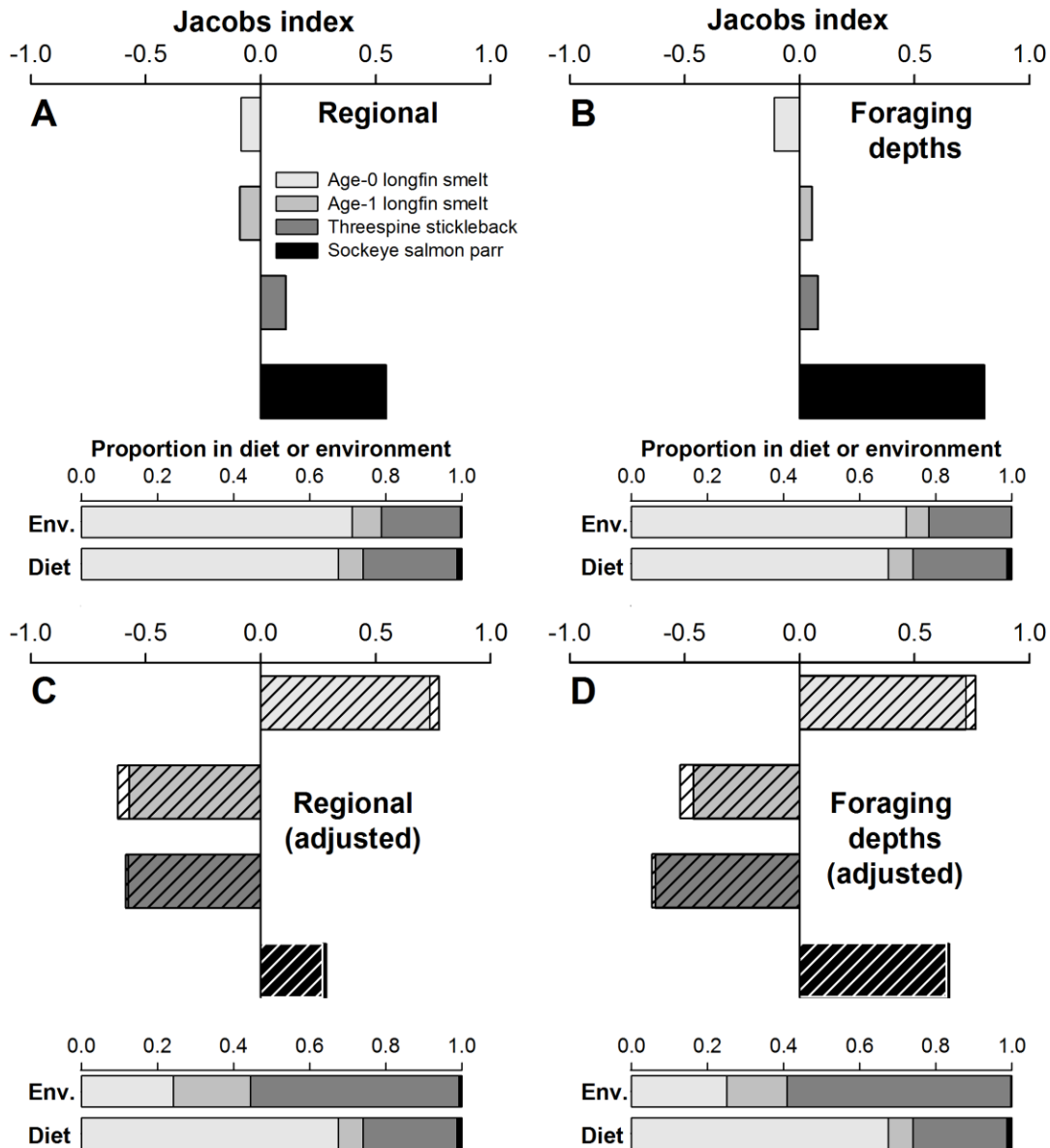


Figure 5.5. Diet selection indices (shaded bars) calculated for cutthroat trout feeding on the dominant planktivores in Lake Washington during fall 2006 using: (A) regional prey abundances summed over all depths, (B) prey abundances only within the key depths occupied by cutthroat trout, and (C and D) the same regional and depth-specific abundances, but adjusted for constraints on detection and capture by piscivores. For comparison, the hatched bars overlaid on the shaded bars in panels C and D denote diet selection indices calculated after applying constraints on visual prey detection only. The hatched bars are meant to show the minimal effect of prey morphology on piscivore capture success and resulting patterns in feeding selectivity. The corresponding stacked horizontal bars show the proportion of each prey group available in the environment versus what appeared in the diet.

Conclusions

By observing through the eyes of pelagic predators and prey, my results show that the foraging-risk environment for planktivores and piscivores can look very different as physical habitat changes over many different dimensions of time and space. Everywhere from broad-scale latitudinal shifts in the diel light environment to seasonal shifts in the thermal environment. Layered on top of this habitat complexity are species and life-stage specific differences in perception, physiological tolerance, behavior, visual prey detection and capture, morphology, and life-history that add variation to pelagic predator-prey interactions. As environmental or ecological conditions in pelagic ecosystems changes in response to future anthropogenic land use, shifts in climate, or the unanticipated introduction on nonnative species, the resulting responses and redistribution of different predators and prey will affect the foraging success of piscivores and predation risk for planktivores in complex ways the will require a mechanistic understanding of key factors and responses. The following sections summarize the primary conclusions from each chapter and areas in need of continued research.

Chapter 2.—Visual prey detection responses of piscivorous trout and salmon: effects of light, turbidity, and prey size

Results from this chapter showed that the functional form of reaction distance over ecologically relevant levels of light and turbidity are conserved across species and life-stages of piscivores, but the magnitude of the response can change considerably. Therefore, to adequately predict the strength of predation-effects in pelagic communities, species and life-stage specific responses must be considered. Given the high potential for the illegal introduction of nonnative piscivores into different systems, additional studies evaluating the light- and turbidity-dependent visual prey detection responses of key cool- and warm-water piscivores are greatly needed. Armed with this type of information for key species, we will be better equipped for evaluating the ecological impacts of current or looming illegal introductions of nonnative piscivores, or alternatively, the potential success and food web implications of native species reintroductions.

Chapter 3.—Latitudinal and photic effects on diel foraging and predation risk in pelagic ecosystems

Results from this chapter showed that the foraging-risk environment for pelagic

planktivores and piscivores, based on different dimensions of the antipredation window, changes in systematic ways with changes in diel patterns in illuminance across a broad latitudinal gradient and to increases in turbidity. These changes have different implications for the structure of pelagic predator-prey interactions and the behavioral strategy needed to effectively cope with the fundamental tradeoff between feeding and avoiding predators at different latitudes. Given that the effect of latitude was so large, there is a general need to evaluate whether the nature of predator-prey interactions changes along this gradient. Additionally, there is a need to relate the visual foraging capabilities (i.e., prey detection and capture) of different predators and prey to the components of pelagic ecosystems (e.g., algae and dissolved organic carbon) most closely linked to productivity and watershed processes other than those that influence sediments. Armed with this type of information, we will be better equipped for evaluating how or why predator-prey interactions change across different classes of lakes.

Chapter 4.—Environmental constraints on piscivory: insights from linking ultrasonic telemetry to a visual foraging model for cutthroat trout

This study demonstrated how dynamic environmental conditions can mediate the foraging success of piscivores and predation risk for planktivores. Here, periods of environmental stress (i.e., high temperature and low dissolved oxygen) greatly reduced both the foraging success of piscivores and predation risk for planktivores by creating thermal refugia for prey above the thermocline during peak summer stratification. However, patterns observed in this study may be dependent on the duration and severity of stress. Asymmetries in physiological tolerance observed between the predators and prey that allowed for the creation of temporally dynamic refuge space may be weakened if conditions become too severe. Consequently, adaptively managing for stressful environmental conditions and associated shifts in predator-prey interactions will require well-designed and established monitoring programs.

Chapter 5.—Effects of prey abundance, distribution, pigmentation, and morphology on apparent selection by a pelagic piscivore

This study showed that the nature of the feeding selectivity of pelagic piscivores can be highly dependent on fluctuations in the abundance and susceptibility of key prey to visual detection and capture. Whether a predator feeds randomly (i.e., opportunistically) or non-

randomly (i.e., targets certain prey), after accounting for predator-prey overlap in time and space and constraints on prey detection and capture, has important consequences for the level of predation risk experienced by different prey groups in diverse pelagic planktivore communities. Therefore, flexibility in the feeding selectivity of a predator is an important factor to consider when designing conservation or management strategies aimed at boosting ecologically or economically important species. Lastly, there is a need to evaluate how the feeding patterns of predators change with seasonal shifts in environmental conditions; particularly during peak thermal stratification in summer when conditions are most limiting to predators and prey.