

Context-dependent diel behavior of upstream-migrating anadromous fishes

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Abstract Variability is a hallmark of animal behavior and the degree of variability may fluctuate in response to environmental or biological gradients. For example, diel activity patterns during reproductive migrations often differ from those in non-breeding habitats, reflecting trade-offs among efficient route selection, reproductive phenology, and risk avoidance. In this study, we tested the hypothesis that diel movements of anadromous fishes differ among freshwater migration habitats. We analyzed diel movement data from ~13 000 radio-, PIT-, and acoustic-tagged adult fishes from five Columbia River species: Chinook salmon, *Oncorhynchus tshawytscha*; sockeye salmon, *O. nerka*; steelhead, *O. mykiss*; Pacific lamprey, *Entosphenus tridentatus*; and American shad, *Alosa sapidissima*. All five species were active

during most of the diel cycle in low-gradient, less hydraulically complex reservoir and riverine habitats. Movement shifted to predominantly diurnal (salmonids and American shad) or nocturnal (Pacific lamprey) at hydroelectric dam fishways where hydraulic complexity and predator density were high. Results suggest that context-dependent behaviors are common during fish migrations, and that diel activity patterns vary with the degree of effort or predation risk required for movement.

Keywords Behavioral plasticity · Migration · Orientation · Predation risk · Sensory ecology

Introduction

Behavioral flexibility allows animals to rapidly and adaptively respond to changing conditions and to environmental stimuli that signal resources or risk. Diel behavior, for example, varies widely along a continuum from almost exclusively nocturnal, to crepuscular, to strongly diurnal. Within species, diel rhythms can be quite plastic across life stages and at a variety of temporal scales in response to proximate and ultimate factors (Helfman 1983; Boujard and Leatherland 1992; Reeb 2002). Diel activity varies in response to environmental conditions (e.g., photoperiod, water temperature), physiological status (e.g., starvation, metamorphosis), predators, and life history requirements (e.g., migration, reproduction). Ecological context additionally affects

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daily rhythms, as individuals attempt to minimize mortality risks while maximizing growth and fitness (Metcalfé et al. 1999; Railsback et al. 2005; Aarestrup et al. 2009).

Diel behavior often significantly changes during animal migrations, particularly for species that encounter environmental and ecological conditions that diverge from those in rearing or other life history-specific habitats. Many neotropical birds, for instance, are typically crepuscular or diurnal but undertake long-distance migrations solely at night (Gwinner 1996). Similarly, diadromous fishes moving between freshwater and marine habitats often have very different diel rhythms than those expressed in other life history stages (Smith and Smith 1997; Metcalfé et al. 1998). Diel activity during fish migration is mediated by the sensory cues present in often dynamic environments that can vary along several gradients that affect the biophysical costs of movement and orientation or perceptions of risk. These include hydraulic and visual complexity (e.g., velocity, turbulence, turbidity), biological context (e.g., presence of predators, competitors, or prey), and requirements associated with orientation and navigation cues (e.g., visual environment, olfactory plumes, temperature gradients, or social interactions). These factors can elicit increasingly nocturnal or diurnal behavior depending on perceived risk-reward tradeoffs. Nocturnal migration may reduce predation risk, for instance, but can exact fitness costs if migrants miss favorable migration windows or arrive late at spawning areas (Einum and Fleming 2000; Drent et al. 2003; Dickerson et al. 2005).

Our primary objective was to assess diel migration activity of five anadromous fish species moving upstream through habitats differing in environmental complexity and passage difficulty in the Columbia River basin, USA. The study species were three native salmonids (Chinook salmon, *Oncorhynchus tshawytscha*; sockeye salmon, *O. nerka*; and steelhead, *O. mykiss*), a native lamprey (Pacific lamprey, *Entosphenus tridentatus*), and a non-native clupeid (American shad, *Alosa sapidissima*). Diel activity was assessed at a suite of relatively low gradient riverine sites and at high gradient environments with evolutionarily-novel hydraulic and physical elements created by large hydroelectric dams. The dams and recent aggregations of large predators in some dam tailraces and fishways have been associated with upstream migration delay and elevated mortality risks (Moser et al. 2002; Caudill et al.

2007; Stansell et al. 2010). Our principal hypothesis was that fish movements would be temporally constrained in high velocity and turbulent environments and areas of increased predation risk. We further expected taxon-specific responses that would correspond with differences in sensory ecology among the study species.

Material and methods

Study species

The five study species exhibit a range of migration strategies and phenologies. The three salmonids are obligate migrants with high natal-site fidelity. Semelparous Chinook salmon (spring-summer and fall-run) and sockeye salmon follow relatively strict spawning migration schedules. Summer steelhead can be either semelparous or iteroparous and the timing of their spawning migration is more variable. All three salmonids pass through the Columbia River migration corridor from spring through late fall and spawn in the year of river entry (Chinook and sockeye salmon) or the following spring (steelhead) (Brannon et al. 2004). Our samples included two Chinook salmon life history types: stream-type salmon return as adults from March to July (spring-summer Chinook) and ocean-type salmon return from July to October (fall Chinook). American shad are mid-summer, iteroparous migrants whose natal site fidelity is geographically coarse (Hendricks et al. 2002) compared to salmonids, whereas Pacific lamprey are semelparous, facultative migrants with no apparent natal homing (Goodman et al. 2008). Pacific lamprey migrate in summer and fall, overwinter, and then spawn the following spring. The salmonids and lamprey are lithophilic spawners that build and defend redds in main stem and tributary substrates, while shad are pelagophilic broadcast spawners in main stem reaches (Balon 1975).

Fish tagging and monitoring

Study fishes were primarily collected at Bonneville Dam (Fig. 1) at a trap facility adjacent to the north-shore fishway (salmon, steelhead, shad) or using passive box traps affixed to fishway walls (Pacific lamprey). Less than 5 % of the tagged shad were captured by angling or electro-fishing in the Bonneville Dam tailrace. Details of salmonid and Pacific lamprey capture, anesthetization,

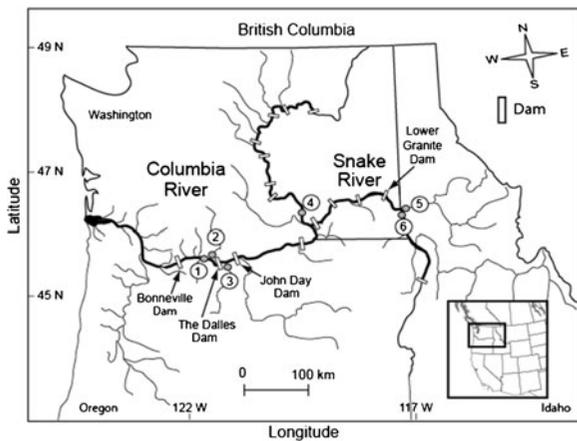


Fig. 1 Map of the Columbia River, U.S.A., basin showing sites where diel activity of tagged adult Chinook salmon, steelhead, sockeye salmon, Pacific lamprey, and American shad was monitored. Upstream migrants were collected at Bonneville Dam and at lower Snake River dams. Activity was monitored at nine dam sites, which included the tailraces, fishways entrances, and fish ladder exits at Bonneville, The Dalles, and John Day dams, and at six riverine and reservoir habitats shown on the map as: (1) Bonneville reservoir; (2) Klickitat River; (3) Deschutes River; (4) Columbia River Hanford Reach; (5) Clearwater River; and (6) Snake River

handling and release protocols, and monitoring systems are in Moser et al. (2002), Naughton et al. (2005), and Keefer et al. (2005, 2009); similar methods were used for American shad. Briefly, radio transmitters were intragastrically inserted into adult salmonids at Bonneville Dam in 1997 (sockeye salmon) and 2000–2003 (Chinook salmon, steelhead), and American shad in 2010. Transmitters used in the salmonid studies were either 3-V (1.4-cm \times 4.3-cm, 11 g in air), 7-V (1.6-cm \times 8.3-cm, 29 g), or data storage tags (2.0-cm \times 9.0 cm, 34 g; Lotek Wireless Inc., Newmarket, Ontario), with the smaller tags used in smaller-bodied sockeye salmon and steelhead. Pacific lamprey collected at Bonneville Dam were surgically implanted with radio transmitters (8.3-mm \times 18.3-mm, 2.1 g in water; Lotek Wireless Inc.) in 2007–2009 and with acoustic transmitters (3-mm \times 5-mm \times 17-mm, 0.55 g in water; Advanced Telemetry Systems, Isanti, Minnesota) in 2010. American shad were tagged with radio transmitters (3.1-mm \times 5.4-mm \times 13.5-mm, 0.4 g in air or 3.1-mm \times 6.3-mm \times 14.5-mm, 0.5 g; Lotek Wireless Inc.) in 2010. Additionally, passive integrated transponders (PIT) tags were used in Pacific lamprey in 2006–2009 (half-duplex tags; 4-mm \times 23-mm or 4-mm \times 32 mm; Texas Instruments,

Dallas, Texas) and American shad in 2005–2007 (full-duplex tags; \sim 2-mm \times 12 mm; Texas Instruments). All of these fishes were released at sites downstream or upstream from Bonneville Dam and monitoring occurred after recovery and natural resumption of upstream movements. Two groups of fish were collected and radio-tagged at lower Snake River dams: transmitters (8.3-mm \times 18.3-mm, 2.1 g in water; Lotek Wireless Inc.) were surgically implanted in Pacific lamprey in 2006–2008 (McIlraith 2011) and were intragastrically inserted (1.1-cm \times 4.3-cm, 7.7 g in air; Lotek Wireless Inc.) into sockeye salmon in 2000 (Keefer et al. 2008). These fishes were released upstream from Lower Granite Dam (Fig. 1).

Fifteen monitoring sites were used in the diel evaluation (Fig. 1). These were nested within five habitat types that varied qualitatively along environmental and ecological gradients: (1) unimpounded tributaries (Klickitat, Deschutes, and Clearwater rivers, Fig. 1); (2) large main stem reaches (Bonneville reservoir, Snake River above Lower Granite reservoir, and Hanford Reach of the Columbia River); (3) dam tailraces; (4) fishway entrances; and (5) fishway ladders (Table 1). Habitat types differed in substrate, water depth, channel cross-section, water velocity and turbulence, and the density of other fishes and predators that we hypothesize were produced largely by differences in hydraulic slope (i.e., animals congregated at sites where upstream fish passage was challenging). Hydraulic gradients (i.e., slope) were very high (\sim 10 %) at fishway entrances and inside pool-and-weir fishways and were very low ($<$ 0.1–1 %) at tributary, main stem, and tailrace sites. Tributaries were monitored using aerial radio antennas located \sim 2 km upstream from confluences with the Columbia or Snake rivers. Tagged fishes experienced cooler water temperature, increasing water velocity and turbulence, and decreasing depth upon tributary entry and often encountered intensive fisheries. Large main stem reaches were monitored with aerial radio antennas. These sites were characterized by seasonally stable environmental conditions, relatively deep water, low turbulence, low to moderate current velocity, and salmonid fisheries. Lamprey were additionally monitored with an underwater acoustic detection array at the Bonneville reservoir site in 2010.

Conditions at dams were generally more complex and potentially evolutionarily novel (e.g., Waples et al. 2007). Tailraces had relatively deep water, moderate to high water velocity and turbulence, and predator aggregations. Predators in all tailraces

Table 1 Qualitative descriptions of environmental and biological attributes affecting movement at the Columbia River basin sites where migrating anadromous fishes were monitored

	Migration habitat type				
	Tributaries	Main stem	Dam tailrace	Fishway entrance	Fishway ladder
Environmental attributes					
Hydraulic slope	< 1 %	<0.1 %	<0.1 %	~10 %	~10 %
Channel width	~50–250 m	~500–2000 m	~500–2000 m	~1–5 m	~3–10 m
Turbulence	Moderate	Low	Moderate-High	High	Moderate-High
Depth	~1–10 m	~1–30+ m	~1–30+ m	~2–15 m	~2–5 m
Daily temperature	Diel variation	Seasonally stable	Seasonally stable	Seasonally stable	Diel variation
Substrate type	Mixed riverine ^a	Mixed riverine ^a	Concrete, bedrock	Concrete	Concrete
Biological attributes					
Predator density	Low-Moderate	Low-Moderate	High	High	Low ^b
Conspecific density	Low-Moderate	Low	High	High	High
Fish density	Low-Moderate	Low	High	High	High
Human fisheries	High	Moderate-High	Low	None	None

^a Rock, cobble, gravel, sand, fine sediment, woody debris

^b Density of white sturgeon (a Pacific lamprey and American shad predator) was high inside some entrance areas but was low at top-of-ladder sites

included white sturgeon (*Acipenser transmontanus*), double-crested cormorants (*Phalacrocorax auritus*), and osprey (*Pandion haliaetus*). Piscivorous California sea lions (*Zalophus californianus*) and Steller sea lions (*Eumetopias jubatus*) were intermittently present in the Bonneville Dam tailrace (Stansell et al. 2010). Tailraces were monitored with aerial radio antennas 2–3 km downstream from Bonneville, The Dalles, and John Day dams. Fishway entrances were relatively small (3–4 m wide, 10–15 m deep) and were characterized by high water velocity and turbulence, elevated predator presence, novel physical structures (i.e., concrete weirs, ceilings, metal grating, water diffusers, artificial lights), and often dense concentrations of conspecific and other fish species. Fishway ladder sites were similar to entrances in fish density, width, and maximum velocities, but these sites were shallower and somewhat less hydraulically complex. Entrances and ladders were monitored with underwater radio antennas, and ladders also had half- and full-duplex PIT antennas (see Downing and Prentice 2004 and Keefer et al. 2009 for details).

Data analysis

We assembled a database on the movements of approximately 13 000 fishes monitored in prior studies

(Table 2). Chinook salmon and steelhead were monitored at all sites and had the largest sample sizes (*means*=1550–2372 fish/site). Sample sizes were smaller for sockeye salmon (*mean*=425 fish/site), Pacific lamprey (334), and American shad (211). For all species, more unique individuals were detected at dam tailraces and fishways than at tributary and main stem sites due to fish dispersal among spawning sites, harvest (salmonids), transmitter battery life limitations (Pacific lamprey), and monitoring effort (American shad).

Fish movement was estimated using detections at each monitoring location. At aerial radiotelemetry sites (tributaries, main stem, tailraces), the time of first detection per fish was used and additional times were included when fish moved in and out of antenna detection range (time gap ≥ 30 min). At fishway entrances (underwater radiotelemetry), each unique entry time per fish was used. Inside fishway ladders (underwater radiotelemetry or PIT antenna), the time of last detection was used. These records were closest in time to fish exit into reservoirs. Typically, 1–4 unique detections were used from each tagged fish at each site. The highest numbers of detections per fish were at fishway entrances (i.e., many fish entered fishways multiple times) and the lowest numbers per fish were in ladders (i.e., most passed fishway ladders only once). We note that individual fish data at

Table 2 Numbers of unique tagged anadromous fish detected at Columbia River basin study sites, all years combined. All data for Chinook salmon, steelhead, and sockeye salmon were from radiotelemetry. Data for Pacific lamprey were from radiotelemetry (tributaries, Snake River, dam tailraces, fishway entrances), acoustic telemetry (Bonneville reservoir), and PIT-tag detections (fishway ladders). Data for American shad were from radiotelemetry at all sites except the Bonneville fishway ladder, where they were from PIT-tag detections

Site	Spring–summer Chinook salmon	Fall Chinook salmon	Steelhead	Sockeye salmon	Pacific lamprey	American shad
Tributaries						
Klickitat River	82	310	393	–	9	–
Deschutes River	293	288	872	–	31	–
Clearwater River	311	84	580	–	62	–
Main stem						
Bonneville reservoir	2,928	1,336	1,942	–	23	–
Hanford Reach	982	1,163	529	362	–	–
Snake River	1,008	86	906	27	29	–
Dam tailrace						
Bonneville	3,612	2,461	3,037	568	–	–
The Dalles	3,010	1,911	2,819	559	84	28
John Day	2,650	1,679	2,594	402	57	35
Fishway entrance						
Bonneville	3,524	2,413	2,893	469	707	–
The Dalles	3,522	2,627	3,162	376	184	40
John Day	3,097	1,961	2,859	441	33	–
Fishway ladder						
Bonneville	3,818	2,517	3,126	559	1,591	1,105
The Dalles	3,617	2,623	3,270	485	835	45
John Day	3,121	1,794	2,782	430	694	15

tailrace, fishway entrance, and ladder sites were not independent at each dam.

Differences in diel activity were assessed by calculating the percentage of passage events that were nocturnal by species and habitat type. Percent nocturnal was defined as the percent of detections that occurred between 21:00 and 05:00 h (Pacific Daylight Time). This 8 h block was between sunset and sunrise on all days except for ≤ 4 min/day near the summer solstice. Differences among species and habitat types were tested using unbalanced ANOVAs followed by Tukey’s HSD pairwise comparisons (e.g., percent nocturnal_{tailraces} = species; percent nocturnal_{steelhead} = environment type). All data were logit-transformed prior to analyses to account for their binomial distribution. After testing for the main habitat type effects, a nested ANOVA tested for site effects within habitat types (e.g., percent nocturnal_{steelhead} = habitat type + site[-habitat type]) where ‘sites’ were the 15 nested monitoring locations. In all ANOVAs, site×year was the replicate and spring–summer Chinook salmon and fall Chinook salmon were treated as separate species.

Results

Diel activity patterns varied among species, habitat types, and study sites (Fig. 2). Pacific lamprey were more nocturnal than salmonids or American shad in all habitat types (Table 3). In addition, steelhead were more nocturnal than spring–summer Chinook salmon at fishway entrances. Crepuscular activity was most evident for salmonids at tributary sites and Pacific lamprey in the Bonneville reservoir and Klickitat River.

Variability in movement timing was lowest for all species at high gradient fishway entrance and ladder sites (Fig. 3; Table 3). For salmonids, mean percent nocturnal was higher at tributary, main stem, and tailrace sites than at fishway entrances and inside ladders (Tukey’s HSD tests significant in 21 of 22 pairwise tests). Mean percent nocturnal for salmonids among tributary, main stem, and tailrace sites generally did not differ (significant in 1 of 10 tests) and there were no differences for salmonids between fishway entrances and fishway ladders (4 tests). No HSD-adjusted pairwise tests were significant for American shad (not monitored in main stem or tributary

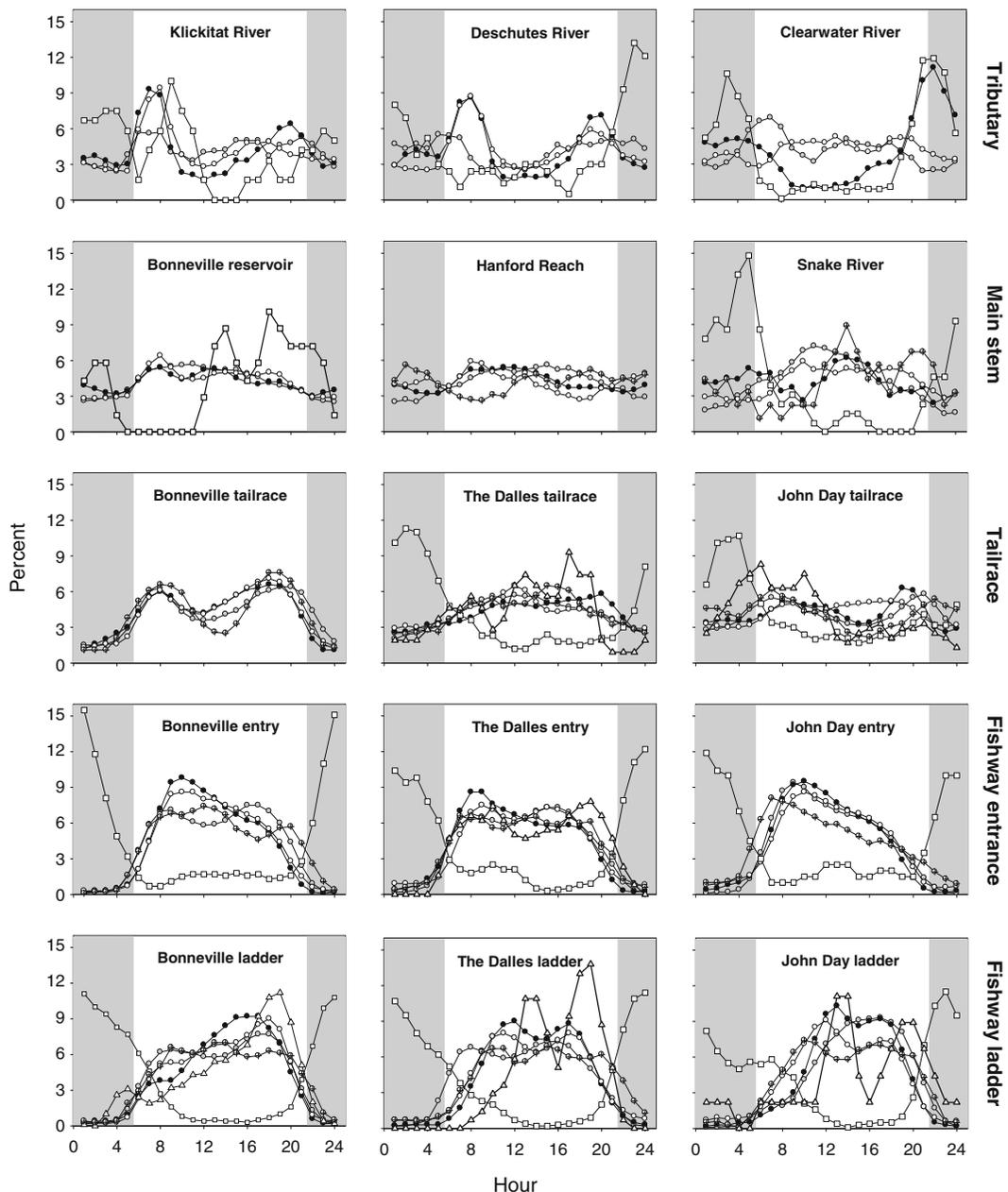


Fig. 2 Three-hour moving averages of diel movement by tagged spring–summer Chinook salmon (*grey circle*), fall Chinook salmon (*black circle*), steelhead (*white circle*), sockeye salmon (*crossed \circ*), Pacific lamprey (*white square*), and

American shad (*delta*). Data combined across years for each species at each site. Shaded areas cover 21:00–05:00 h (Pacific Daylight Time), the hours defined as nocturnal for analyses

habitats) or Pacific lamprey in the non-nested models. However, both habitat type and the nested term (site[type]) were significant ($3.8 \leq F \leq 4.3$, $P \leq 0.010$) for lamprey in the nested model, with more nocturnal movements at fishway entrances than in tailraces. In nested models for the salmonids, the site(type)

term was significant for fall Chinook salmon ($F=6.7$, $P<0.001$) and steelhead ($F=6.0$, $P<0.001$) but not spring–summer Chinook salmon ($F=2.0$, $P=0.055$) or sockeye salmon (only one study year). Site effects were inconsistent among species and habitat types.

Table 3 ANOVA results for among-habitat type and among-species tests of logit-transformed mean percent nocturnal (2100–0500 h) activity by tagged adult anadromous fish

Among-environment			Among-species		
Species	F _{df}	P	Environment	F _{df}	P
Spring–summer Chinook salmon	130.4 _{4,55}	<0.001	Tributary	20.6 _{3,39}	<0.001
Fall Chinook salmon	102.2 _{4,55}	<0.001	Main stem	22.6 _{4,37}	<0.001
Steelhead	40.7 _{4,55}	<0.001	Tailrace	22.8 _{5,41}	<0.001
Sockeye salmon	8.0 _{3,7}	0.012	Fishway entry	78.1 _{5,41}	<0.001
Pacific lamprey	2.5 _{4,31}	0.065	Fishway ladder	39.5 _{5,51}	<0.001
American shad	0.7 _{2,6}	0.535			

Discussion

Diel activity patterns of upstream-migrating adult fishes systematically varied across habitat types in ways that supported our hypotheses. In the most challenging environments (i.e., high-gradient, high-risk fishway entrances and ladders), fish movements became primarily diurnal (salmonids and shad) or nocturnal (Pacific lamprey), whereas fishes of all species were active over more hours of the diel cycle at lower gradient and less risky sites. These findings demonstrate that diel behavior patterns can be highly context-dependent along migration routes. Furthermore, shifts in activity occurred over relatively small spatial (kilometers to 10 s of

kilometers) and temporal (hours to days) scales, highlighting the substantial behavioral plasticity of these species.

Variability in fish behavior among habitat types likely reflected taxon-specific differences in sensory ecology and responses to visual, rheotactic, tactile, and olfactory cues. At sites with low hydraulic and ecological complexity, the common orientation strategy of odor-conditioned rheotaxis (Finelli et al. 1999; Vickers 2000) may have allowed safe and efficient upstream passage for all taxa. Thus, in large main stem and tributary environments, fishes could exploit stable currents and persistent chemical signals to navigate upstream in all light conditions, with minimal dependence on visual or tactile cues. In contrast, the turbulent, high-velocity conditions at dams may have required additional sensory inputs for successful route finding.

Visual cues may have been especially important for sight-oriented salmonids and shad in the more challenging environments. American shad, for example, rely on visual cues to orient upstream inside fishways during the day, but often change their heading or retreat downstream under low light conditions (Haro and Kynard 1997; Kynard and Buerkett 1997). Similarly, electromyogram studies of adult Atlantic salmon (*Salmo salar*) and Chinook salmon inside fishways have shown reduced night-time activity, reduced swim speeds, and cessation of upstream movements (Gowans et al. 2003; Brown et al. 2006). These behaviors have parallels in hydraulically challenging reaches of unimpounded rivers. For instance, sockeye and pink salmon (*O. gorbuscha*) migrating through river rapids spend proportionately more time searching for efficient passage routes and often significantly restrict night-time movements (Hinch and Rand 1998; Standen et al. 2002).

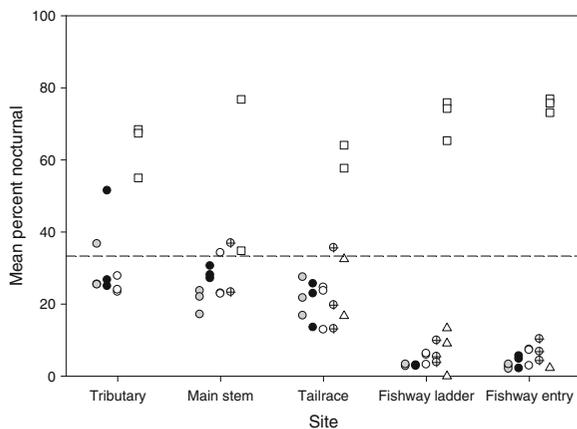


Fig. 3 Mean percent nocturnal (21:00–05:00 h) movement by tagged spring–summer Chinook salmon (grey circle), fall Chinook salmon (black circle), steelhead (white circle), sockeye salmon (crossed ○), Pacific lamprey (white square), and American shad (delta). Symbols are means across years at individual sites (n=15) and are grouped within migration environment. Dashed horizontal line represents 33 % nocturnal. Fish behavior was more temporally constrained at fishway entry and ladder sites, which had relatively high hydraulic slope and predator density compared to the more riverine tributary, reservoir, and tailrace sites

In contrast with the visually-oriented species, Pacific lamprey likely relied on rheotactic and tactile cues at more challenging sites. The role of lamprey vision during migration appears to be limited, as behaviors of experimentally-blinded adult sea lamprey (*Petromyzon marinus*) were nearly identical to those of non-blinded lamprey (Binder and McDonald 2007). In that study, both blinded and non-blinded lamprey used tactile and hydraulic cues to locate daytime refuges and vision appeared incidental. When confronted with turbulent or high-velocity conditions like those inside fishways, Pacific lamprey use their oral discs to remain in near-constant tactile contact with substrate (Reinhardt et al. 2008; Keefer et al. 2011). Persistent upstream orientation in these environments is presumably rheotaxis-based, although olfaction may also play a role. Experiments with anosmic sea lampreys indicate that adults use a sequence of rheotactic and olfactory cues to locate rivers, move upstream, and identify spawning sites (Vrieze et al. 2010, 2011). These studies imply context-dependent switching among sensory mechanisms across habitat types and/or integration of multiple mechanisms, supporting our general hypothesis.

Predator effects on diel behaviors are well known from predation-avoidance studies of vertically-migrating zooplankton (Hays 2003) and drifting stream invertebrates (Flecker 1992). Strong diel periodicity in these taxa, with most activity at night, is considered an adaptive strategy to avoid visual predators. The most dense predator gauntlets in our study were formed by white sturgeon at Bonneville and The Dalles dams, where hundreds of sturgeon can reside inside lower sections of fishways for extended periods (e.g., Parsley et al. 2007). The prey species (American shad and Pacific lamprey) presumably could use visual or chemosensory cues to detect sturgeon and assess predation risk (e.g., Kats and Dill 1998). These species may temporally restrict passage through hazardous areas or increase their passage speed to reduce exposure time (e.g., Gilliam and Fraser 2001). Either behavior potentially contributed to the strongly diurnal (shad) and nocturnal (lamprey) patterns we recorded in and near fishways. Nocturnal movements by lamprey may also represent adaptive, anti-predator behavior in natural high-gradient habitats like waterfalls, where adults often ascend via routes with very shallow (< 10 cm) water and can be vulnerable to diurnal predators.

We did not directly test for effects of sea lions on salmonids. However, diel behaviors of spring Chinook

salmon was nearly identical in years with (2002–2003) and without (2000–2001) significant aggregations of sea lions at Bonneville Dam. These predators hunt at the dam almost exclusively during daytime (Stansell et al. 2010), and salmon potentially could have reduced predation risk by using fishways at night. That we did not detect a large Chinook salmon behavioral shift when sea lions were present may indicate that the sensory requirements that elicit daytime fishway use outweighed the perceived predation risk or that visual cues are simply important for predator avoidance. Alternately, some pinnipeds and other predators (i.e., brown bears, *Ursus arctos*) efficiently prey on adult salmon at night (Klinka and Reimchen 2002; Wright et al. 2007), and the salmon behavior we recorded may reflect past selection pressures to avoid sites with perceived night-time predation risk.

Social cues have been shown to critically affect how animals respond to threats and navigate through ecologically complex environments (Torney et al. 2009; Guttal and Couzin 2010). The importance of such interactions to migrating anadromous fishes is essentially unknown, and likely differs among species and among habitat types. For example, visually-oriented species may avoid energetically inefficient night-time movement in demanding environments like fishways or rapids. Such avoidance would preserve endogenous reserves needed for reproduction (Bernatchez and Dodson 1987; Castro-Santos and Letcher 2010) and could be cued by either collective behaviors or individual adaptive responses. Similarly, timing movement to minimize predation risk may increase individual or group fitness, particularly if increased prey density results in lower risk through predator swamping (Ims 1990) or reduced predator attack success (e.g., Neill and Cullen 1974).

In conclusion, we think it is likely that challenging environments act as behavioral filters in animal movement systems ranging from migration to routine foraging and that such filters reinforce the among-habitat behavioral shifts we observed. An important next step is to quantitatively identify the specific factors affecting variability in behavior along the environmental and biological gradients we qualitatively identified. Future studies should explicitly measure how physical and biological complexity differs among habitat types and well-constructed experiments may then identify factors that constrain behaviors. Potentially informative hypotheses include: 1) whether migrants alternate

among sensory systems in different environments; 2) whether sensory cues in novel environments affect the expression of behaviors; 3) if there are environmental or ecological thresholds that predictably elicit behavioral changes; 4) how migrants respond to diel fluctuations in predator density or activity; 5) the degree to which migrants use social interactions to modify behaviors; 6) whether behaviors change seasonally or in response to life history phenology; and 7) the relative influence these mechanisms have on migrant behavior and fitness.

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