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First Documentation of Pelagic Larvae of Prickly Sculpin *Cottus asper* in Willamette Basin Reservoirs Using a Novel Light Trapping Method

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Although sculpin can play important ecological roles, serving as abundant key meso-predators in freshwater aquatic systems, much remains to be learned about their development and ecology. Depth discrete light traps effectively captured larval sculpin from Lookout Point Reservoir in the Willamette Basin, Oregon, USA. We confirm that these larvae were Prickly Sculpin (*Cottus asper*) based on morphology and genetics. We also document larval size and development and examine monthly vertical distributions and sympatric invertebrate taxa. We captured 1,048 pelagic larval Prickly Sculpin from 4.21 to 42.0 mm total length. Sampling occurred in traps set up to 20 m above the substrate, with Prickly Sculpin captured at all sampled depths. Captures shifted toward deeper reservoir habitats corresponding to increases in average body sizes as the season progressed from early spring to fall. We found most larval Prickly Sculpin at locations within the main reservoir body, several kilometers downstream of riverine areas. In addition to trap location, the abundance of larval Prickly Sculpin per trap was strongly associated with aquatic mites (absent from Prickly Sculpin stomachs). These findings suggest potentially shared ecological drivers of the observed distributions of larval Prickly Sculpin and mites. Collectively, we demonstrate that light trapping can be a useful method for collecting pelagic juvenile sculpins from reservoirs, in this case Prickly Sculpin, with the potential to improve our understanding of distribution, life-history patterns, and ecology throughout their range.

FRESHWATER sculpins (Cottidae; most in the genus *Cottus*) encompass more than 100 species restricted to the Northern Hemisphere (Kinziger et al., 2005; Goto et al., 2015; Young et al., 2022; Cortés, 2024). Sculpin can play important ecological roles, serving as abundant key meso-predators in freshwater aquatic systems and linking energy flow within and across ecosystems as important prey items (Beauchamp, 1990; Hodgens et al., 2004). As such, a focus on freshwater and diadromous sculpins has been proposed as a promising avenue for management and conservation of cool- and coldwater ecosystems broadly (Adams and Schmetterling, 2007). However, knowledge of sculpins remains surprisingly limited, especially for early life-history characteristics and habits, which are important both for resolving taxonomic confusion and for producing a holistic understanding of the ecological roles of these understudied fishes.

Diversity in the life history of sculpins includes species with either benthic or pelagic larvae, with most species of freshwater sculpins (genus *Cottus*) exhibiting either a fluvial or lacustrine life history (Goto, 1990; Baek et al., 2018; Goto et al., 2015). Pelagic larvae of sculpins have been generally associated with amphidromy, while benthic larvae, like the lake-dwelling Slimy Sculpin (*Cottus cognatus*; Arciszewski et al., 2015), are linked to only freshwater lifecycles (including fluvial and lacustrine) and are presumed to be a derived condition (Goto, 1990; Baek et al., 2018). Interestingly, Prickly Sculpin (*Cottus asper*) have pelagic larvae but express the full range of life-history ecotypes, with documented populations in coastal and far inland areas (Dennenmoser et al., 2014). Dennenmoser et al. (2014) demonstrated that Prickly Sculpin colonized the northern-most freshwater reaches of its modern distribution after the last glacial maximum (∼14,000 years BCE). However, the distribution of sculpins broadly in freshwaters south of this region, including this study area, likely occurred 2.5–6.2 mya (Yokoyama and Goto, 2005). The boundaries of amphidromous, fluvial, and lacustrine Prickly Sculpin populations, and the potential effect of artificial impoundments within their current distributions, are uncertain.

In historical synoptic fish sampling, Dimick and Merryfield (1945) documented Prickly Sculpin in the Willamette River Basin, OR, USA. Thirteen high-head and re-regulating dams (>15 m) were constructed primarily during the 1950s and 1960s in the headwaters and tributaries of the Willamette River (USACE, 2019). Similar surveys conducted in 1983 found abundant Prickly Sculpin only in the lower river, generally below river km 40, with two individuals captured at rkm 77 (Hughes and Gammon, 1987). In 2011–2013, synoptic sampling efforts by Williams (2014) in the same region documented this species throughout the entire 283 rkm sampling effort (75% of all sampled sites). More recent records now include Prickly Sculpin above these major Willamette River Basin impoundments (e.g., Monzyk et al., 2015). While the mechanisms of these changes in distribution are unclear, there is genetic evidence for widespread translocation of sculpins, including Prickly Sculpin (Young et al., 2013, 2022). It may be that reservoirs have facilitated the spread of Prickly Sculpin and that the use of this species as baitfish or movement of pelagic larvae with gamefish stockings could account for these patterns (Drake and Mandrak, 2014). Alternatively, they may have been historically present in lower numbers or in poorly

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sampled habitats and are now more abundant or easily sampled (White and Harvey, 1999). Likewise, it's possible that misidentifications in the field due to sexual dimorphism, allometry, convergence, and other evolutionary processes have led to erroneous historical estimates of sculpin diversity, distribution, and abundance.

Where sculpin exist in lentic systems, much remains to be known about their spatial distribution or behavior. Traditional methods of fish capture are often limited to larger individuals and shallower depths (Portt et al., 2006). As such, the ecological role of sculpins in reservoirs, and potential patterns related to ontogenetic shifts, remain unclear (Adams and Schmetterling, 2007). In nearshore marine systems along the Pacific Northwest, Richardson and Washington (1980) documented Prickly Sculpin larval development up to 9.9 mm standard length (SL) and noted that they retain a blennioid shape until this point, after which they begin to develop juvenile pigmentation and possess fully developed fins and juvenile characters. Pigmentation was considered to be an important characteristic for differentiating between species of sculpin larvae in coastal areas, in addition to morphology and meristics (Richardson and Washington, 1980). To what extent nearshore Prickly Sculpin ontogeny matches lentic systems is unknown and is not documented in either system past 9.9 mm SL or through pelvic fin development. The transition to a benthic ecology in sculpins is likely why larval and juvenile descriptions past 9.9 mm SL are lacking. Difficulties related to sampling lentic systems, especially small young sculpin, have limited our understanding of their life-history expression in these reservoirs and their use of pelagic habitat. This limitation is problematic given that sculpin are a part of reservoir communities and food webs in this region supporting species of conservation interest, such as Chinook Salmon (*Oncorhynchus tshawytscha*). Improving our understanding of reservoir sculpins, including their diversity and ecology, habitat use, diet, and development, may contribute to understanding their role in these highly modified ecosystems.

Light trapping can be an effective way to measure planktonic taxa exhibiting positive phototaxis, including fishes. There are numerous light trap designs that fundamentally rely on a light source and an opening that narrows toward the interior of the trap (McLeod and Costello, 2017); however, designs can be limited in their ability to withstand pressure at depth and often rely on consumable light sources that are limited in duration. In 2019, vertical arrays of LED light traps developed for sampling deep freshwater reservoirs (Murphy et al., 2022) were effective for capturing larval fishes, in particular larval sculpin in the Willamette River Basin. In this study, we used vertical light trapping and integrated results with morphology, meristics, and genetics to identify larval sculpin; we examined vertical distribution of abundance and size over the summer–fall period. Collectively, we show that vertical light trapping is an effective method to collect larval and juvenile Prickly Sculpin from reservoirs, and it may be used to improve our understanding of distribution, life-history patterns, and ecology throughout their range.

MATERIALS AND METHODS

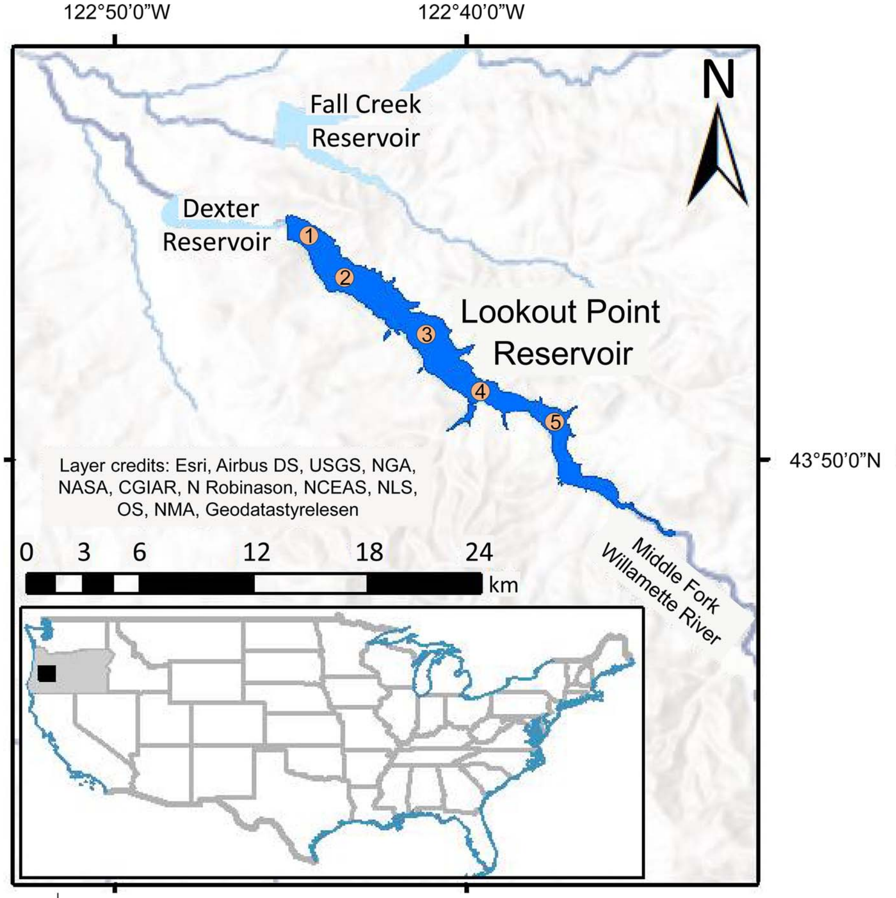
Study area.—Our study area was Lookout Point Reservoir, Oregon, located on the Middle Fork Willamette River (43°53′48″N, 122°43′34″W; Fig. 1). This and the other Willamette River Basin storage reservoirs have been conventionally managed with water retention times of around 1.5–3 months (Johnson et al., 1985), with some exceptions for more recent operational measures for downstream fish passage (Murphy et al., 2019). Sculpin species recorded broadly in the Willamette Valley include *C. aleuticus*, *C. asper*, *C. bairdii*, *C. beldingii*, *C. confusus*, *C. gulosus*, *C. perplexus*, and *C. rhotheus* (Markle et al., 1996). The construction of Lookout Point Dam in 1954 led to the origin of Lookout Point Reservoir, which is owned and operated by the U.S. Army Corps of Engineers to serve multiple purposes, including flood control infrastructure. For the century prior to dam construction, this free-flowing river stretch was potentially impacted by transport of logs to sawmills, instream gravel extraction, and removal of large wood (Keith et al., 2023). The Middle Fork Willamette River is also impounded upstream by Hills Creek Dam, constructed in 1961. At full pool, Lookout Point Reservoir is the largest reservoir in the Willamette River Basin (5.9×10^8 m^3) has a maximum depth of 71.3 m and a mean depth of 31.7 m (Johnson et al., 1985) at an elevation of 286.8 m National Geodetic Vertical Datum. The reservoir stratifies during summer months (temperature, light, chlorophyll, and plankton profiles are available in Murphy et al., 2023). We conducted light trap sampling each month in Lookout Point Reservoir from June through December 2019.

Field methods.—We set light traps (details of construction in Murphy et al., 2022) for 48 hours at fixed distances from the reservoir bed floor at five locations throughout Lookout Point Reservoir (1. Shallow, 2. Central, 3. Low, 4. Mid, 5. Top sites; Fig. 1). We constructed the traps with funnels consisting of a 4.5 mm or 5 mm stem opening. While we did not expect this difference to influence zooplankton, it could be size-limiting for larger taxa. We recorded differences in trap construction and performance (e.g., if the light had flooded, the presence of mud) upon deployment and pickup, respectively.

At each location, we set traps at 2.5, 5, 10, 15, and 20 m above the reservoir bed monthly from June through December 2019. We added an extra trap set at 1 m above the reservoir bed floor for all sampling except June. Reservoir water levels were dynamic (see Murphy et al., 2020 and https://www.nwd-wc.usace.army.mil/nwp/teacup/willamette/). In seven cases, traps placed 1 m above the bed floor appeared to have hit bottom during sampling, based on the presence of mud inside and outside of the trap, and thus we did not process these samples. Additionally, due to water level fluctuations during a portion of the study period, we could not set the 20 m trap at the 'Top' and 'Mid' stations (Fig. 1).

Upon retrieval, we processed light traps in the field by first emptying samples into a sorting tray. When sculpins were present, we placed trap contents in an ice bath until cessation of fish movement (including visible opercular movement) prior to filtering through a 106 μm sieve. We rinsed samples from the sieve and stored them in 95% ethanol for later identification and enumeration of target zooplankton and non-target taxa (including sculpins) in the laboratory. During the first deployment day of each month, we measured light and temperature at the deepest sampling location (the 'Central' site) near the dam.

Laboratory methods.—In the laboratory, we first removed all visible fish specimens from light trap samples for identification and counting. We then filtered the remaining sample contents through stacked 500 μm and 106 μm standard sieves and enumerated non-target zooplankton and other invertebrates



Site	Depth (m)						
	June	July	August	September	October	November	December
1. Shallow	22.8	26.3	25.5	21.3	22.2	30.7	9.0
2. Central	59.7	55.0	46.6	43.7	43.0	40.3	39.0
3. Low	26.2	26.0	23.6	21.5	24.9	18.9	18.0
4. Mid	25.8	22.8	15.4	21.6	20.7	18.0	16.8
5. Top	15.0	14.9	16.9	13.0	11.3	10.0	6.2

Fig. 1. Map of study location (Lookout Point Reservoir) including trap string placements (top, indicated by numbered circles) and corresponding table with trap line placement depths (m) by month. The inset U.S. map shows the study region (black square) within Oregon (gray). Other states are outlined in gray (land border) and blue (water border).

by subsampling and microscopy as described in Murphy et al. (2020); we identified zooplankton to broad taxonomic groups (e.g., Cladocera, Calanoida) or finer resolution and used them as potential predictor variables as described in 'Statistical analyses' below.

Using Markle et al. (1996), we identified all previously removed larval fish to family and selected a subset of sculpins to represent the observed size and color pattern variation of sampled individuals. We sent eyes from three specimens for sequencing of the mitochondrial COI barcode gene (mtCOI; Lifescanner division of Biolytica, Inc., Guelph, Ontario, Canada). The resultant sequences were compared to other sequences in the Barcode of Life (BOLD) database using the BOLD Identification Engine (IDE; Ratnasingham and Hebert, 2007; Meiklejohn et al., 2019), which returns a calculated probability of correct species identification. We then uploaded these mtCOI sequences to the BOLD database, with two uploaded to GenBank. Using 10MP microscope camera and the associated measurement software (AmScope, United Scope, Irvine, CA), we measured total length and standard length of all sculpin samples to the nearest 0.01 mm (Fig. 2). To analyze stomach contents, we selected a subset of sculpins—representing a variety of months, sizes, and depths—and dissected and removed their digestive tracts (Table 1). Digestive tracts were cut open, and prey organisms were identified and enumerated. When partially digested or damaged organisms were present, we counted microcrustacean carapaces and chironomid midge head capsules to avoid overestimating abundances based on fragments of organisms.

Statistical analyses.—To compare traps with different funnel sizes, we tested for differences in mean and median sculpin lengths using the two-sample t-test and Mood's median test using the software R, version 4.2.0 (R Core Team, 2022). We then used the R "partykit" package (Hothorn and Zeileis, 2015) to construct classification and conditional inference trees. This method allowed us to determine whether sculpin presence/absence or quantity during June and July were related to numbers of any zooplankton taxa found in light traps. We

Fig. 2. Representative Prickly Sculpin (*Cottus asper*) specimens captured throughout the study period and used for morphology, meristics, and descriptions. Oregon State University Ichthyology Collection (OS) accession numbers: (A) 26627, 8.57 mm SL; (B) 26629, 8.72 mm SL; (C) 26628, 9.05 mm SL; (D) 26630, 10.61 mm SL; (E) 26631, 14.04 mm SL; (F) 26632, 15.33 mm SL; (G) 26633, 23.84 mm SL.

performed similar analyses to test the relevance of temperature, light, depth, or station. Classification and conditional inference trees are non-parametric methods of analyzing data, and thus they can be useful when many predictor variables are under consideration. We used the "ctree" function, which selects the optimal predictor variable and point for splitting the data through permutation-based significance tests. We used a Bonferroni correction to account for multiple tests performed simultaneously and adopted node split size of five, a minimum bucket size of three, and specified the *P*-value for a split to be performed at a threshold of 0.05. We excluded data from August onward since sculpin captures were limited to five or fewer traps during those months.

Morphology and meristics.—A subset of individuals were selected for morphological and meristic evaluations (Fig. 2,

Table 1. Stomach contents (as number of each taxa identified in a stomach) of individual *Cottus asper* captured in light traps in 2019 in Lookout Point Reservoir. Although Trombidiformes were significantly associated with quantities of *C. asper* captured, they were not found as a diet item.

Month	Depth (m from bottom floor)	Sculpin total length (mm)	Cladocera	Chironomidae	Amphipoda	Copepoda	Trombidiformes (aquatic mites)	Other
June	2.5	12	0	0	0	5	0	0
June	2.5	13	4	3	0	4	0	1
June	2.5	13	1	0	0	1	0	0
June	2.5	14	1	0	0	0	0	0
June	2.5	14	2	4	1	0	0	0
June	20	12	0	0	0	4	0	0
June	20	13	0	0	0	1	0	0
June	20	14	1	1	0	0	0	0
August	1	17	1	5	0	1	0	0
August	1	17	0	0	0	7	0	0
August	1	24	0	0	0	0	0	0
August	1	25	0	0	0	0	0	0
August	1	27	0	0	0	0	0	1
August	1	33	0	2	0	0	0	0
August	1	33	1	5	0	1	0	0
August	1	35	0	5	0	0	0	0

Table 2). The smallest individual examined for meristic counts was 8.57 mm SL, as the condition of smaller individuals would have led to incomplete meristic data. We captured all fish images used for morphology and pigment descriptions with a 61MP digital camera (Sony A7Riv) paired with a macro lens (Sigma Art 105mm DG DN). Measurements were taken by converting pixels to nearest 0.01 mm via a photographic scale placed near the specimen during imaging and using a digital measurement tool (Adobe Photoshop v24.1.1). We measured meristics by examining specimens under a microscope. We deposited all sculpins captured in the Oregon State Ichthyology Collection (OS).

RESULTS

We caught 1,048 sculpin from 4.21 to 42.0 mm total length (TL) in light traps from Lookout Point Reservoir in 2019 (Fig. 2, Table S1; see Data Accessibility). All identified sculpin were Prickly Sculpin based on identification keys (Markle et al., 1996), and the BOLD IDE indicated that specimens were correctly identified as Prickly Sculpin based on their mtCOI sequences (BOLD sequence IDs: MOBIL9843-19, MOBIL9844-19, and MOBIL9845-19; GenBank sequence IDs: OQ872367 and OQ872368). Light traps built with funnels containing a stem opening of 5 mm caught slightly larger Prickly Sculpin than traps constructed with 4.5 mm funnel stems (Fig. S1; see Data Accessibility). A two-sample t-test comparing the mean Prickly Sculpin total lengths between traps with different funnel sizes was statistically significant ($P < 0.01$), although the means only differed by 1.13 mm. The larger Prickly Sculpin caught in the 5 mm funnel stem likely influenced this difference. This resulted in a mean total length that skewed slightly larger since Mood's median test did not detect a significant difference ($P = 0.88$) in the median total length of Prickly Sculpin between traps with different funnel stem openings.

External Anatomy

We describe the external anatomy (Fig. 2) and meristics (Table 2) for the Prickly Sculpin larvae captured during this study; these are the first larval descriptions to include larvae greater than 9.9 mm standard length and to document development through pelvic fin formation.

Head.—The four preopercular spines described by Richardson and Washington are already present in the smallest specimen in this study (Richardson and Washington, 1980). In the largest individual (Fig. 2G), the fourth, most ventral spine matches that of the adult stage (Markle et al., 1996) and is reduced and blunt, thus not included in the spine count (Table 2). Like adult Prickly Sculpin, the first, most dorsal spine is large and directed up, and the second spine is directed posteroventrally. The eyes gradually change from a more lateral position (Fig. 2A–D) to a dorsal position (Fig. 2E, F).

Fins.—The pectoral fins are the first fully formed fins in the smallest specimen (meristics listed in Table 2). The pelvic fins are indicated initially by a small fin bud and appear fully formed with a spine and four fin rays in our 11.5 mm SL specimen (not visible in Fig. 2). The fin rays of the dorsal fin develop before the spines and are present in our 8.7 mm SL specimen but have not reached their full height (Fig. 2B), which happens shortly after (Fig. 2C). The development of the anal fin progresses more rapidly but follows a pattern similar to that of the soft-ray portion

Table 2. Larval morphology (mm) and meristics measured from Prickly Sculpin (*Cottus asper*) specimens outlined in Figure 2. Blanks indicate unobservable characters on the specimens or measurements that were not possible. OS refers to the Oregon State Ichthyology Collection.

OS catalog number (specimens A–G)	Standard length	Total length	Head length	Snout length	Eye diameter	Snout–anus length	Body depth	Pectoral fin length	2nd preopercular spine length
Morphology									
26627	8.57	9.96	1.81	0.43	0.66	3.69	1.20	1.46	0.12
26629	8.72	10.14	2.21	0.44	0.66	3.99	1.45	1.48	—
26628	9.05	10.62	2.40	0.41	0.75	4.02	1.63	1.91	0.21
26630	10.61	12.44	2.94	0.60	0.88	4.88	2.04	2.31	0.24
26631	14.04	16.93	3.76	0.77	1.16	6.52	2.80	3.44	0.22
26632	15.33	18.54	4.41	0.85	1.30	7.46	3.30	3.58	0.22
26633	23.84	29.04	6.97	1.24	2.20	10.93	4.82	6.00	0.23

	Dorsal-fin spines	Dorsal-fin rays	Anal-fin rays	Left pectoral-fin rays	Pelvic-fin spine and rays	Preopercular spines	Ventral midline-melanophores
Meristics							
26627	8	19	18	16	—	4	17
26629	8	19	17	15	—	4	17
26628	8	20	17	16	4	4	17
26630	9	21	15	15	4	4	0
26631	8	21	17	16	4	4	0
26632	9	20	16	15	4	4	0
26633	8	—	18	15	4	3	0

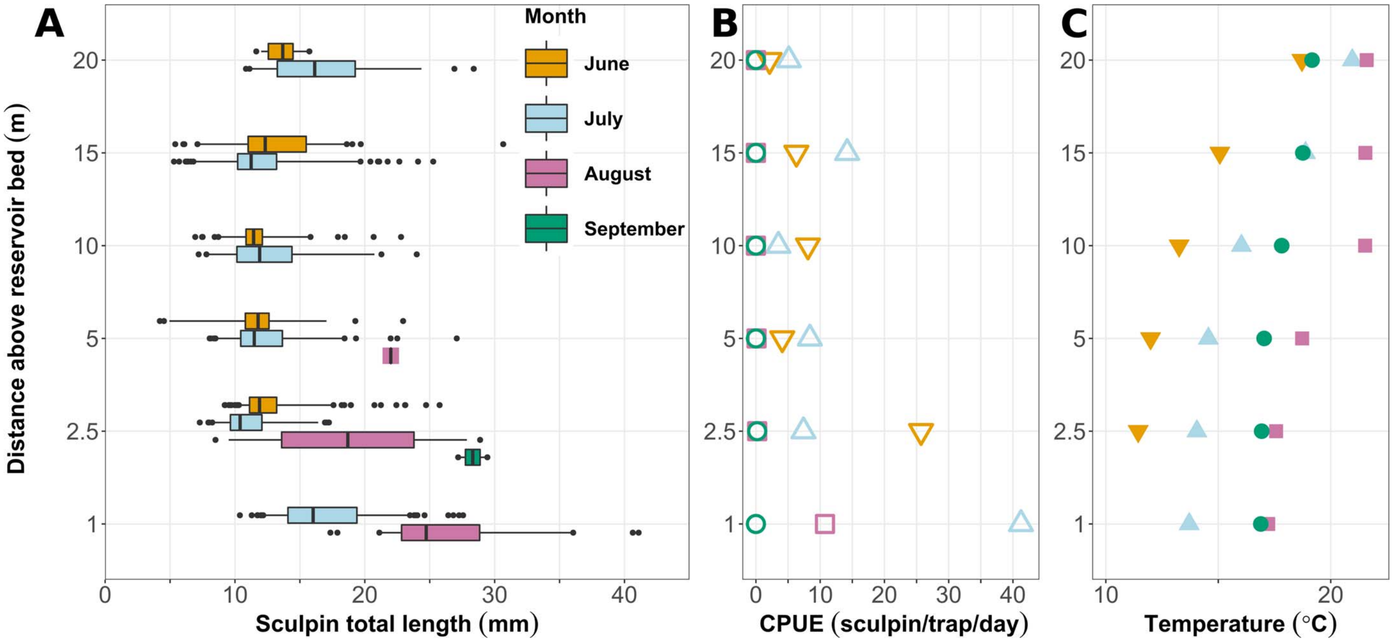


Fig. 3. Data from larvae of Prickly Sculpin (*Cottus asper*) caught in light traps during 2019 sampling in Lookout Point Reservoir, Oregon. Traps 1 m above reservoir bed floor were not set during June. (A) Boxplots depict ranges of sculpin body sizes (total length) each month based on light trap relative depth above the reservoir bed floor. The solid vertical line inside the boxplot is the median, the edges of the box represent the 25th to 75th percentile range, and the boxplot whiskers extend to the 5th and 95th percentiles. Points indicate outliers beyond the 5th–95th percentile range. Only one sculpin was caught in a trap 5 m above reservoir bed during August. (B) The sculpin catch per unit effort (CPUE) is displayed as the number of sculpins caught per light traps per day. Symbols correspond to sampling month, with upside down triangles representing June, upright triangles representing July, squares representing August, and circles representing September. (C) Water temperature recorded during light trap deployment each month. Symbols correspond to sampling month, with upside down triangles representing June, upright triangles representing July, squares representing August, and circles representing September.

of the dorsal fin. In our 8.7 mm SL specimen, the anal fin is already fully formed but has yet to reach its full height. As shown in Figure 2C, a membranous connection to the caudal fin remains, paralleling the condition seen in the dorsal fin. The caudal fin already has the full complement of fin rays in our smallest specimen (Fig. 2A).

Pigmentation

Head.—The pigmentation on the head starts with a large internal melanophore posterior to the eye and a second at the jaw joint (Fig. 2A). In later stages, large stellate melanophores fill in the space on the hind and the forebrain (Fig. 2B) until the entire dorsal section from the ethmoid region to the nape is filled (Fig. 2C–G). A darker pigment stripe runs diagonally from the dorsoposterior corner of the eye to the nape. The stripe starts with a few large melanophores (Fig. 2B, C) and becomes most apparent in the 10.6 mm and 14.0 mm specimens (Fig. 2D, E) and merges in with the rest of the pigmentation (Fig. 2F, G).

Ventral to the eye, including the lower jaw, remains sparsely pigmented with a few melanophores until the adult stage (Fig. 2). In the adult stage, the melanophores densely cover the region of the dentary (Fig. 2G).

Body.—The body is unpigmented primarily in the smaller larvae except for 22 melanophore arrangements along the base of the anal-fin rays and the ventral larval fin fold. Dorsally the gut is covered by pigmentation (Fig. 2A). In the larger stages, a medial band of pigments runs from the isthmus to the pelvic fins (not visible in the figure). The distinct vertical pigment stripe running vertically along the proximal base of the fin rays, characteristic for the larger stages (Fig. 2C–F), starts early as two minor fields of few melanophores (Fig. 2B). The dorsal pigment saddles just ventral to the dorsal fin begin with three small melanophores at the anterior and three at the posterior end of the soft-ray section of the dorsal fin (Fig. 2B). They progressively fill in, eventually forming the five saddles present in the larger larval stages (Fig. 2C, D). Two more rows of pigment patches are in the 9.0 mm specimen and located on the epaxial and hypaxial musculature (Fig. 2C–F), although the entire dorsal and lateral parts of the body fields remain noticeable (Fig. 2E, F). The abdominal and caudal regions remain mostly unpigmented (Fig. 2).

Ecology

Most Prickly Sculpin captures occurred during June and July, the earliest portion of our sample period (Table S1; see Data Accessibility). Although sampling occurred from June through December, only one Prickly Sculpin was caught after September, during the month of December. The size of Prickly Sculpin captured generally increased over the season (Fig. 3). We found Prickly Sculpin throughout the water column during June and July, but only found them in traps near the reservoir bed floor later in the summer (August and September; Fig. 3). Captures were not clearly associated with depths from the surface in the same way as distance from the substrate, and captures were never highest at the shallowest depth sampled with the exception of the central site in July (Table S1; see Data Accessibility), although traps did not always include the shallowest, near surface depths

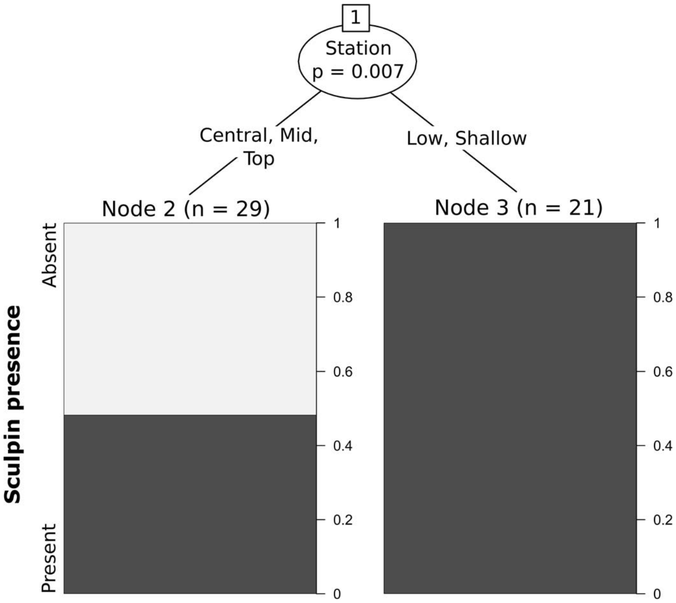


Fig. 4. Classification tree depicting sampling station as the only variable used to determine whether larvae of Prickly Sculpin (*Cottus asper*) were present or absent from a given light trap during June and July in Lookout Point Reservoir during 2019 (see map in Fig. 1).

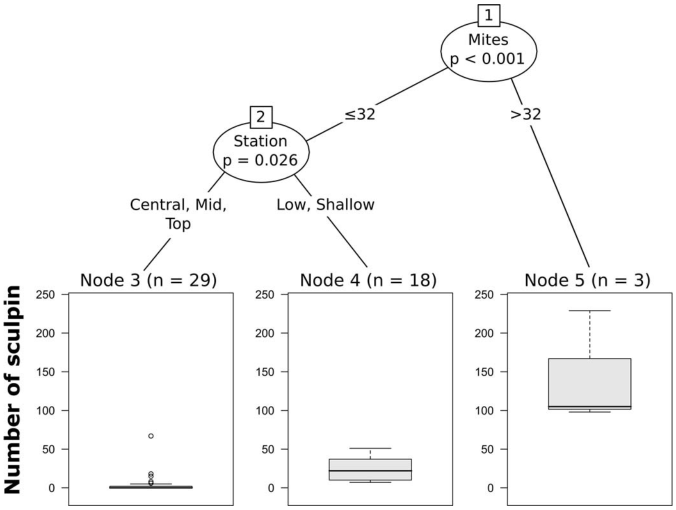


Fig. 5. Regression tree showing splits used to determine the number of larvae of Prickly Sculpin (*Cottus asper*) captured in light traps during June and July of 2019 in Lookout Point Reservoir, Oregon (see map in Fig. 1). Boxplots depict the median (bold horizontal line), interquartile range (box extent), and outliers (open circles) for the number of sculpin captured by traps within the data subset corresponding to each of the terminal nodes.

(Fig. S2; see Data Accessibility). Prickly Sculpin presence by each light trap sample was strongly associated with station, as evidenced by classification tree analyses (Fig. 4). All light traps set in the main body of the reservoir at both low and shallow stations caught sculpin during June and July.

While presence and absence of Prickly Sculpin was associated with station (Fig. 4), the quantity of Prickly Sculpin in a light trap sample was associated with the presence of aquatic mites in the order Trombidiformes, as evidenced by regression tree analyses (Fig. 5). Traps with the most numerous mites also contained the largest number of Prickly Sculpin. Interestingly, we did not find aquatic mites during the examinations of Prickly Sculpin stomach contents (Table 1). Instead, larval Prickly Sculpin fed primarily on copepods (37% ± 44%) and chironomids (34% ± 40%).

DISCUSSION

Light traps effectively captured small pelagic freshwater Prickly Sculpin with up to 229 larvae and juveniles in a single trap set for 48 hours. These captures included Prickly Sculpin up to almost one order of magnitude below the body size ranges typically observed during more traditional fish sampling surveys (e.g., 4 mm in the present study vs. 34 mm minimum captured during fish sampling in the reservoir in 2013; Monzyk et al., 2014). Discrete depth placement of traps provides additional insight into patterns of vertical distribution that are not well documented for sculpin species in general. While this study focused on traps placed consistently with respect to distance from the substrate, traps could be deployed with respect to surface depths. Because the design of the light trap appears important for limiting Prickly Sculpin body sizes (e.g., funnel size did not impact the median size of Prickly Sculpin caught in a trap, but did appear to limit the mean and maximum sizes caught), it may be possible to tailor trapping efforts for particular pelagic fishes or life stages of interest; these data could further allow for approximate growth by month and detailed diet analyses considering the vertical distribution of larval Prickly Sculpin in the reservoir.

This is the first study to track the larval development and distribution of Prickly Sculpin in an inland freshwater reservoir. According to Krejsa (1967), Prickly Sculpin hatch at a mean of 6 mm TL, while our captures were as small as 4.21 mm TL, suggesting that they were likely susceptible to capture shortly after hatching. Rickard (1980) found spawning from April–June, with possible preference for gravel habitats. This could explain both the timing and locations of captures observed for the smallest larvae in our study. We observed individuals reaching sizes of 41.09 mm TL by August, while Rickard (1980) estimated total first year growth at 47.4 mm TL and calculated that about half of that growth occurred from November to March, suggesting that Lookout Point Reservoir may offer exceptional rearing and growth opportunities for some individuals. Presumably, previous larval development in marine environments was documented to 9.9 mm SL because larger individuals settled and were less susceptible to nearshore collections (Richardson and Washington, 1980). This is roughly consistent with our observations where Prickly Sculpin appeared to remain pelagic through around 11 mm SL (~13 mm TL) based on vertical capture positions in the water column and the shift in eye position from more lateral to more dorsal. Some larger individuals remained in the water column early in the summer, including one individual over 30 mm that was captured 15 m above the reservoir bed in June. Beginning in August, even though smaller Prickly Sculpin were still captured, no captures occurred more than 5 m above the reservoir bed.

Sculpin presence is associated with certain locations within the reservoir, in particular, the 'Shallow' (<27 m) site near the dam, with few sculpins found at the deepest ('Central') station (44–60 m), suggesting that larval Prickly Sculpin are not uniformly distributed. This could be the result of either larval sculpin habitat preferences or, more likely, proximity to nesting sites. The presence of larval sculpin near the dam (approximately 18 km downstream of the run-of-river) indicates that sculpins are likely successfully reproducing within the reservoir and that larvae and juveniles use them as rearing habitats. The presence of Prickly Sculpin above this large high-head dam is particularly intriguing, since smaller (>15 cm) perch height barriers, including fish ladders, have been associated with upstream limits in other systems, presumably through the inhibition of adult upstream movement (LeMoine and Bodensteiner, 2014). That Prickly Sculpin persist above considerable barriers in the Middle Fork Willamette River suggests that a sufficient proportion of the population retained within and above the reservoirs is self-sustaining. Still, gene flow may be more limited than what may have occurred historically in an unimpounded system.

The abundance of Prickly Sculpin in light traps was surprising, given that they are infrequently encountered in these reservoirs using more traditional fisheries methods, though they are commonly found in stomachs of some piscivorous fishes (Monzyk et al., 2014). The pelagic larvae of Prickly Sculpin may be well suited to these highly fluctuating novel reservoir habitats and associated pelagic productivity, since the constant exposure of littoral habitats and limited vegetation mean that zooplankton may be more abundant than benthic macroinvertebrates (Whitmore et al., 2017). The relative abundance of Prickly Sculpin captured may indicate that they play important, and likely overlooked, roles in structuring ecological interactions and trophic relationships in these reservoirs, as has been documented in other systems (Beauchamp, 1990). Lookout Point Reservoir is on a historically free-flowing system, which may explain why a sculpin life history associated with lacustrine populations and potential migration is present. However, this species has not been documented in the upper river during historical sampling (Hughes and Gammon, 1987). This absence of records could indicate that the species was absent or that it was present but less abundant or poorly sampled.

Stomach contents indicate that larval Prickly Sculpin feed on zooplankton and chironomid midges and seem to move deeper in the water column as they develop. The reliance of some pelagic sculpins on benthic aquatic macroinvertebrates is puzzling, given the more limited capacity to move between habitats than would be expected in stream reaches. Further, aquatic mites are sympatric with sculpin captures, but they are absent of the sculpin stomach contents, and other zooplankton were not predictors of sculpin presence or abundance. The environmental drivers determining the distributions of both mites and sculpin may be shared, but further research could examine such relationships. Diel vertical migration, documented in Bear Lake Sculpin *C. extensus* and a dwarf form of Coastrange Sculpin, could also drive the distribution patterns observed (Ikusemiju, 1975; Neverman and Wurtsbaugh, 1994), and perhaps a mismatch with relatively stationary invertebrate zooplankton distributions (Murphy et al., 2023). Alternatively, larval sculpin may be attracted to light away from the feeding locations they would otherwise occupy. Finally, sculpin may be limited in their foraging under high light conditions and thus Prickly Sculpin may have had difficulty foraging on items within our light traps even if those items were attractive (Tabor et al., 2004). Larval Prickly Sculpin themselves may be a suitable prey item for larger fishes (Monzyk et al., 2014). Thus, the overall diet and behavior of Prickly Sculpin is likely important for predation risk and interactions with other taxa, where stratified reservoir conditions result in more introduced warm-water fish taxa near surface waters and more native cold-water fish taxa at depth.

Importantly, while we describe Prickly Sculpin here based on morphology and mitochondrial COI information, preliminary analyses of more complete genomic information suggest that Prickly Sculpin may be part of a species complex across its range (Cortés, 2024). This probability would not be surprising given that species in the genus can be morphologically similar and COI may provide incomplete lineage sorting (Young et al., 2022).

Additional methods for capturing larval fishes, such as light traps deployed as vertical arrays, could allow for greater understanding of their morphology and ecological importance. In this case, light trapping allowed us to capture Prickly Sculpin throughout larval development, examine their distribution, and concurrently document Prickly Sculpin and pelagic zooplankton dynamics, revealing an interesting non-trophic correspondence of sculpins and mites. We expect that the updated description of the larvae presented here will be helpful to taxonomists and that the information about sculpin diet and depths could provide a more holistic understanding of reservoirs and of a previously overlooked fish that, based on captures here, may be a surprisingly important part of the in-reservoir ecosystems.

DATA ACCESSIBILITY

Supplemental material is available at https://www.ichthyologyandherpetology.org/i2024026. Total captures of *Cottus asper* in light traps by month and depth are presented in Table S1. Retained specimens are available via the Oregon State Ichthyology Collection (https://ichthyology.oregonstate.edu/). Questions about limnological data can be directed to Ivan.Arismendi@oregonstate.edu. Unless an alternative copyright or statement noting that a figure is reprinted from a previous source is noted in a figure caption, the published images and illustrations in this article are licensed by the American Society of Ichthyologists and Herpetologists for use if the use includes a citation to the original source (American Society of Ichthyologists and Herpetologists, the DOI of the *Ichthyology & Herpetology* article, and any individual image credits listed in the figure caption) in accordance with the Creative Commons Attribution CC BY License.

AI STATEMENT

The authors declare that no AI-assisted technologies were used in the design and generation of this article.

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