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[Article]

Age-0 Lost River Sucker and Shortnose Sucker Nearshore Habitat Use in Upper Klamath Lake, Oregon: A Patch Occupancy Approach

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Abstract.—We examined habitat use by age-0 Lost River suckers *Deltistes luxatus* and shortnose suckers *Chasmistes brevirostris* over six substrate classes and in vegetated and nonvegetated areas of Upper Klamath Lake, Oregon. We used a patch occupancy approach to model the effect of physical habitat and water quality conditions on habitat use. Our models accounted for potential inconsistencies in detection probability among sites and sampling occasions as a result of differences in fishing gear types and techniques, habitat characteristics, and age-0 fish size and abundance. Detection probability was greatest during mid- to late summer, when water temperatures were highest and age-0 suckers were the largest. The proportion of sites used by age-0 suckers was inversely related to depth (range = 0.4–3.0 m), particularly during late summer. Age-0 suckers were more likely to use habitats containing small substrate (<64 mm) than those containing large substrate (>64 mm) and habitats with vegetation than those without vegetation. Relatively narrow ranges in dissolved oxygen, temperature, and pH prevented us from detecting effects of these water quality features on age-0 sucker nearshore habitat use.

Lost River suckers *Deltistes luxatus* and shortnose suckers *Chasmistes brevirostris* were listed as endangered under the Endangered Species Act in 1988 after dramatic declines in abundance and a lack of recruitment into the adult spawning populations (NRC 2004). Factors thought to contribute to the decline of these species included poor water quality, interactions with exotic species, overharvest, and habitat alteration, including the draining of wetlands (USFWS 2002). The majority of the remaining Lost River and shortnose suckers are found in Upper Klamath Lake and its tributaries (Moyle 2002). Since being listed as endangered, infrequent recruitment into adult populations and periodic mass mortality of adult suckers in Upper Klamath Lake (most notably in 1995–1997) have probably limited the recovery of Lost River and shortnose suckers (NRC 2004).

Historically, juvenile suckers had access to rearing habitat in vast wetlands along the northern portions of Upper Klamath Lake and in the Williamson River delta. However, extensive diking and draining of wetlands for agriculture between 1915 and 1995 eliminated an estimated 31% of wetlands in the Upper Klamath River basin (Gearheart et al. 1995). Upper Klamath Lake, which covers approximately 271 km^2 (67,000 acres) at full pool, is uniformly shallow, averaging less than 2.13 m in depth at mean summer lake surface elevation except at a trench along the western shore, which has depths between 6.40 and 9.45 m (NRC 2004). This shallow bathymetry makes the volume and area of remaining inundated wetlands sensitive to minor changes in surface elevation caused by irrigation diversions, downriver releases over the Link River Dam, and variation in annual precipitation (Reiser et al. 2001; NRC 2004). For example, most presently occurring marsh habitat in Upper Klamath Lake is inundated at a lake surface elevation of 1,262.2 m (4,141.0 ft), but nearly all marsh habitats are dewatered at a lake surface elevation of 1,261.3 m (4,138.0 ft; Reiser et al. 2001). Before the construction of the Link River Dam in 1921, the surface elevation of Upper Klamath Lake only varied by approximately 1 m over the entire year (NRC 2004). The construction of the dam allowed surface elevation to be drawn down by an additional meter (NRC 2004), such that in a typical year under present lake level management, about half the remaining emergent and submergent macrophytes are dewatered by midsummer (Reiser et al. 2001).

Recruitment failure documented in Lost River and shortnose sucker populations (NRC 2004) can be at least partially explained by diminishing rearing habitat and declining water quality due to the decreased wetland acreage adjacent to Upper Klamath Lake. The loss of these wetlands have been implicated as the cause of more rapid increases in summer water

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TABLE 1.—Substrate size-classes in nearshore areas of Upper Klamath Lake, Oregon, based on work by Terwilliger et al. (2004). Substrate classes (examined in relation to sucker habitat use) were considered separately and in small and large groupings.

Substrate	Group	Particle size (mm)
Fines	Small	<0.06
Sand	Small	0.06–2
Gravel	Small	2.0–64, or >75% <64
Intermix	Large	0.06–4,000
Cobble	Large	64–250
Boulder	Large	250–4,000, or >75% >64

temperatures and low summer dissolved oxygen (DO) concentrations throughout Upper Klamath Lake (Wood et al. 1996; NRC 2004). Wetlands retain and filter nutrients and maintain pH balance (Wetzel 1983); thus, reduced wetland acreage has increased the frequency of high summer pH levels (>9.5) in Upper Klamath Lake (Terwilliger et al. 2003; Wood et al. 2006).

Recently, several restoration projects have attempted to reconnect these wetlands with Upper Klamath Lake to provide critical habitat for larval and juvenile suckers. In 1999, the U.S. Fish and Wildlife Service (USFWS) and U.S. Bureau of Land Management restored approximately 566 ha (1,400 acres) of permanent marsh and open-water habitat and 646 ha (1,600 acres) of seasonal wetlands near the mouth of the Wood River, a tributary to Agency Lake (USBLM 2005). However, only a small portion of these restored wetlands is presently connected to the lake and available to suckers. The Nature Conservancy is restoring more than 2,020 ha (5,000 acres) of potential age-0 sucker habitat consisting of open-water habitat (depth = 2.75–3.96 m), deepwater wetlands (depth = 1.53–2.74 m), and emergent vegetation wetlands (depth = 0.61–1.52 m) in the vicinity of the Williamson River delta (Miller et al. 2005). A proposed expansion to the Upper Klamath Lake National Wildlife Refuge along the western shores of Upper Klamath and Agency lakes may additionally restore approximately 3,919 ha (9,700 acres) of agricultural land to marsh and open-water habitats (USFWS 2005).

Despite the extensive effort allocated to wetland restoration in Upper Klamath Lake, the importance of submerged and emergent vegetation for age-0 sucker rearing habitat remains unclear. Emergent macrophytes such as bulrushes *Scirpus* spp. exist in patches along some shorelines of Upper Klamath Lake, and submerged macrophytes such as pondweeds *Potamogeton* spp. inhabit some shallow bays and shoreline areas, especially in the northern portions of the lake. Larval suckers, which are mainly dispersed by major lake currents, are found in these vegetated shoreline areas starting in May and June of each year (Cooperman and Markle 2004). Reiser et al. (2001), who sampled emergent vegetation with seines, identified nearshore vegetation as important for juvenile sucker rearing. Conversely, Buettner and Scoppettone (1990) found few juvenile suckers in surveys of vegetated areas using backpack electrofishers, seines, and dip nets.

Previous surveys have reported that the presence of a wide range of substrate sizes is an important rearing-habitat component for juvenile suckers (Reiser et al. 2001; Terwilliger et al. 2004). Most substrates in Upper Klamath Lake are composed of fine organic material; however, the perimeter of the lake consists of boulders or mixed larger substrates (18.6%), cobble (10.4%), gravel or mixed smaller substrates (8.4%), sand (8.3%), fine sediments (45.8%), and a mixture of small and large substrates (8.4%; (D. Simon, Oregon State University [OSU], personal communication; Table 1).

Poor water quality in Upper Klamath Lake, often associated with massive blooms of the blue-green alga *Aphanizomenon flos-aquae*, can affect juvenile sucker survival and may also influence their behavior and distribution. Acutely lethal pH levels, water temperature, and DO for juvenile Lost River and shortnose suckers were determined by Saiki et al. (1999). With the exception of water temperature, acutely lethal levels of these factors occur locally in areas of Upper Klamath Lake almost every year (Wood et al. 1996; Terwilliger et al. 2003). Of the previously mentioned water quality variables, Martin and Saiki (1999) found that DO is the most critical factor affecting juvenile Lost River sucker survival in Upper Klamath Lake.

Loftus (2001) developed stress indices (SIs) for juvenile suckers based on DO, pH, water temperature, and a combination of all three metrics. Based on available data, Loftus (2001) determined the concentrations or levels of water quality variables that are likely to initiate physiologically adaptive responses (low stress thresholds) and at which adverse sublethal effects are likely to occur (high stress thresholds). The Loftus (2001) SIs place the effect of water quality metrics between high and low stress thresholds on a scale between 0 and 1. Sublethal stress may cause suckers to avoid otherwise suitable habitats. For example, Terwilliger et al. (2004) observed that age-0 suckers were less likely to be captured in open-water areas of Upper Klamath Lake close to shore when daytime DO concentrations were low.

The inconsistency in habitat descriptions for age-0 juvenile suckers among previous surveys may be due to heterogeneity in sampling efficiency across habitat types and among gears. The efficiency of gear in detecting individuals is not often taken into account in fisheries habitat studies; imperfect detection of a

species, if unaccounted for, can lead to biased conclusions about habitat use (MacKenzie 2005; MacKenzie et al. 2006). Studies assessing capture efficiency for amphibians and stream-dwelling salmonids have found that gear bias varied among sampling sites and sampling occasions and was dependent upon environmental variables (Bailey et al. 2004a; Peterson et al. 2004; Weir et al. 2005). Some examples of factors that may affect detection of age-0 suckers in Upper Klamath Lake are the presence or absence of vegetation, depth of water, type of nets used, number of hours for which nets were fished, seasonal or developmental changes in fish behavior, fish abundance, water temperature, and substrate type.

Site occupancy rates of rare species can be estimated in the presence of imperfect detection by conducting multiple sampling events at a site within a short period of time (MacKenzie et al. 2006). Individual covariates describing the habitat at each site also can be modeled, and the influence of habitat characteristics on site occupancy can be estimated (Weir et al. 2005). This relatively new methodology of assessing site occupancy, called patch occupancy estimation, is already commonly applied in wildlife studies (Tyre et al. 2003; Bailey et al. 2004b; Stauffer et al. 2004; Ball et al. 2005; Linkie et al. 2006). To our knowledge, this is the first fisheries application of this analytical technique.

The purpose of our study was to evaluate the influence of physical habitat characteristics on nearshore habitat use by age-0 Lost River and shortnose suckers in Upper Klamath Lake. Our approach allowed us to evaluate the importance of submerged vegetation, substrate type, water quality, and time period in relation to habitat use by age-0 suckers while accounting for imperfect detection. We also assessed the effects of several environmental variables on detection probability. The information we present on rearing habitat characteristics for age-0 suckers and effects of water quality and seasonal habitat use will help managers make informed decisions related to management of water resources, endangered species, and direction of restoration efforts.

Methods

From mid-July to early September 2004 and 2005, we investigated nearshore habitat use by age-0 Lost River and shortnose suckers in two shoreline areas of Upper Klamath Lake (Figure 1). We limited our sampling to these sites to better assess habitat use in areas where age-0 suckers are known to congregate (Terwilliger et al. 2004) and because the system is too large for an adequate survey of the entire lake.

We divided the shoreline into 50-m bands based on a substrate survey conducted in 1994, when water levels were low and substrate was exposed (Terwilliger et al. 2004). Six substrate classes were defined based on dominant particle size in the substrate survey (Table 1). Previous work indicated that these substrate groupings were important for age-0 sucker habitat use (Terwilliger et al. 2004). We used stratified random sampling to allocate effort proportional to the total area of the six substrate classes in the two areas (north and south; Figure 1). When possible, substrate composition was confirmed by probing the lake bottom with a piece of plastic pipe; confirmation was always positive, indicating that substrate was also correctly classified at unchecked sites. When depth prevented confirmation, we assumed that substrate remained unchanged since 1994. We believe that this assumption is reasonable given that only 20 cm of sediment has accumulated in Upper Klamath Lake over the last 150 years (Eilers et al. 2004). Each site was assigned a secondary habitat classification for vegetation based on the presence or absence of emergent macrophytes (e.g., bulrushes) and submerged macrophytes (e.g., pondweeds). Sites with only overhanging vegetation that did not provide in-water cover were considered unvegetated for this study.

All sampling was conducted with overnight sets of 0.61- or 0.91-m-diameter fyke nets (0.61-m net: one 0.61 × 9.10-m lead, two 0.61 × 4.60-m wings, five 0.61-m-diameter hoops; 0.91-m net: 0.91 × 9.10-m lead, two 0.91 × 4.60-m wings, five 0.91-m-diameter hoops). All fyke nets had 6.4-mm bar mesh and two internal fykes. Net pairs were arranged so that one was facing toward shore and the other was facing away from shore. In some cases, the lead of the net facing toward shore extended onto shore. Paired nets were set so that their mouths were at similar depths. We measured the depth at the mouth of each net and calculated a mean depth for each pair. This average depth was included as a covariate in our models. The depths at which we sampled represent the depth range found in Upper Klamath Lake, with the exception of very shallow (<0.40 m) wetlands and the narrow, deep trench located along the western shore. Sampling began on 18 July 2004 and 19 July 2005 before age-0 suckers fully recruited to our nets. Sampling ceased after catches declined; the final sampling dates were 8 September 2004 and 9 September 2005. In 2004, we sampled the north end of the lake 2 d/week and the south end of the lake 3 d/week, and we set seven pairs of nets per sampling day. In 2005, we sampled both the north and south ends of the lake 2 d/week and set six pairs of nets per sampling day.

We monitored water quality for the duration of overnight net sets on each sample date at two paired-net sites in 2004 and five paired-net sites in 2005. In

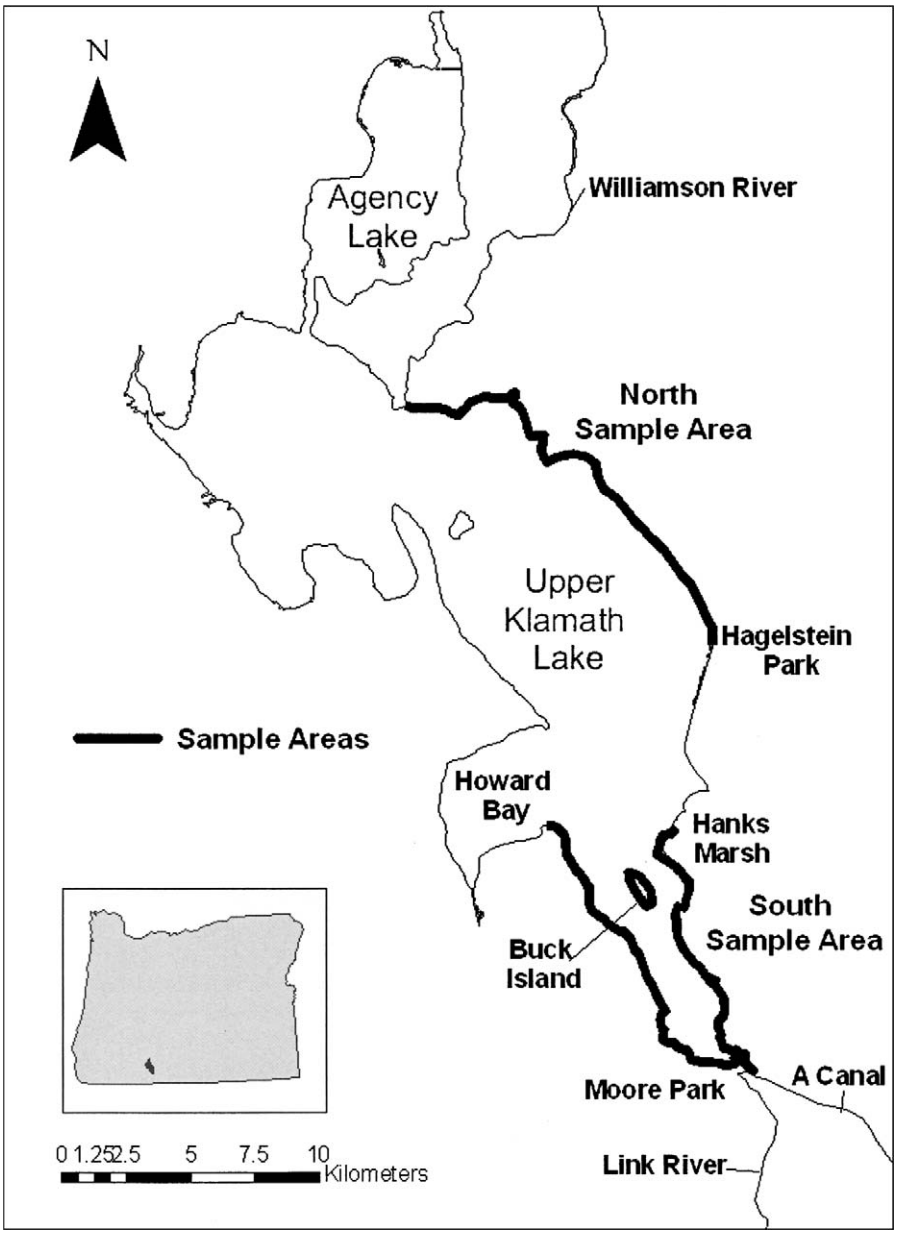

FIGURE 1.—Map of the study area in Oregon, including Upper Klamath Lake and the Williamson River. The north sampling area extended from the Williamson River mouth to Hagelstein Park; the south area extended from Hanks Marsh south to the outlet at the Link River near Moore Park and from Moore Park to the southeastern tip of Howard Bay (sampled area includes Buck Island).

2004, water quality sampling sites were chosen from seven possible paired-net sites to represent average daily water quality conditions over all sampling locations on each day; in 2005, sites were picked randomly from six possible paired-net sites. Water quality measurements were collected at 15-min intervals with Hydrolab DS-3 multiprobes (2004) or YSI XLM600 multiprobes (2005). Multiprobes were suspended 1 m off the bottom or within the middle of the column (whichever was deeper) at a location that was midway between the two nets in a pair and at the same distance from shore as the net mouths. Measured

variables included DO concentration (mg/L), pH, and water temperature (°C). We calibrated multiprobes before each weekly deployment and checked precision and accuracy against a reference multiprobe upon retrieval following U.S. Geological Survey (USGS) established protocols (USGS 1997 to 2007).

Fish captured in fyke nets were identified to the lowest taxonomic group possible in the field and were counted. Standard length (SL) was taken for all catostomids and a random selection of 10 fish each for nonsucker species. When catches exceeded 2–3 kg, juvenile fish of all species except suckers were subsampled and the number of each nonsucker species in the total catch was estimated by extrapolation. Due to difficulty in making positive identifications in the field, juvenile suckers were not identified to species at the time of capture. A proportion of juvenile suckers (approximately 35%) captured in paired nets were sacrificed and preserved in 95% ethanol for later identification to species. By means of a method that employs a combination of techniques (i.e., vertebral counts, lip morphology, and gill raker counts; Markle et al. 2005), sacrificed juvenile suckers were identified as one of three sucker species present in Upper Klamath Lake (Lost River, shortnose, or Klamath largescale sucker *Catostomus snyderi*). Because only a subset of suckers was identified to species, we were unable to model habitat use separately for each sucker species. Therefore, all analyses presented here were conducted on the combined grouping of age-0 suckers, not on individual species. Captured suckers smaller than 100 mm SL were considered to be age 0 based on work by Markle and Cooperman (2002), who reported that suckers in Upper Klamath Lake can reach approximately 75–100 mm SL by the end of their first summer.

Analyses.—We estimated age-0 habitat use with a suite of occupancy models (MacKenzie et al. 2006) in which we accounted for detection probabilities concurrently with occupancy probabilities. We defined a site as a 50-m band of shoreline where a pair of nets was set on a particular day. Sites in our study corresponded to sites sampled for substrate by Terwilliger et al. (2004). With two nets at each site there were four possible outcomes and corresponding capture histories: (1) suckers could be caught in both nets (coded as 11), (2) only in the net facing away from shore (coded as 10), (3) only in the net facing towards shore (coded as 01), or (4) in neither net (coded as 00). In each capture history, detection was represented by a 1 and nondetection was indicated by a 0. The probabilities of observing each outcome, known as encounter histories (h), are as follows:

$$\begin{aligned}
\Pr(h_{11}) &= \psi p_a p_s, \\
\Pr(h_{10}) &= \psi p_a (1 - p_s), \\
\Pr(h_{01}) &= \psi (1 - p_a) p_s, \quad \text{and} \\
\Pr(h_{00}) &= \psi (1 - p_a)(1 - p_s) + (1 - \psi),
\end{aligned}$$

where ψ is the probability that a site is occupied by age-0 suckers at the time of sampling, and p_a and p_s are the probabilities of detecting suckers at the nets facing away from shore and toward shore, respectively, given sucker presence at a site. We estimated p_a, p_s, and ψ using a maximum likelihood approach in Program MARK (White and Burnham 1999). Based on observed data, Program MARK maximizes the likelihood function:

$$L(p, \psi | h_i) = \prod_{i=1}^{s} \Pr(h_i),$$

which represents the product of probabilities of all observed encounter histories (h_i).

We used a logit link function to model the effect of covariates on the odds of detection and occupancy. The logit function is defined as:

$$\ln[\theta_i/(1 - \theta_i)] = \beta_0 + \beta_1 x_{i1} + \cdots + \beta_j x_{ij},$$

where β_j determines the size of the effect of covariates x_{ij}, and θ_i is the parameter of interest (p or ψ). We assumed that (1) age-0 suckers were never falsely detected at a site (no false positives due to misidentification) and (2) detection and presence of age-0 suckers were independent among sites. We also assumed that detection was independent between samples. For example, if an age-0 sucker was detected in one net, we assumed that at least one other age-0 sucker was available for capture in the second net. In modeling site occupancy, a necessary assumption is that sites are closed to extinction and colonization events during sampling periods if sampling events at a single site do not occur simultaneously. Our sample periods were the length of each overnight net set at each site. Given that both nets were fished in unison, this requirement was met for our analysis. Also, this assumption could be relaxed because we were interested in site occupancy on a daily time scale rather than in using our results to model metapopulation dynamics.

Sites were grouped by time period and substrate type. Three time periods were defined in each year based on age-0 sucker catch per unit effort (CPUE; fish/net-hour; Figure 2). In 2004, the prepeak period was defined as 18 July–1 August, the peak period was defined as 2–27 August, and the postpeak period was defined as 28 August–8 September. In 2005, the prepeak period was 19–30 July, the peak period was 2–18 August, and the postpeak period was 19 August–9

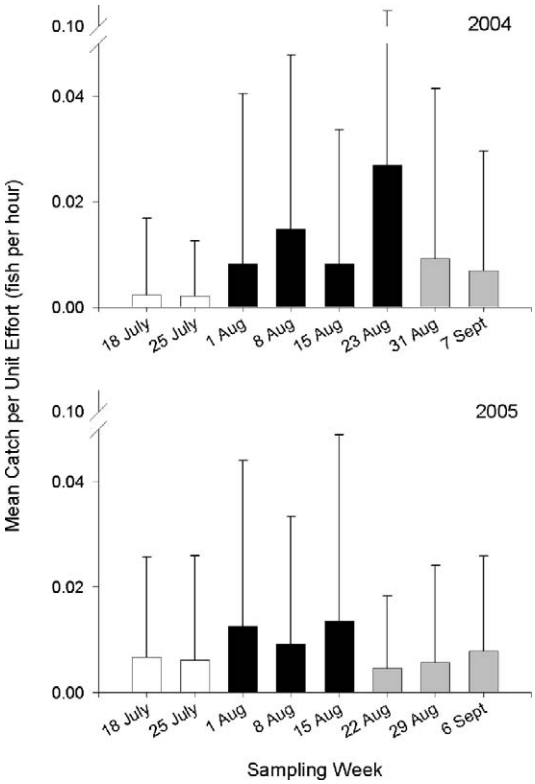

FIGURE 2.—Mean age-0 sucker catch per unit effort (CPUE; fish/h) in fyke nets set in the north and south sampling areas of Upper Klamath Lake, Oregon, by sampling week during 2004 and 2005. Time period was used as a group variable in patch occupancy analysis. Three time periods (white = prepeak; black = peak; gray = postpeak) were defined based on age-0 CPUE in each year (2004: prepeak = 18 July–1 August, peak = 2–27 August, postpeak = 28 August–8 September; 2005: prepeak = 19–30 July, peak = 2–18 August, postpeak = 19 August–9 September). Peak periods began when the mean weekly CPUE more than doubled and ended when CPUE decreased by at least 50% and remained low for the remainder of the sampling season.

September. Peak periods in both years began when the mean weekly age-0 sucker CPUE more than doubled; peak periods ended when CPUE decreased by at least 50% and remained low for the remainder of the sampling season (Figure 2). Occasionally, bands of shoreline were sampled multiple times in different time periods. These were considered separate sites in our analysis; however, this occurred too infrequently to model the local extinction and colonization processes directly. We used time period as a group variable because temporal changes in abundance (Royle and Nichols 2003), movement rates, and average size of age-0 suckers may cause heterogeneity in detection probability. We grouped substrate in two ways; we first modeled six substrate classifications as designated by Terwilliger et al. (2004), and then we grouped the three largest (i.e., boulder, cobble, and intermix) and three smallest (i.e., fines, sand, and gravel) classes to make two substrate size-groups (Table 1).

Physical habitat models.—To model the factors associated with age-0 sucker detection probability (p) and habitat use (ψ), we developed a set of a priori candidate models based on a literature review and our previous observations. Each candidate model was a mathematical description of a working hypothesis that explained age-0 sucker distributions in Upper Klamath Lake (Table 2). In our most basic candidate model (H18; Table 3), age-0 suckers were assumed to be ubiquitous and equally detectable across all sites. We fit models having parameters for detection probability (our nuisance parameter) first; using our best model for detection probability, we then added parameters for site occupancy. We considered detection probability a nuisance parameter because it was fundamental to the probabilistic model but was not of particular interest independently. We considered year of sampling, net type, orientation of the net mouth (towards or away from shore), presence or absence of aquatic vegetation, mean depth at net mouths for each net pair, time period (prepeak, peak, or postpeak), the length of time for which the net was in the water, substrate class, and small and large substrate groupings as factors that could influence detection probability. Physical habitat characteristics considered as possible factors in site occupancy were year, substrate class, small or large substrate grouping, vegetation, depth at mouth, time period, and area (north or south) of the lake (Figure 1). The biological rationale for inclusion of each model parameter is given in Table 2. As a final check to ensure that we had not undervalued the importance of any of the detection parameters by fitting them first, we fitted a model that was fully expanded for detection probability and that had the best fit for occupancy.

Water quality models.—Water quality data were not collected at all sites; therefore, we were unable to include DO, pH, and temperature covariates in our analysis of the full data set. We separately modeled the influence of water quality on site occupancy using a subset of sites for which we had water quality data (Table 4). The highest-ranking habitat model (H1) was used as a starting point for constructing water quality models. Water temperature, DO, and pH were averaged across sampling intervals within a net set, standardized to a value between 0 and 1, and used as covariates in separate candidate models. Stress indices for DO, pH, and a combined variable (incorporating means of all three water quality variables) (Loftus 2001) were also used as covariates in some of our models. A temperature

TABLE 2.—Biological interpretation of predictor variables used in candidate models describing factors influencing age-0 sucker habitat use (HU) and detection probability (DP) within Upper Klamath Lake, Oregon, during summer 2004 and 2005.

Predictor variables	Biological inference to HU	Biological inference to DP
VEG	HU varies with the presence or absence of vegetation	DP is influenced by the presence or absence of vegetation
SUB	HU varies with substrate size (six size-classes)	DP is influenced by substrate size (six size-classes)
SMALL_LARGE	HU depends on whether or not substrate is large or small	DP depends on whether or not substrate is large or small
DEPTH	HU varies with depth	DP is influenced by depth
NET	—	DP is influenced by fyke-net type (large or small)
ORENTATION	—	DP is influenced by fyke-net orientation (toward or away from shore)
AREA	HU varies by area of the lake (north or south)	—
HOURS	—	DP is influenced by soak time
YEAR	HU is influenced by interannual variation in abundance or environmental conditions	DP is influenced by interannual variation in abundance or environmental conditions
PERIOD	HU varies among sampling periods (prepeak, peak, and postpeak)	DP is influenced by variation in abundance or behavior of age-0 suckers within the size range susceptible to our gear among the three sampling periods
PERIOD × DEPTH	HU varies with both the sampling period and water depth	—
PERIOD × AREA	HU varies with both the sampling period and area of lake	—
TEMP	HU varies with mean daily temperature within the observed range	Temperature affects the behavior of juvenile suckers and therefore influences DP
PH	HU varies with mean daily pH within the observed range	—
DO	HU varies with mean daily dissolved oxygen concentration within the observed range	—
SI	HU can be predicted by a stress index that accounts for mean daily temperature, dissolved oxygen, and pH	—

SI was not modeled due to a lack of nonzero values for this parameter. The biological rationale for including each variable in our models is given in Table 2.

Model selection.—Physical habitat and water quality models were ranked using Akaike's information criterion (AIC) corrected for small sample size (AIC_c; Burnham and Anderson 2002). Use of AIC provides a method of ranking models based on $\log_e$(likelihood); to encourage parsimony, this method applies a penalty for the number of parameters. Burnham and Anderson (2002) recommended use of the small sample size correction (AIC_c) when the ratio of sample size (n) to number of parameters is less than or equal to 40. Because this adjustment approaches 0 as n becomes large, we used the adjustment regardless of sample size. We further modified AIC_c ranks to account for potential lack of independence among sites by substituting the effective sample size (M) for n in the small sample size adjustment (Cooch and White 2006). To calculate M, we subtracted the number of repeat visits to a shoreline band from the total number of visits to all shoreline bands (n).

We examined the fit of our global model (Tables 3, 4) to the physical habitat and water quality data sets using Pearson's chi-square goodness-of-fit test, which we evaluated at an α level of 0.05 (MacKenzie and Bailey 2004). This test was not available in Program MARK for the two-sample case; therefore, we conducted the test in Microsoft Excel. The chi-square test compares the frequency of occurrence of each possible encounter history to observed data. Our global model had a total of 36 parameters (six substrate classes in three time periods for both occupancy and detection probabilities). A variance inflation factor (c) was estimated by dividing Pearson's chi-square statistic by the degrees of freedom (Cooch and White 2006). An estimated variance inflation factor ($\hat{c}$) greater than 1.0 indicated overdispersion and was used to adjust the variance and AIC_c rankings. Overdispersion indicates a lack of fit and the potential for lack of independence among sites. Variance-adjusted rankings are indicated by quasilikelihood AIC_c ($QAIC_c$) values in the Results. Differences (Δ) in AIC_c and AIC_c normalized weights (w_i) were calculated in Program MARK for each model. Normalized weights are calculated by dividing each model weight ($\exp[-\Delta AIC_c/2]$) by the sum of all model weights from the considered group of models (Cooch and White 2006). A confidence set of models

TABLE 3.—Akaike information criterion (AIC) rankings for Upper Klamath Lake age-0 sucker physical habitat models that were fitted using the full data set and adjusted for a small sample size and overdispersion (quasilikelihood AIC_c [$QAIC_c$]). The $QAIC_c$, normalized weights (w_i), and number of parameters are given. Model parameters considered for detection probability include net type (NET), orientation of the fyke-net mouth (ORIENTATION; toward or away from shore), number of hours of net soak time (HOURS), year (YEAR), presence or absence of submerged aquatic vegetation (VEG), average depth at mouths of paired nets (DEPTH), time period (PERIOD; prepeak, peak, and postpeak), substrate class (SUB), and small and large substrate groupings (SMALL_LARGE). Model parameters considered for site occupancy included YEAR, VEG, DEPTH, PERIOD, SUB, SMALL_LARGE, and area of the lake (AREA; north or south). Models including "." were those that assumed a homogenous distribution of age-0 fish throughout the sampling area. Variances were adjusted by an inflation factor ($\hat{c}$) of 1.07.

Model	Model number	$QAIC_c$	w_i	Number of parameters
p(PERIOD)ψ(PERIOD × DEPTH)	H1	988.20	0.993	7
p(PERIOD)ψ(DEPTH)	H2	999.02	0.004	5
p(PERIOD)ψ(PERIOD)	H3	1,002.64	0.001	6
p(PERIOD)ψ(.)	H4	1,003.09	0.001	4
p(PERIOD)ψ(SMALL_LARGE)	H5	1,003.66	0.000	5
p(PERIOD)ψ(AREA)	H6	1,004.17	0.000	5
p(PERIOD)ψ(VEG)	H7	1,004.87	0.000	5
p(PERIOD)ψ(YEAR)	H8	1,004.95	0.000	5
p(SUB + PERIOD)ψ(PERIOD × DEPTH)	H9	1,005.64	0.000	22
p(PERIOD)ψ(PERIOD × AREA)	H10	1,006.38	0.000	7
p(DEPTH)ψ(.)	H11	1,006.95	0.000	3
p(PERIOD)ψ(SUB)	H12	1,008.69	0.000	9
p(YEAR)ψ(.)	H13	1,019.84	0.000	3
p(SMALL_LARGE)ψ(.)	H14	1,020.86	0.000	3
p(VEG)ψ(.)	H15	1,021.56	0.000	3
p(ORIENTATION)ψ(.)	H16	1,022.42	0.000	3
p(SUB)ψ(.)	H17	1,023.27	0.000	7
p(.)ψ(.)	H18	1,023.30	0.000	2
p(NET)ψ(.)	H19	1,024.23	0.000	3
p(HOURS)ψ(.)	H20	1,025.14	0.000	3
p(SUB + PERIOD) ψ(SUB + PERIOD)	GLOBAL	1,033.69	0.000	36

was defined as models having w_i values no less than 10% of the top model's w_i value (Burnham and Anderson 2002). To incorporate model uncertainty, we averaged all habitat models to estimate probability of detection and habitat use and the variances associated with these estimates (Burnham and Anderson 2002; MacKenzie et al. 2006).

Models with high AIC ranks identify which parameters are important for site occupancy or habitat use but do not indicate the direction or magnitude of parameter effects. To examine the effects of habitat and water quality parameters on occupancy and detection, we calculated odds ratios (ORs) and their confidence limits for all occupancy and detection variables contained in at least one model in the confidence set of models for each data set (MacKenzie et al. 2006). Odds ratios for a single unit of change were calculated as $\exp(\beta_i)$ from the highest-ranking model containing the covariate of interest. Odds ratios indicate the direction and magnitude of parameter effects and allowed us to understand how habitat variables affected site occupancy and detection.

TABLE 4.—Odds ratios and 95% confidence limits (CLs) for Upper Klamath Lake (Oregon) physical habitat categorical covariates found in selected age-0 sucker habitat use models. Odds ratios greater than 1.0 favor sucker presence in habitats of the first category over the second.

Variable	Ratio	Odds ratio	Odds ratio CLs	
			Lower	Upper
Substrate	Small : large	1.80	0.66	4.88
Vegetation	Vegetated : unvegetated	1.44	0.32	6.46
Year	2004 : 2005	1.24	0.47	3.30
Area	South : north	1.60	0.61	4.17

Results

We sampled 232 sites in 2004 and 195 sites in 2005; 274 shoreline bands were visited only once, 56 were visited twice, 11 were visited three times, 2 were visited four times, and 2 were visited five times. Distance between sites sampled on the same day averaged approximately 1 km. Net capture of age-0 suckers between 30 and 40 mm SL began during the first 2 weeks of sampling. We captured age-0 suckers at 55.2% of sites in 2004 and 51.3% of sites in 2005 (total for all sites and both years = 53.4%). The majority of sacrificed juvenile suckers were identified as Lost River suckers in 2004 (60%) and 2005 (56%).

The second-largest percentages of sacrificed juvenile suckers were identified as shortnose suckers in 2004 (32%) and 2005 (40%). Among sacrificed juvenile suckers, 2% were identified as Klamath largescale suckers and 4% were unidentifiable with our methodology. The ratio of shortnose suckers to Lost River suckers in samples of identified suckers was 0.53:1.00 in 2004 and 0.71:1.00 in 2005.

Nonsucker fish species were caught at high rates and had wide spatial distributions in 2004 and 2005. Juvenile tui chub *Gila bicolor*, which were captured in 92% of the nets in 2004 and 94% of nets in 2005, were nearly ubiquitous. Juvenile blue chub *G. coerulea*, fathead minnow *Pimephales promelas*, and juvenile yellow perch *Perca flavescens* were also widely distributed and were captured in 79–92% of all net sets in each year. Mean annual CPUE in nearshore areas was greater in 2005 than 2004 for juvenile blue chub and juvenile yellow perch and was greater in 2004 than 2005 for fathead minnow and juvenile tui chub. Periods of peak catch for fathead minnow in 2004 and for juvenile tui chub in both years overlapped periods of peak sucker catch. Peak catch rates for juvenile blue chub occurred slightly earlier in 2004 and later in 2005 than peak sucker catches. In both years, the seasonal peak in juvenile yellow perch CPUE occurred before the peak in sucker CPUE.

Mean daily temperatures were similar in both areas (north and south) and years. Daily mean temperatures were highest between 18 and 29 July and between 11 and 18 August in 2004 and between 26 July and 9 August in 2005. Mean daily temperatures exceeded the low stress threshold for juvenile suckers of 25.0°C on two occasions in each year but never exceeded the high stress threshold of 28.0°C (Loftus 2001). Peak temperatures were observed on 26 July 2004 (28.6°C) and 8 August 2005 (28.3°C). In both years, the mean daily temperature steadily declined in the last week of August to mean daily lows in September of 18.3°C in 2004 and 16.5°C in 2005. Minimum temperatures were observed on 24 August 2004 (14.9°C) and 9 September 2005 (9.9°C).

Mean daily DO concentration across all sites ranged from 2 to 10 mg/L in 2004 and from 5 to 12 mg/L in 2005. Values were similar in the northern and southern areas in both years. Mean daily DO concentration dropped below 6.0 mg/L, the low stress threshold for juvenile suckers (Loftus 2001), at 23.1% of monitored sites in 2004 and at 9.6% of monitored sites in 2005; mean daily DO was below 4.0 mg/L, the high stress threshold, at one site in 2004 but no sites in 2005.

Mean daily pH did not vary greatly among areas or time periods in either year. Values ranged from 7.6 to 9.4 in 2004 and from 8.6 to 9.8 in 2005. Mean daily pH values exceeded 9.0, the low stress threshold for juvenile suckers (Loftus 2001), at 32.7% of monitored sites in 2004 and at 88.4% of monitored sites in 2005. A mean daily pH of 9.75, the high stress threshold for juvenile suckers (Loftus 2001), was not recorded in either year.

Physical Habitat Models

Our global model provided a good fit to the full data set used to evaluate physical habitat characteristics (Pearson's chi-square goodness-of-fit test: $P = 0.38$, df $= 18$). We estimated a $\hat{c}$ of 1.07 for this model, which we used to adjust variances for all physical habitat models. All other candidate models had lower $QAIC_c$ values and therefore were considered better than the full model when parsimony was taken into account (Table 3). The top physical habitat model, which carried 99.3% of the model weight, indicated that detection probability varied by time period and that site occupancy varied by a depth × period interaction. Models that included depth, year, vegetation, substrate, net type, and net orientation as factors affecting detection probability ranked low (Table 3). Models having site occupancy parameters for year, vegetation, substrate, and area all ranked lower than the model that assumed a homogenous distribution of age-0 suckers throughout the sampling area (designated by "." in Table 3). Models containing a substrate variable expressed as six classes (H12 and H17; Table 3) resulted in lower deviances but had more parameters (therefore were ranked lower) than models with substrate described as either small or large (H5 and H14).

Model-averaged estimates of detection probability and site occupancy varied by period but not by substrate. Our estimates of overall detection probability for 2004 and 2005 were higher during peak (0.49 ± 0.04) and postpeak (0.49 ± 0.07) periods than during prepeak periods (0.40 ± 0.07). Estimated site occupancy was higher during peak catch periods (0.92 ± 0.07) than during prepeak (0.63 ± 0.11) and postpeak (0.65 ± 0.09) periods in both years.

Age-0 Lost River and shortnose suckers were more likely to inhabit shallow sites than deep sites during prepeak and postpeak periods in 2004 and 2005. Odds ratios indicated that for every 1-m increase in depth, sites were 0.26 (95% confidence interval [CI] = 0.10–0.65) times as likely to be occupied by age-0 suckers during prepeak periods and 0.25 (95% CI = 0.11–0.57) times as likely to be occupied by age-0 suckers during postpeak periods in both years. During peak periods in both years, however, all sites were equally likely to be occupied regardless of depth (OR = 0.82, CI = 0.28–2.49).

Odds ratios suggested that age-0 suckers were more

TABLE 5.—Akaike information criterion (AIC) rankings for Upper Klamath Lake water quality models that were fitted using a subset of sites and adjusted for a small sample size (quasilikelihood AIC_c [$QAIC_c$]). The $QAIC_c$, normalized weights (w_i), and number of parameters are given. Covariates considered in these models included mean dissolved oxygen (DO), mean temperature (TEMP), mean pH (PH), stress indices (SIs) for DO (DO SI) and pH (PH SI), and a three-metric SI based on DO, TEMP, and PH. Variances were adjusted by an inflation factor ($\hat{c}$) of 1.68. The confidence set of models includes all but the GLOBAL model.

Model	Model number	$QAIC_c$	w_i	Number of parameters
p(PERIOD)ψ(DEPTH × PERIOD + TEMP)	WQ1	292.56	0.369	8
p(PERIOD)ψ(DEPTH × PERIOD + PH)	WQ2	294.24	0.159	8
p(PERIOD)ψ(DEPTH × PERIOD)	WQ3	294.35	0.151	7
p(PERIOD + TEMP)ψ(DEPTH * PERIOD)	WQ4	295.42	0.089	8
p(PERIOD)ψ(DEPTH × PERIOD + DO SI)	WQ5	295.77	0.074	8
p(PERIOD)ψ(DEPTH × PERIOD + DO)	WQ6	296.37	0.055	8
p(PERIOD)ψ(DEPTH × PERIOD + PH SI)	WQ7	296.45	0.053	8
p(PERIOD)ψ(DEPTH × PERIOD + SI)	WQ8	296.53	0.051	8
p(SUB + PERIOD)ψ(SUB + PERIOD)	GLOBAL	346.57	0.000	36

likely to occupy sites with small substrates or submerged vegetation (Table 4). Sites also had a higher probability of being occupied in 2004 than 2005 (Table 4). Southern sites were more likely to be occupied than northern sites. However, the low rank of model H10 (Table 3), which includes a period × area interaction for occupancy, implies that a north to south migration did not occur, as would be expected if age-0 suckers moved in the direction of predominant lake currents along the eastern shore (Wood et al. 2006). With the exception of depth, 95% CIs for all physical habitat ORs included 1.0, indicating that these differences were not strongly supported with our available sample sizes (Tables 4).

Water Quality Models

The reduced data set used to evaluate water quality characteristics fit our global model poorly (Pearson's chi-square goodness-of-fit test: $P = 0.03$, df = 18). A $\hat{c}$ of 1.69 was estimated and used to adjust model rankings. With the exception of the global model, all water quality models fell within the confidence set (Table 5). When fit to the water quality subset of data, the top physical habitat model ranked third (WQ3; Table 5). The first- and second-ranked water quality models (WQ1 and WQ2; Table 5) contained parameters for mean temperature and mean pH and carried a combined 47.4% of model weights. The top-ranked model, which contained a parameter for temperature, fit the water quality data set 2.31 times better than the second model, which contained a parameter for pH. A model that used mean pH to predict occupancy (WQ2) fit the data 3.01 times better than a model that used the pH SI (WQ7; Table 5). In contrast, model WQ5, which included the DO SI as an occupancy variable, fit the water quality data 1.35 times better than model WQ6, which contained mean DO as a water quality variable. A model that included the three-metric SI ranked eighth, contained only 5.1% of the total water quality model weights, and provided a 6.53 times poorer fit to the data than the top-ranked model (Table 5). Odds ratios suggested that age-0 suckers were more likely to occupy areas with warmer temperatures, higher pH, and higher DO concentrations than elsewhere (Table 6). However, 95% CIs for all water quality ORs included 1.0, indicating that these differences were not strongly supported with our available sample sizes (Table 6).

Discussion

We demonstrated the utility of patch occupancy methods for estimating habitat use by two endangered

TABLE 6.—Estimates of covariate effect size (β) and standard errors (SEs) from logistic regression, odds ratios, and 95% confidence limits (CLs). Odds ratios greater than 1.0 indicate an increase in probability that age-0 suckers will occupy a site with a 1.0-unit increase in the given variable. Variables are listed from the best- to poorest-fitting models according to the quasilikelihood Akaike information criterion adjusted for small sample size (Table 5). Values are given for mean temperature (TEMP), mean dissolved oxygen (DO), mean pH (PH), stress indices (SIs) for dissolved oxygen (DO SI) and pH (PH SI), and a three-metric SI based on DO, TEMP, and PH. The β-value was not estimable for the temperature stress index.

	β			Odds ratio CLs	
Parameter	Estimate	SE	Odds ratio	Lower	Upper
TEMP	0.11	0.08	1.12	0.97	1.30
PH	0.21	0.14	1.23	0.95	1.61
DO SI	0.51	1.19	1.66	0.16	17.22
DO	0.02	0.03	1.02	0.95	1.09
PH SI	−0.06	0.30	0.94	0.52	1.69
SI	0.00	0.15	1.00	0.74	1.35

species of fish. The advantage of this method is the ability to separate true absences of species from false absences caused by incomplete detection, which can be a substantial problem in fisheries (Bayley and Peterson 2001; Peterson et al. 2004). Lack of significant ORs for features other than water depth may indicate that age-0 suckers use a wide variety of habitats or may have resulted from combining the analysis across three sucker species that use habitats with different characteristics. Lack of significant effects may also be an artifact of small sample sizes, because when data are sparse, AIC favors models with fewer parameters. Therefore, low ranking but highly parameterized models may still have some value in determining site occupancy by age-0 suckers. We believe some of these nonsignificant effects may still be biologically relevant and thus are worth reporting.

Major violations of assumptions were unlikely to have occurred in our study. The assumption that no fish were falsely identified as age-0 suckers is supported by subsamples that were preserved and later identified to species and by examination of weekly length frequency distributions for all suckers captured. In subsamples, 100% of fish identified as suckers in the field were verified as catostomids in the laboratory. Bimodal distributions in weekly length histograms strongly suggest that age-0 fish were correctly classified throughout the prepeak and peak periods; however, age distinctions based on length became slightly less clear in the postpeak period. Our use of passive sampling gear insured that detections were independent among sites sampled on the same day. Occasionally, 50-m bands of shoreline were visited multiple times and were considered as separate sites in our analysis. This could violate the assumption of independent sample sites, especially if age-0 suckers tended to remain in one location. Estimated $\hat{c}$-values of 1.07 for physical habitat data and 1.69 for water quality data, however, suggest that the independence assumption was violated rarely if at all.

We only collected two samples at each site (nets facing away from and toward the shore). MacKenzie et al. (2002) found that when only two samples are collected per site, estimates of occupancy are accurate when detection probability is at least 0.5. When detection probability is less than 0.5, the probability of occupancy tends to be overestimated if true occupancy rates are low ($\leq$0.7) and underestimated if true occupancy rates are high ($\geq$0.9; MacKenzie et al. 2002). Therefore, during peak and postpeak periods in both years when detection was 0.49, our estimates of occupancy can be considered relatively unbiased. We may have overestimated occupancy, however, during prepeak periods in each year, when detection was 0.40.

Physical Habitat

Our results show that time period was a primary factor in estimating site occupancy and suggest that age-0 sucker abundance within the gear-selected size range affected the proportion of available habitat that was occupied. Higher occupancy rates estimated for peak periods corresponded to high nearshore catch rates in August and were followed by declines in early September, mirroring a well-established trend (Terwilliger et al. 2004). The results suggest that when more age-0 suckers are present in nearshore areas, more habitats are occupied (rather than higher fish densities being concentrated only in selected habitats).

Age-0 suckers were more likely to be found in shallow habitats during prepeak and postpeak periods than during peak periods in both 2004 and 2005. The use of shallow nearshore habitats by age-0 Lost River suckers was also observed by Buettner and Scoppettone (1990), who primarily caught these fish in water depths less than 0.5 m but did not note seasonal differences in catch rate. One explanation is that age-0 suckers move to deeper offshore habitats in midsummer after undergoing an ontogenetic shift in diet related to attainment of a size threshold (~20–30 mm SL) that makes them less vulnerable to predation by other fishes (Markle and Clauson 2006). In contrast, our results suggest that a late-summer offshore migration did not occur in 2004 or 2005, as age-0 suckers were more likely to occupy shallower (thus, nearshore) than deeper habitats during this period within the range of depths sampled (0.4–3.0 m).

Sites with submerged and emergent aquatic vegetation were more likely to be occupied by age-0 suckers than sites with no vegetation (Table 4). Age-0 suckers may concentrate in and around vegetation due to greater food availability; however, it seems unlikely food is a limiting factor in hypereutrophic Upper Klamath Lake. Vegetation may also provide places to hide from predators (e.g., yellow perch) or may provide refuge from wind-induced wave action. It is possible that water quality is better in highly vegetated areas; however, this hypothesis has not been tested in Upper Klamath Lake. Reiser et al. (2001) also identified vegetation as an important habitat characteristic for age-0 suckers. In contrast, Buettner and Scoppettone (1990), who used dip nets and beach seines, reported that juvenile suckers did not use vegetated areas. It is, however, possible that their gear was ineffective in the dense vegetation present in Upper Klamath Lake. This problem was reported by Reiser et al. (2001), who sampled the vegetation in Upper Klamath Lake using a beach seine and found that nets would snag and

become clogged with debris and the leadline would rise up over vegetation, allowing fish to escape.

Age-0 suckers in our study occupied sites with fines, sand, and gravel more frequently than sites with intermix, cobble, or boulder substrates (Table 4). Our findings support observations by Buettner and Scoppettone (1990), who captured juvenile Lost River suckers primarily over sand and mud. In cast-net surveys, Terwilliger et al. (2004) caught age-0 suckers more frequently over larger substrates, such as gravel and cobble. Small substrates in the lake, however, tend to be associated with vegetation, which was avoided by Terwilliger et al. (2004) because of the propensity for vegetation to clog nets. The higher probability for age-0 suckers to occupy sites with smaller substrates may be due to the high occurrence of vegetation at these sites. Another possibility is that food resources for 30–70-mm SL suckers, which primarily eat benthic invertebrates and crustaceans (Markle and Clauson 2006), may be greater in areas of small substrate. As mentioned previously, however, we believe that food is not a limiting resource in Upper Klamath Lake.

Dynamic habitat use by age-0 suckers may be partially explained by interactions with nonsucker species, such as fathead minnow, juvenile tui chub, juvenile blue chub, and juvenile yellow perch. Interactions among species, however, were not obvious from our data. The nearly ubiquitous distributions and seasonal trends in catch rate made incorporation of nonsucker species into patch occupancy models inappropriate. Because the resource use by sucker and nonsucker species probably coincides, species co-occurrence patterns may be more appropriately examined with another type of multivariate analysis.

Detection Probability

Low detection probability in prepeak periods in both years suggests that age-0 suckers were too small to be fully recruited to our nets during these periods. Larval suckers rear in nearshore habitats of Upper Klamath Lake (Cooperman and Markle 2003) and would be present but not susceptible to our gear until reaching approximately 30–40 mm SL. Therefore, occupancy estimates only apply to suckers large enough to be captured by our nets. Failing to account for seasonal heterogeneity in detection probability would have led us to overestimate occupancy during peak catch periods and underestimate it during pre- and postpeak periods in both years.

As shown by ORs, the probability of detecting age-0 suckers in fyke nets was negatively correlated with depth within the sampled range (0.4–3.0 m). Detection probability increases with localized abundance (Royle and Nichols 2003); therefore, it is possible this result is an artifact of a higher abundance or density of age-0 suckers in shallow water. Another explanation is that fyke nets are less effective in deeper water. Thus, the effect of depth on detection probability may reflect a shortcoming of our chosen gear. Our ability to detect age-0 suckers, however, was not significantly influenced by vegetation, year, water temperature, net soak time, net size, net mouth orientation, or substrate, which may bias other gear types commonly used to capture juvenile suckers in Upper Klamath Lake (Rozas and Minello 1997). Accounting for incomplete detection in probabilistic models is an advantage to using a patch occupancy approach. If we had not adjusted for differential detection probabilities by depth, estimates of occupancy would be erroneously low in deeper water.

Water Quality

We were unable to detect significant effects of water quality on site occupancy, probably because data were insufficient or the range of values observed was too small to produce an effect. Water quality at our sample sites was generally within the acceptable range for juvenile suckers, and extremes were rare except in pH. Relatively narrow ranges in DO and temperature values may have limited our ability to detect significant effects of these variables on age-0 sucker habitat use. Our temporal resolution may also have been too coarse to detect changes in age-0 sucker habitat use. Despite the imprecise effects suggested by our water quality ORs, they are biologically interesting and deserve attention here and in future studies.

Odds ratios for mean temperature imply that age-0 suckers were slightly more likely to occupy sites with warmer water (Table 6). The effect of temperature on site occupancy may be confounded with depth, because shallower areas of Upper Klamath Lake tend to warm faster than deep areas. Maximum mean daily water temperature coincided with peak CPUE in both years. Therefore, the effect of temperature on the percentage of occupied sites as seen in our results could be attributed to seasonal increases in abundance.

We found that age-0 suckers were slightly less likely to inhabit sites with lower mean daily DO concentrations or higher DO SI values. Telemetry studies in Upper Klamath Lake have shown that adult Lost River and shortnose suckers move out of areas with low DO (<2 mg/L; B. Adams, USGS, personal communication). Our results suggest that age-0 suckers are also able to avoid areas with low DO concentrations. These findings also agree with observations by Buettner and Scoppettone (1990) and Terwilliger et al. (2004), who captured fewer juvenile suckers in nearshore areas when DO concentrations were low. Loftus (2001)

determined that DO concentrations below 6 mg/L would invoke a low-level stress response and that concentrations below 4 mg/L would cause adverse sublethal effects in Lost River and shortnose suckers.

Site occupancy rates increased slightly with daily mean pH. However, a model containing the pH SI (WQ7; Table 3), which scales values between 0 and 1 based on known stress responses to higher levels of pH, performed poorly due to a lack of contrast in the data (Table 5). In Upper Klamath Lake, pH and DO are positively correlated as a result of increased photosynthetic activity by massive blooms of *A. flos-aquae* (Wood et al. 2006). Therefore, it is not surprising that age-0 suckers are using areas with moderately high levels of pH, as these areas also have higher DO levels. Buettner and Scoppettone (1990) reported that juvenile Lost River suckers were rare in samples when pH was greater than 9.0; however, they collected few samples when pH was in this range.

Summary

By separating heterogeneity in detection from habitat use, we clearly demonstrated that age-0 suckers use shallow nearshore areas more than deeper habitats. With less certainty, we showed the importance of other factors in the determination of site occupancy, such as small substrate, presence of submerged or emergent vegetation, and good water quality. Ongoing and planned restoration of shallow nearshore areas with small substrate and emergent vegetation in Upper Klamath Lake should benefit Lost River and shortnose suckers by increasing the quantity and quality of juvenile rearing habitat. Our results indicate that age-0 suckers occupy open-water, deepwater-wetland, and emergent-vegetation habitats, which are the focus of restoration efforts by government agencies and The Nature Conservancy in the northern portion of Upper Klamath Lake. Furthermore, management of water resources in Upper Klamath Lake that promote access to marsh habitats during peak age-0 sucker rearing periods should be beneficial to these species.

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