Wetlands (2020) 40:2097–2108
https://doi.org/10.1007/s13157-020-01364-8

CONSTRUCTED WETLANDS

# Do Existing Constructed Ponds on Pelee Island, Ontario Match the Habitat Requirements of Endangered *Ambystoma* Larvae?

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Received: 15 May 2020 / Accepted: 13 August 2020 / Published online: 5 September 2020

## Abstract

Global loss of wetlands has significantly reduced the habitat available for amphibians. Various organizations now regularly construct wetlands to provide areas for amphibian reproduction and larval development. To support wetland taxa, including federally-endangered salamanders, numerous ponds have been constructed in Southern Ontario. We examine natural and constructed ponds to address three questions: 1) What environmental variables govern the presence of salamander larvae in ponds?, 2) What environmental variables predict relative abundance of salamander larvae?, and 3) Do constructed ponds match the habitat needs for salamander larvae as observed in natural ponds? Presence of larvae was associated with high canopy cover and crayfish burrow presence, whereas catch-per-unit-effort increased with the amount of leaf litter in the substrate and presence of submergent vegetation. Constructed ponds had less canopy cover, less leaf litter in the substrate, warmer water, and fewer contained submergent vegetation. Larvae were caught in only 33% of constructed ponds, and catch-per-unit-effort was ~4-10x lower than in natural ponds. Constructed ponds on Pelee Island therefore require additional restoration support or naturalization before they are of substantial conservation value to salamanders. Protecting natural breeding sites remains critical for amphibian conservation, as created ponds may not adequately alleviate the loss of this habitat.

**Keywords** Amphibians · Habitat creation · Habitat suitability · Salamanders · Species-at-risk · Vernal pools

## Introduction

A wide range of taxa have been negatively impacted by habitat loss (e.g., Gaston et al. 2003; Gibbons et al. 2000; Meyer et al. 2010), but the impact on amphibians has been particularly widespread and severe (Wood et al. 2003; Cushman 2006; Gallant et al. 2007). In part, amphibians are vulnerable because their biphasic life history requires both aquatic and terrestrial habitat (Hanken et al. 1997; Becker et al. 2007). Wetlands and vernal pools are essential for many amphibians because they provide places to breed, places for their larvae to develop, refugia from terrestrial predators, and important non-breeding habitat (Porej and Hetherington 2005; Gorman et al. 2009; Ryan and Calhoun 2014). Despite their ecological importance (Gibbs 2000), the decline in pond and wetland habitat is ongoing (Wood et al. 2003; Watmough and Schmoll 2007; Davidson 2013). Southern Ontario, Canada, offers an extreme example, with a more than 72% reduction in wetland coverage over the last 150 years, and where net loss continues today (Ducks Unlimited Canada 2010; Environmental Commissioner of Ontario 2018).

In an effort to mitigate wetland loss, restoration actions have increasingly turned to the construction of new vernal pools, ponds, and wetlands (Mitsch and Wilson 1996; Calhoun et al. 2014). The primary goal of pond and wetland creation is to increase the amount of suitable habitat available for wetland biota, often with an interest in preserving amphibian populations (Pechmann et al. 2001; Rannap et al. 2009; Calhoun et al. 2014). Yet, our capacity for designing and creating new wetland habitat for imperilled amphibians relies on our ability to replicate core characteristics of their natural habitat (Zedler 1998). Unfortunately, long-term monitoring of created wetlands is typically lacking. The research results that

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**Electronic supplementary material** The online version of this article (https://doi.org/10.1007/s13157-020-01364-8) contains supplementary material, which is available to authorized users.

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are available have indicated that created wetlands often do not effectively replace lost habitat (e.g., Mitsch and Wilson 1996; Turner et al. 2001; Vasconcelos and Calhoun 2006; Kihslinger 2008). The contribution of constructed ponds to supporting imperilled, pond-breeding amphibians therefore remains unclear.

In addition to attaining habitat use by target species, created ponds should be designed to effectively support amphibian populations by facilitating sustainable levels of recruitment (Calhoun et al. 2014). Patterns of use and relative abundance at potential amphibian breeding sites are determined both by environmental conditions, such as canopy cover and pond-surface area (Skelly et al. 1999; Werner et al. 2007a; Felix et al. 2010; Ousterhout et al. 2015), as well as a range of biotic interactions, including interspecific competition and predator-prey dynamics (e.g., Wellborn et al. 1996; Porej and Hetherington 2005). Many amphibians also require aquatic habitats with vernal hydroperiods (Semlitsch 1987a and b; Ryan 2007, Chandler et al. 2017), and other landscape-level environmental features can dictate patterns of occupancy (e.g., Lehtinen et al. 1999, Werner et al. 2007b; Groff et al. 2017). Mechanistically, differences in use and recruitment between natural and created ponds should therefore reflect the extent to which they differ in habitat suitability. We should also expect created ponds to generally support a lower abundance of developing amphibian larvae when they fail to effectively replicate the environmental characteristics of natural ponds (Turner et al. 2001; Lichko and Calhoun 2003; Moreno-Mateos et al. 2012). Identifying how existing natural and created ponds differ in these dimensions is key to directing efforts to improve created habitats.

Constructing ponds that are likely to have significant conservation value requires a thorough understanding of the ecology and life history requirements of the species that restoration efforts seek to assist (Zedler 1998). One group that stands to benefit significantly from well-designed constructed ponds is *Ambystoma* salamanders (COSEWIC 2014; Linton et al. 2018; Hossie 2018). Previous research has highlighted a number of variables that influence *Ambystoma* occupancy and relative abundance in their aquatic habitat. These include high canopy cover (Peterman et al. 2014), the presence of aquatic vegetation (Thompson et al. 1980; Bartlet et al. 2011; Groff et al. 2017), as well as characteristics of the pond substrate that can influence prey abundance (Dodson and Dodson 1971) and provide refugia to escape predation (Thompson et al. 1980). Presence of fish or crayfish can negatively impact habitat suitability and relative abundance because they rapidly consume *Ambystoma* eggs and developing larvae (Semlitsch 1987a and b; Ireland 1989; Porej and Hetherington 2005). Alternatively, terrestrial crayfish presence may facilitate colonization or recruitment of new ponds through the provisioning of burrows around the ponds that can act as terrestrial retreats for adult or juvenile salamanders (Williams 1973; Regosin et al. 2003; Owen and Juterbock 2013). Additional variables such as pond temperature (Thompson et al. 1980) and proximity to forest (Felix et al. 2010) are also known to influence patterns of occupancy of potential breeding sites (see also: Bartelt et al. 2011; Cosentino and Brubaker 2018).

Our study sought to answer three related questions: 1) What environmental variables influence the presence of *Ambystoma* salamander larvae at potential breeding sites?, 2) What environmental variables predict the relative abundance of developing larvae?, and 3) Do existing constructed ponds adequately match the habitat requirements for *Ambystoma* larvae as observed in natural ponds? We investigated these questions by surveying natural and created ponds across Pelee Island, Ontario. We hypothesized that the presence of *Ambystoma* salamander larvae at potential breeding sites would be influenced by a combination of biotic (i.e., fish presence, crayfish presence, canopy cover, presence of submergent vegetation, amount of leaf litter in the substrate) and abiotic (water temperature, pond surface area, pond maximum depth, proximity to forest edge) environmental factors. Further we hypothesized that the environmental variables which predict the presence of larvae would also predict their relative abundance, and that the existing constructed ponds would poorly match the environmental requirements for *Ambystoma* larvae habitat as observed in natural ponds.

## Methods

### Study System

Pelee Island, Ontario is home to an endangered *Ambystoma* salamander complex, which includes Canada's only population of small-mouthed salamanders (*A. texanum*), blue-spotted salamanders (*A. laterale*), and unisexual *Ambystoma* (small-mouthed salamander dependent population) salamanders (COSEWIC 2014; COSEWIC 2016; Hossie 2018). In the mid-1880s more than 20 km$^2$ of wetlands (nearly half of the island) was drained for conversion to farmland, and since then additional wetland habitat has been lost (Hossie 2018). Consequentially, small-mouthed salamanders, and the associated unisexual salamanders, have been listed as *Endangered* in Canada by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC 2016) and within Ontario by Committee on the Status of Species at Risk in Ontario (COSSARO 2016) and under Ontario's Endangered Species Act (Hossie 2018; NatureServe 2020). Over the last decade, however, several new ponds have been constructed on the island in an attempt to restore habitat and protect rare biota. Ecosystem-centered habitat remediation efforts began over a decade ago, and are ongoing, but have included the creation of vernal pools, semi-permanent ponds, and larger wetlands, thereby creating potential breeding sites for *Ambystoma* salamanders across the island. Salamanders on the island currently use both natural and constructed ponds for reproduction, but substantial variation in pond use and relative abundance of developing larvae suggests that not all sites are equally suitable. We therefore examined natural and constructed ponds distributed across the island. We divided potential breeding ponds on Pelee Island into two categories: natural ponds (i.e., naturally occurring vernal pools, semi-permeant ponds, and wetlands) and constructed ponds (i.e., ponds created by private landowners or conservation groups to provide habitat for wetland taxa including amphibians). Constructed ponds ranged in age from 1 to 15 years old at the time of our study. Two abandoned agricultural lands have ponds that were initially dug for livestock watering and are filled by artesian wells, but have subsequently naturalized and now act as established breeding ponds for *Ambystoma* salamanders. These ponds were > 50 years old at the time of our study and completely dry by late summer in most years. For our purposes, we consider these two ponds alongside our natural ponds as additional reference sites that currently meet the habitat requirements to sustain viable populations. Ponds were located on a variety of land tenures, however, in all cases written permission was secured from landowners prior to our surveys. On Pelee Island, unisexual *Ambystoma* (i.e., the “small-mouthed salamander dependent population”) possess nuclear DNA from both *A. laterale* and *A. texanum*, co-occur with either or both *A. texanum* and *A. laterale* at all sites, and represent ~95% of all *Ambystoma* salamanders on the island (Hossie 2018).

## Sampling Design

We sampled 32 ponds between May 27 and June 3, 2019 for salamander larvae. Eight of these ponds were natural and 24 were constructed ponds built to support wetland biodiversity. Natural and constructed ponds were distributed across the island, but for data sensitivity reasons specific locations cannot be provided here. Ponds were dispersed across the island, and we sought to include natural and constructed pond types from each area of the island to avoid problems with spatial autocorrelation. Of the eight natural ponds, four were from the northern half of the island and four were from the southern half; six were on the eastern half of the island and two were from the western side. Of the 24 constructed ponds, 16 were in the northern half of the island and eight were in the southern half; 10 were on the eastern half and 14 were on the western side. We tested for spatial autocorrelation in our data using permutation tests for Moran’s I statistic with 1000 simulations and found no evidence of spatial autocorrelation in pond type (see Electronic Supplementary Material).

All ponds were sampled for *Ambystoma* larvae using a systematic dip-net approach consisting of 80 sweeps per pond using Ward’s® Aquatic D Frame Net (1200-μm mesh). In this population, salamanders breed in the last two weeks of March and larvae were ~ 33.4 mm in total length (range: 12.6 to 58.0 mm) at the time of our surveys. Two surveyors conducted the dip-net surveys in each pond by conducting 40-sweeps each, seeking to sample the entire pond area and all microhabitat types. For each sweep, D-shaped nets were held at arm’s length in front of each surveyor and run along the bottom of the pond. All captured larvae were collected, and total number of larvae collected after 80 sweeps was recorded. This was converted to catch per unit effort (CPUE: total number of individual larvae caught / number of sweeps). We visited each pond only once and were therefore unable to explicitly account for imperfect detection of salamander larvae. However, in our experience, this approach is a reliable indicator of salamander larva presence and relative abundance (see also Van Buskirk 2005). Maximum depth of each pond was estimated to the nearest 5 cm before leaving the pond. Google Earth was used to estimate proximity to the nearest forest edge and pond-surface area. In some cases, ponds did not show up on Google Earth imagery (e.g., because they were too new), and in such cases we estimated surface area of the ponds by measuring length, width, and perimeter of each using a measuring tape in the field. Specifically, length and width were used to estimate perimeter of a rectangle and an oval. We then estimated surface area assuming the shape which had an estimated perimeter that most closely matched the measured perimeter.

At each pond we measured a number of abiotic and biotic characteristics. Canopy cover was estimated at each of four points along the perimeter of the pond (i.e., by taking four readings at each of the four cardinal points around the pond) using a convex spherical crown densiometer (Jennings et al. 1999*).* We then averaged these values to estimate the mean canopy cover for the pond perimeter. We measured temperature using both a Hoskin Scientific pH Meter and an ExStik II dissolved oxygen meter (ExTech Instruments®), and then calculated an average from these readings. These were consistently recorded within 1 m of the pond edge, just below the water surface. Given that pond temperature fluctuates over time and ponds were sampled at different times of day, we applied a correction to standardize temperature values (see Electronic Supplementary Material). This point sample for temperature is admittedly coarse, but we contend that following standardization it reflects the broad differences across ponds. Point samples for dissolved oxygen (mg/l), pH, and total dissolved solids (ppm) were recorded but not included in our analyses because all readings fell within the broad range of suitable conditions for *Ambystoma* larvae (Shrode 1972; Pierce and Wooten 1992; Sacerdote and King 2009, Table 1). Presence of crayfish burrows around the pond margin was assessed by two personnel walking the perimeter of the pond to visually encounter burrows up to ~5 m from the pond margin and recorded as present

**Table 1** Median and range of environmental variables for 32 ponds sampled on Pelee Island, Ontario between May 27 and June 3, 2019. Data is summarized to facilitate comparison between natural vs. constructed ponds vs. all ponds where *Ambystoma* larvae were detected. Water temperature values have been standardized to reflect water temperature at noon

| Environmental Variable | Natural Ponds $n = 8$ | Constructed Ponds $n = 24$ | Occupied Ponds $n = 15$ |
|---|---|---|---|
| Larval CPUE (larvae / sweep) | Median: 0.53 | Median: 0.00 | Median:0.43 |
| | Range: 0.00–1.05 | Range: 0.00–0.44 | Range: 0.01–1.05 |
| Pond Surface Area ($m^2$) | Median: 1396 | Median: 44.69 | Median: 197 |
| | Range: 166–11,930 | Range: 6–10,118 | Range: 1875–11,930 |
| Maximum Pond Depth (m) | Median: 0.75 | Median: 1.00 | Median: 0.90 |
| | Range: 0.40–2.00 | Range: 0.20–2.00 | Range: 0.30–2.00 |
| Canopy Cover (% covered) | Median: 75.7 | Median: 50.7 | Median: 64.74 |
| | Range: 46.7–84.8 | Range: 0.00–13.4 | Range:1.4–85.8 |
| Proximity to Forest Edge (m) | Median: 0.00 | Median: 56 | Median: 0 |
| | Range: 0.00–0.00 | Range: 0.00–259 | Range: 0.00–259 |
| Percent with Fish Present | 0% (0/8) | 12.5% (3/24) | 0% (0/15) |
| Percent with Submergent Vegetation | 87.5% (7/8) | 12.5% (3/24) | 46.7% (7/15) |
| Water Temperature (°C) | Median: 19.04 | Median: 20.38 | Median: 19.76 |
| | Range: 11.28–21.54 | Range:16.03–26.08 | Range: 11.38–21.54 |
| Percent with Crayfish Present | 75% (6/8) | 50% (12/24) | 80% (12/15) |
| Substrate* | 0: 0 ponds (0%) | 0: 6 ponds (25.0%) | 0: 0 ponds (0%) |
| | 1: 1 pond (12.5%) | 1: 14 ponds (58.3%) | 1: 6 ponds (40.0%) |
| | 2: 7 ponds (87.5%) | 2: 4 ponds (16.7%) | 2: 9 ponds (60.0%) |
| pH | Median: 7.5 | Median: 7.7 | Median: 7.5 |
| | Range: 7.1–7.8 | Range: 7.1–8.3 | Range: 7.1–8.1 |
| Dissolved Oxygen (mg/l) | Median: 2.6 | Median: 5.3 | Median: 4.0 |
| | Range: 1.1–7.5 | Range: 1.8–10.1 | Range: 1.0–9.7 |
| Total Dissolved Solids (ppm) | Median: 287 | Median: 174 | Median: 222 |
| | Range: 147–417 | Range: 76–321 | Range: 123–417 |

*Substrate: 0 = bare clay, 1 = some leaf litter, 2 = complete layer of leaf litter covering pond bottom

/ absent. Presence of submergent aquatic vegetation was also recorded as a binary variable. Presence of fish was determined during the dip-netting surveys. If no fish were caught or observed while dip-netting, we scored the pond as fish-free. The amount of leaf litter in the pond substrate was recorded on a scale of 0 to 2 (0 = pond bottom is bare, no leaf litter present; 1 = some woodland detritus [leaf litter, sticks, etc.], but parts of the pond bottom are still visible; 2 = pond floor completely covered in a layer of woodland detritus [leaf litter, sticks, etc.]).

## Statistical Analysis

To assess the predictive power of environmental variables on presence and abundance of *Ambystoma* larvae, we began by examining the correlations between each pair of predictors using the *cor* function in R to test for collinearity among our predictors ($r \geq 0.70$). We found that *canopy cover* and *substrate* were strongly correlated ($r = 0.71$) and we therefore did not include *canopy cover* and *substrate* together in the same model when determining the predictors of presence or abundance. Prior to analysis we centered and scaled our predictor variables by the standard deviation using the *scale* function in R to facilitate direct comparison of predictors.

To determine the environmental variables that best predicted presence of *Ambystoma* larvae in potential breeding sites, we used a model selection approach to compare logistic regression models with *presence* as our binary response variable (Anderson et al. 2000). Due to the limited number of ponds we were able to sample ($n = 32$), we only considered additive models with up to 2 predictor variables (Harrell et al. 1996; Jenkins and Quintana-Ascencio 2020). All potential combinations of up to two predictors were considered, except for models with correlated predictor variables. In a second set of analyses we similarly used a model selection approach to determine the environmental variables that best predict abundance of larvae in breeding ponds. In this case our response variable, CPUE, was continuous. Therefore we used general linear models. A Shapiro-Wilks Test indicated that the residuals from these models were not normally distributed, so CPUE was square-root transformed to achieve normality of the residuals. As above, we considered all models with up to two predictor variables excluding models with correlated predictor variables ($r \geq 0.70$). For both sets of analyses we included a null model (i.e. intercept only) in the candidate set, and the full candidate set of models is included in our supplement (ESM Table S1, S2). Model fit was assessed using Akaike's Information Criterion (AIC) corrected for small sample sizes (AICc; Burnham and Anderson 2002), calculated with the R package 'MuMIn' (Bartoń 2019). Models within ΔAICc <2 of the best-fit model were considered statistically indistinguishable. The weight of support for each model was estimated using AICc model weights. We further evaluated whether the best-fit model was a significantly better fit than the null model, using a Likelihood Ratio Test (LRT).

A third set of analysis sought to compare the environmental characteristics of natural and constructed ponds. Specifically, we conducted a Principle Component Analysis (PCA) using the package 'FactoMineR' (Lê et al. 2008), including all of the biotic and abiotic environmental predictors listed above. We then extracted principal components (PCs) that explained ≥10% of the variation in the dataset. These PCs were included as response variables in a MANOVA with pond type (i.e., natural vs. constructed) as a categorical predictor. Following a significant value in the MANOVA analysis we conducted univariate ANOVAs on each PC to determine in what ways natural and constructed ponds differ. Welch's *t*-tests were used to compare the CPUE between natural and constructed ponds. All analyses were conducted in R, version 3.6.1 (R Core Team 2019).

## Results

We captured *Ambystoma* salamander larvae in 15 of the 32 (46.9%) ponds we surveyed. Of the 15 ponds where larvae were captured, seven were natural and eight were constructed ponds. Larvae were captured in ponds from all four quadrants of the island (i.e., northeast, northwest, southeast, southwest). CPUE in natural ponds was significantly greater than in constructed ponds (mean (range): natural = 0.583 larvae/sweep (0.000–1.05), constructed = 0.058 larvae/sweep (0.000–0.438); $t = 3.86$, $P = 0.005$, $df = 7.63$; Table 1). Overall, ponds where we captured larvae had a median CPUE of 0.45 larvae/sweep (range: 0.013–1.05). When comparing only those ponds where larvae were captured, natural ponds still had a significantly higher CPUE than constructed ponds (mean (range): natural = 0.666 larvae/sweep (0.225–1.05), constructed = 0.175 larvae/sweep (0.013–0.438); $t = 3.56$, $P = 0.005$, $df = 9.75$).

Natural and constructed ponds had a similar range in surface area, with natural ponds tending to have a larger surface area than constructed ponds (Table 1), and ponds where we captured larvae ranged in surface area from 1875 to 11,930 $m^2$ (median: 197 $m^2$). Maximum pond depth was also similar for the two pond types (Table 1), and ponds with larvae had a maximum depth ranging from 0.30 to 2.00 m (median = 0.90 m). Canopy cover around the pond margin was substantially higher in natural ponds than constructed ponds (Table 1), although canopy cover of ponds with larvae ranged widely (1.4–85.8%, median = 50.7%). Natural ponds were all immediately adjacent to the forest edge, whereas constructed ponds ranged from 0 to 259 m (median = 56 m) from the nearest forest edge. Larvae were captured in the most distant pond we examined (i.e., 259 m from forest edge), but all other ponds where larvae were captured were within ~100 m from the forest edge (Table 1). Fish were detected in three out of 24 (12.5%) constructed ponds, but were not detected in any natural ponds, nor in any ponds where salamander larvae were detected. Submergent vegetation was present in many natural ponds, but few constructed ponds, and was present in roughly half of the ponds where we captured larvae (i.e., 7/15, Table 1). Natural ponds tended to have cooler water temperatures than constructed ponds (by ~1.5 °C), but the water temperature of ponds with larvae ranged widely (range: 11.4–21.5 °C (noon-corrected values); Table 1). Crayfish were present at most of the natural ponds, but only half of the constructed ponds (Table 1). Notably, 80% of the ponds where we captured larvae had crayfish burrows around the pond margin. All natural ponds had some leaf litter present in the substrate, whereas the amount of leaf litter in the substrate of constructed ponds varied greatly (Table 1). Larvae were never captured in ponds lacking leaf litter in the substrate.

The presence of *Ambystoma* larvae in a pond was best predicted by the amount of canopy cover around the pond margin and the presence of crayfish burrows (AICc weight = 0.38, Table 2). The only other model within two AICc units of this model included the amount of leaf litter in the pond substrate and the presence of crayfish burrows (AICc weight = 0.14, Table 2). The similar fit of these models was not surprising given that *canopy cover* and *pond substrate* were positively correlated ($r = 0.71$). Salamander larvae were more likely to be present in ponds that had more canopy cover around their perimeter (Odds Ratio: 0.07 ± 0.03, $z = 2.55$, $P = 0.011$), more leaf litter in the pond substrate (Odds Ratio = 2.63 ± 1.10, $z = 1.10$, $P = 0.017$), and if they had crayfish burrows around the pond margins (Odds Ratio = 3.47 ± 1.64, $z = 2.12$, $P = 0.034$, Fig. 1). The best fit model performed significantly better than the NULL model (ΔAICc = 17.45, LRT: Deviance: -18.58, $P << 0.001$). CPUE was best predicted by the amount of leaf litter in the pond substrate and the presence of submergent vegetation (AICc weight = 0.77, Table 3). This model performed significantly better than the NULL model (ΔAICc = 21.42; LRT: Deviance = 2.19, $P << 0.001$; Table 3). CPUE increased with both the amount of leaf litter in the substrate ($t_{29} = 3.99$,

**Table 2** Summary of the top five models predicting the presence of *Ambystoma* salamander larvae in ponds on Pelee Island, Ontario during surveys between May 27 and June 3, 2019. Null model (intercept-only) also included for comparison

| Ecological Parameters | df | AICc Value | ΔAICc | AICc Weights |
|---|---|---|---|---|
| Canopy Cover + Crayfish Burrow Presence | 3 | 32.51 | 0.00 | 0.375 |
| Substrate + Crayfish Burrow Presence | 3 | 34.48 | 1.97 | 0.140 |
| Submergent Vegetation Presence + Crayfish Burrow Presence | 3 | 35.77 | 3.26 | 0.074 |
| Substrate | 2 | 35.87 | 3.36 | 0.070 |
| Fish Presence + Canopy Cover | 3 | 36.43 | 3.92 | 0.053 |
| NULL* | 1 | 46.37 | 13.86 | 0.000 |

$P < 0.001$), and the presence of submergent vegetation ($t_{30} = 3.08$, $P = 0.005$; Fig. 2). No other models had a ΔAICc value <2 (Table 3).

We found that the top three principal components (PCs) each explained $\geq$10% of the variation in our data set of environmental variables (variance explained: PC1 = 30.6%, PC2 = 19.8%, PC3 = 16.2%; ESM Fig. S1, Table S3). A positive PC1 indicated ponds with high canopy cover around their perimeter, submergent vegetation present, lower pond water temperature, and high levels of leaf litter in the pond substrate (ESM Fig. S1, Table S4). A larger PC2 value primarily reflected ponds with crayfish burrows present, located further from the nearest forest edge, had a greater maximum pond depth, and where fish were absent (ESM Fig. S2, Table S4). A positive PC3 value reflected ponds with greater maximum depth, fish present, large surface area, and little leaf litter in the substrate (ESM Fig. S2, Table S4).

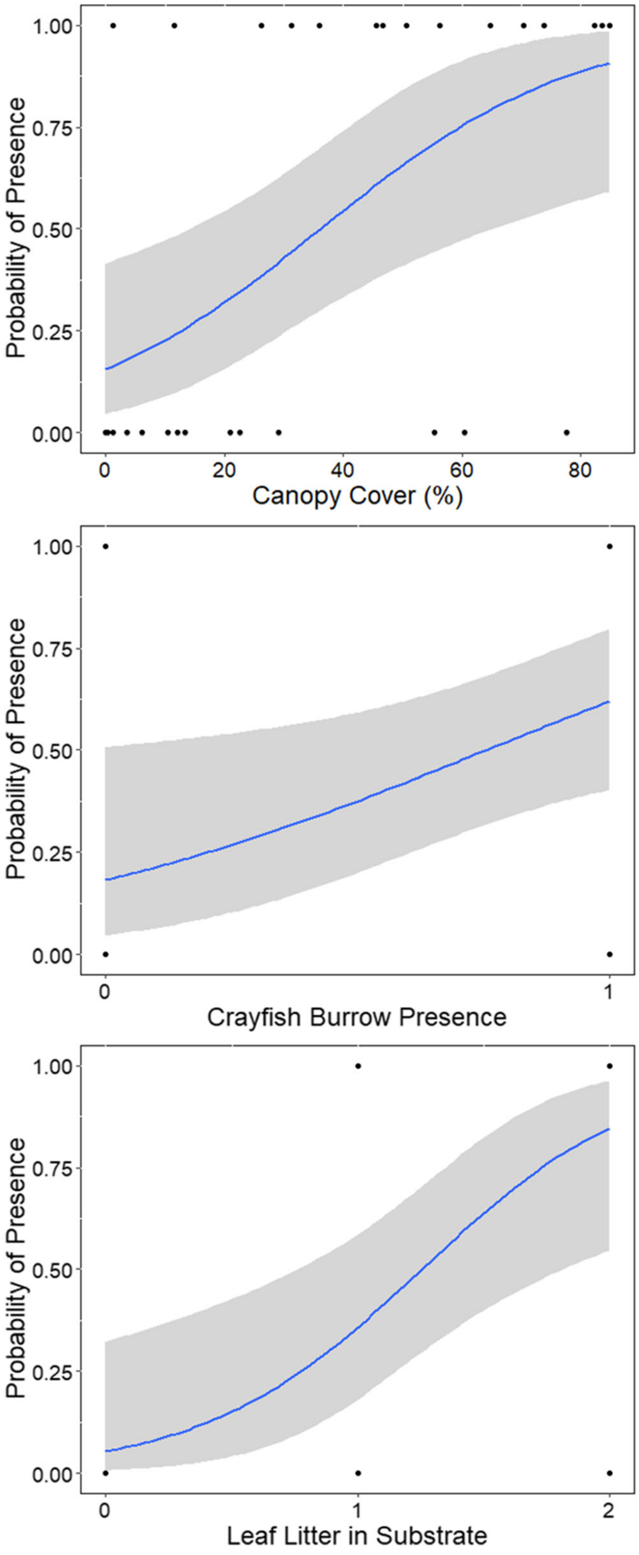
A MANOVA using PC1-PC3 as response variables found a significant effect of pond type ($F_{3,28} = 20.21$, $P << 0.001$). Subsequent univariate ANOVAs found that this effect was driven by a significant effect of pond type on PC1 ($F_{1,30} = 59.68$, $P << 0.001$), indicating that PC1 captured significant variation in environmental conditions between natural and constructed ponds (Fig. 3). Pond type did not have a significant effect on PC2 or PC3 (all $P > 0.49$). We found little evidence of spatial autocorrelation in our data set (ESM Table S5).

## Discussion

In an effort to identify key environmental predictors of *Ambystoma* larvae presence and CPUE, and to determine whether natural and constructed ponds differ in these characteristics, we surveyed natural and constructed ponds across Pelee Island, Ontario. Our analyses indicated that the amount of canopy cover around pond perimeter and the presence of crayfish burrows were the best predictors of pond occupancy by *Ambystoma* larvae, whereas CPUE was best predicted by the amount of leaf litter in the pond substrate and the presence of submergent vegetation. Salamander larvae were never captured in ponds where we detected fish, nor in ponds lacking leaf litter in the pond substrate, but were detected in ponds as far as 259 m away from the nearest forest edge. Larval surveys found that natural ponds had a ~ 4 to 10x higher CPUE of larvae than constructed ponds. Our evaluation of pond characteristics found that, compared to natural ponds, constructed ponds had less canopy cover around the pond margin, had less leaf litter in the pond substrate, were less likely to have submergent vegetation, were smaller in surface area, and had warmer water temperatures. Our study therefore suggests that existing constructed ponds do not currently match the aquatic habitat conditions necessary to be of substantial conservation value to *Ambystoma* salamanders. Below we explore the implications of this, as well as strategies to improve existing constructed ponds.

**Table 3** Summary of the top five models predicting the catch-per-unit-effort (i.e., larvae / dip-net sweep) of *Ambystoma* salamander larvae in ponds on Pelee Island, Ontario during surveys between May 27 and June 3, 2019. Null model (intercept-only) also included for comparison

| Ecological Parameters | df | AICc Value | ΔAICc | AICc Weights |
|---|---|---|---|---|
| Submergent Vegetation Presence + Substrate | 3 | 6.30 | 0.00 | 0.769 |
| Submergent Vegetation Presence + Crayfish Burrow Presence | 3 | 11.91 | 5.61 | 0.047 |
| Substrate | 2 | 12.73 | 6.43 | 0.031 |
| Substrate + Pond Surface Area | 3 | 12.92 | 6.62 | 0.028 |
| Substrate + Proximity to Forest | 3 | 13.32 | 7.02 | 0.023 |
| NULL* | 1 | 27.72 | 21.42 | 0.000 |



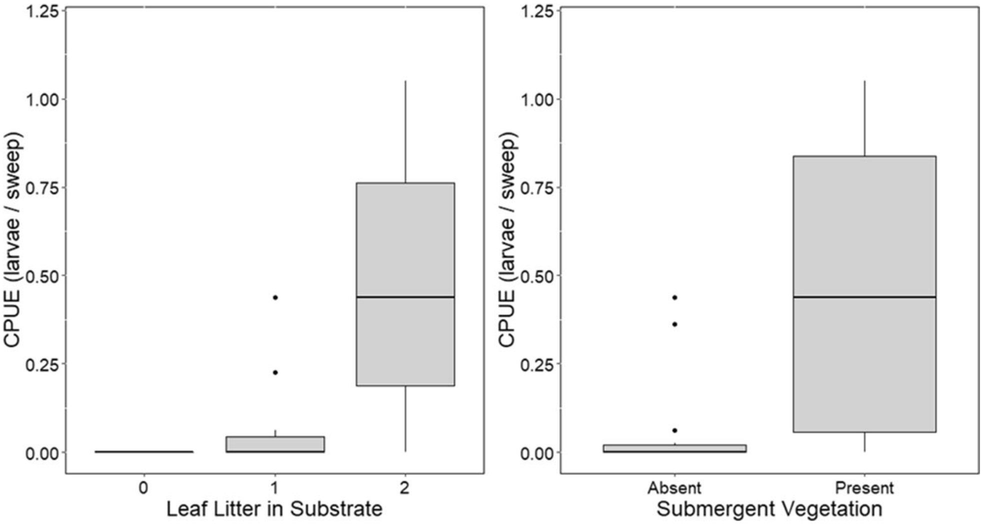
◀ **Fig. 1** Relationship between the probability of *Ambystoma* salamander larva presence and canopy cover around the pond margin (top panel), presence of crayfish burrows around the pond margin (middle panel), and an index of leaf litter in the pond substrate (bottom panel) in potential breeding ponds across Pelee Island, Ontario. For the leaf litter index: 0 = bare (no leaf litter), 1 = some leaf litter (bare patches), 2 = complete layer of leaf litter covering pond bottom. The shaded area around the regression line represents the 95% confidence interval

The probability of a potential breeding site being occupied by *Ambystoma* larvae increased with the amount of canopy cover around the pond margin, which is consistent with previous work (Felix et al. 2010; Peterman et al. 2013; Peterman et al. 2014). Several non-mutually exclusive mechanisms may explain this relationship. First, increased canopy cover might serve to moderate fluctuations in water temperature (Anderson et al. 2015) or to lower average pond-water temperatures (Schiesari 2006), both of which have been found to benefit developing larvae (Moore 1939; Thompson et al. 1980). Consistent with this, we detected a modest negative correlation ($r = -0.63$) between canopy cover and noon-corrected water temperature. Second, dense canopy cover from deciduous trees around the pond margin may improve the pond substrate by increasing the abundance of leaf litter. Indeed, fallen leaf litter provides habitat for *Ambystoma* larvae prey (Dodson and Dodson 1971), as well as refuge for larvae against predators and cannibalistic conspecifics (e.g., Hossie and Murray 2010; Tyler et al. 1998). Finally, adult *Ambystoma* salamanders migrate an average of 125 m during their breeding season (Semlitsch 1998), but often reside much closer to their respective breeding pond. Small-mouthed salamanders, in particular, are thought to remain very close to their breeding pond (i.e., within ~60 m, Parmelee 1993). If the canopy cover along the perimeter of the breeding pond is dense, it may increase pond suitability by providing shelter for migrating adults and/or emerging juvenile *Ambystoma* salamanders from various abiotic stressors (e.g., elevated temperature, low soil moisture).

The presence of larvae in potential breeding ponds was also positively correlated with the presence of crayfish burrows around the pond margin. Terrestrial crayfish are present on Pelee Island and they create ‘chimney’ like burrows in and around various wetlands (Guiasu et al. 1996). *Ambystoma* salamanders regularly use mammal burrows (Madison 1997; Kleeberger and Werner 1983; Douglas and Monroe 1981), and small-mouthed salamanders are known to use crayfish burrows as terrestrial refuges (Williams 1973; Owen and Juterbock 2013). Use of crayfish burrows by adult and juvenile *Ambystoma* salamanders has been observed on Pelee Island (T. Hossie, *personal observation*). One intriguing possibility is that crayfish presence actually increases the suitability of these ponds, or facilitates their colonization, through the creation of burrows. That said, we cannot exclude the possibility that the relationship we observed between larval occupancy and crayfish burrow presence instead simply reflects shared habitat requirements of terrestrial crayfish and *Ambystoma* salamanders on Pelee Island.

The relative abundance of *Ambystoma* larvae appears to be strongly related to pond substrate and the presence of

**Fig. 2** Boxplots depicting the relationship between catch-per-unit-effort (CPUE, larvae / sweep) for *Ambystoma* larvae and an index for the amount of leaf litter in the pond substrate (left), or the presence of submergent vegetation (right) for potential breeding sites across Pelee Island, Ontario. For the leaf litter index: 0 = bare (no leaf litter), 1 = some leaf litter (bare patches), 2 = complete layer of leaf litter covering pond bottom



submergent vegetation. Specifically, CPUE for salamander larvae was greater in ponds with more leaf litter in the substrate, and where submergent vegetation was present. Ponds with abundant leaf litter and submergent vegetation should possess a greater abundance of prey for salamander larvae, which live in and feed on those materials (Dodson and Dodson 1971). Elevated CPUE in ponds with abundant leaf litter and submergent vegetation may therefore reflect increased prey availability. Alternatively, or in addition, higher CPUE in ponds with abundant leaf litter and submergent vegetation could result from the associated increase in structural complexity and refuge habitat for developing larvae (e.g., Kenison et al. 2016). *Ambystoma* face a number of voracious invertebrate predators (e.g., Caldwell et al. 1980; Hossie et al. 2018) and are well known to opportunistically consume other salamander larvae, including conspecifics (Petranka 1998; Wildy et al. 2001). Conspecific aggression (including cannibalism and biting) is often a result of high salamander density and food limitation (Stenhouse et al. 1983; Walls and Jaeger 1987; Wildy et al. 2001). However, structurally complex environments (e.g., ponds with abundant leaf litter and vegetation), may better mitigate the impacts of predation or intraspecific aggression on larval density (Semlitsch 1987a and b; Walls 1995; Tyler et al. 1998). Finally, many *Ambystoma* preferentially oviposit on submergent vegetation and selectively lay their eggs areas where submergent vegetation is denser (e.g., Thompson et al. 1980; Kern et al. 2013). This behaviour minimizes desiccation risk and may also reduce

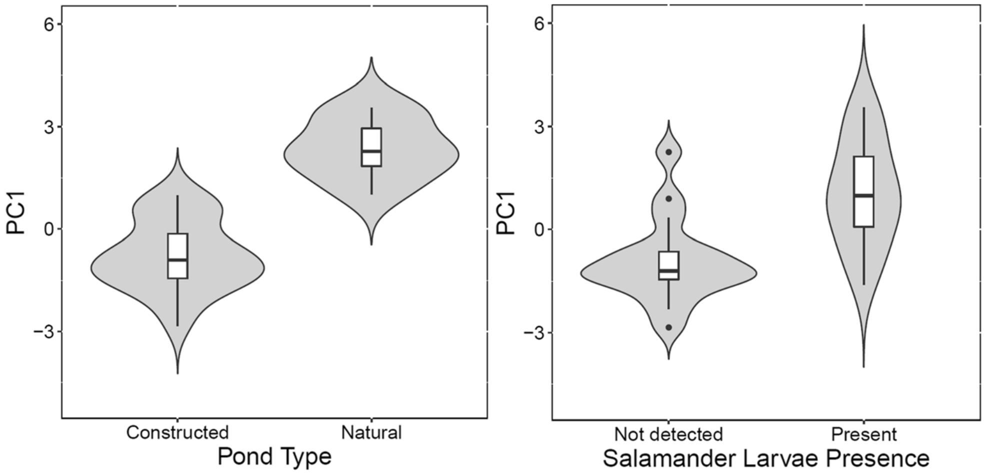


**Fig. 3** Violin plots depicting the relationship between PC1 and pond type (left panel), and presence of *Ambystoma* larvae (right panel) for ponds across Pelee Island, Ontario. A large PC1 reflects ponds with high canopy cover around the pond margin, more leaf litter in the pond substrate, submergent vegetation present, larger pond surface area, and cooler water temperatures. Violin plots depict the probability density of the data across different values and are useful for depicting differences in the observed data distribution across treatments. Nested within each violin plot is a boxplot where the middle line indicates the median, the upper and lower box edges represent the 25th and 75th percentiles, and the whiskers indicate 1.5 × the interquartile range

predation risk in developing embryos (Thompson et al. 1980; Kern et al. 2013). Egg survival may therefore be lower in ponds lacking submergent vegetation.

An important pattern emerging from our results is that different environmental variables predicted salamander larvae presence vs. larval CPUE. Presence of salamander larvae was governed by terrestrial variables (i.e., canopy cover, crayfish burrow presence; Table 2), whereas CPUE was governed by variables from within the ponds (i.e., presence of submergent vegetation, and the mount of leaf litter in the pond substrate; Table 3). One interesting interpretation of this is that factors related to the quality of upland terrestrial habitat promotes the breeding in specific wetlands, whereas the relative abundance of larvae in a pond is related more directly to factors that influence larval survival. If true, this would have important implications for the design and management of constructed wetlands. Van Buskirk (2005) found that both landscape and local factors influenced the occurrence and density of larval amphibians in ponds. The predictive ability of landscape covariates was similarly suggested to reflect the influence of availability of suitable habitat surrounding ponds on patterns of pond occupancy (Van Buskirk 2005). Additional work seeking to disentangle the features and processes that govern occupancy vs. density and recruitment for pond breeding amphibians would assist in the design and management of wetlands constructed to support imperilled species.

Our study found that the natural and constructed ponds we examined differed in the amount of canopy cover around the pond margin, the amount of leaf litter in the pond substrate, pond water temperature, and the presence of submergent vegetation. Specifically, natural ponds had higher canopy cover around their margin, more leaf litter in the substrate, lower water temperature, and larger surface area. They also tended to have submergent vegetation present. Importantly, three of these variables (i.e., canopy cover, leaf litter in the substrate, presence of submergent vegetation) were shown to predict the presence and/or CPUE of *Ambystoma* larvae, highlighting that the habitat provided by natural vs. constructed ponds differ in ways that influence their suitability to *Ambystoma* salamanders. Our results are therefore consistent with previous suggestions that the structural or functional features of constructed ponds are not equivalent to natural ponds (Pechmann et al. 2001; Denton and Richter 2013). That said, these differences may be remedied with time, given that constructed ponds can increase in suitability over a range of 10 to 20 years, occasionally requiring even more time than this (Confer and Niering 1992; Mitsch et al. 2012). With this in mind, constructed ponds should be built in ways that increase the likelihood that they will naturalize into ponds that provide suitable habitat, and may need to be supported by additional restoration efforts over the lengthy naturalization period. It is important to acknowledge this at the outset of pond creation. In addition, many *Ambystoma* salamanders have high fidelity to their breeding ponds (e.g., Zamudio and Wieczorek 2007), and constructed ponds should be built in close proximity to established natural ponds to increase the likelihood of colonization (Patrick et al. 2007; Shulse et al. 2010; Groff et al. 2017).

In conclusion, our study cautions that the construction of new ponds may not functionally replace established natural breeding sites, at least in the short-term. While constructing new ponds may benefit amphibian populations over time (Mitsch et al. 2012), our results warn against the presumption that the loss of natural ponds can be offset by building new ponds. Constructed ponds may remain unsuitable for a considerable amount of time (i.e., 15–20+ years, Mitsch and Wilson 1996), and are therefore unlikely to fully mitigate the immediate loss of natural breeding sites. In a time of ongoing wetland loss and land conversion (Ducks Unlimited Canada 2010; Davidson 2013), it is important to recognize that the construction of new ponds may not compensate for the loss of natural ponds (Turner et al. 2001; Kihslinger 2008). Protection of existing natural breeding sites for amphibians therefore remains imperative, with constructed ponds providing an important supporting role when habitat has already been lost or when conserving existing ponds is impossible (Petranka et al. 2007; Calhoun et al. 2014; Environment Canada 2016). Still, for constructed ponds to provide significant conservation value they must be designed carefully, located within dispersal distance of source populations, and supported by restoration efforts over a suitable period of time to ensure improvements in habitat suitability over time.

**Acknowledgements** The authors thank Species at Risk Stewardship Fund for financial support. G. Smith, and personnel from Scales Nature Park assisted with field work. The Nature Conservancy of Canada, Ontario Parks, Essex Region Conservation Authority, J. Ambrose, D. Kraus, and J. DeMarco provided land access. Research protocols were approved by Trent University Animal Care Committee, Ontario Ministry of Natural Resources and Forestry Wildlife Animal Care Committee. Wildlife Scientific Collector's Authorization No. 1092367. Endangered Species Act Confirmation of Registration ID: M-102-9225853169.

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