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GEOGRAPHIC VARIATION IN LIFE CYCLE STRATEGIES OF A PROGENETIC TREMATODE

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ABSTRACT: Numerous parasite species have evolved complex life cycles with multiple, subsequent hosts. In trematodes, each transmission event in multi-host life cycles selects for various adaptations, one of which is facultative life cycle abbreviation. This typically occurs through progenesis, i.e., precocious maturity and reproduction via self-fertilization within the second intermediate host. Progenesis eliminates the need for the definitive host and facilitates life cycle completion. Adopting a progenetic cycle may be a conditional strategy in response to environmental cues related to low probability of transmission to the definitive host. Here, the effects of environmental factors on the reproductive strategy of the progenetic trematode *Stegodexamene anguillae* were investigated using comparisons among populations. In the 3-host life cycle, *S. anguillae* sexually reproduces within eel definitive hosts, whereas in the progenetic life cycle, *S. anguillae* reproduces by selfing within the metacercaria cyst in tissues of small fish intermediate hosts. Geographic variation was found in the frequency of progenesis, independent of eel abundance. Progenesis was affected by abundance and length of the second intermediate fish host as well as encystment site within the host. The present study is the first to compare life cycle strategies among parasite populations, providing insight into the often unrecognized plasticity in parasite developmental strategies and transmission.

Organisms commonly inhabit variable and unpredictable environments, in which those that have phenotypic plastic traits and are able to adjust their strategies in response to environmental cues should experience increased fitness (West-Eberhard, 2003; Schoeppner and Relyea, 2008). Like free-living organisms, parasites also inhabit an unpredictable world, resulting in differential transmission success and life cycle completion (Fenton and Hudson, 2002). Transmission depends on host availability, which is variable both spatially and temporally (Crossan et al., 2007). Selection could favor parasites with plastic life history traits and abilities to perceive and respond to cues related to host presence and transmission probability (Poulin and Cribb, 2002). Even when hosts are abundant, individual hosts are discrete units dispersed throughout the environment, and thus the probability of a parasite contacting a suitable host is typically low and unpredictable (Fenton and Hudson, 2002; Crossan et al., 2007).

Low, or variable, abundance of the definitive host is most likely the main selective force in the evolution of truncated life cycles (Poulin and Cribb, 2002). Many helminth parasites have dropped the definitive host from their life cycle, making it easier to complete (Poulin and Cribb, 2002; Lefebvre and Poulin, 2005a). For some species, the shortened life cycle has become obligatory, whereas in others it is a facultative strategy with both normal and abbreviated cycles occurring in the same population. In trematodes, facultative life cycle truncation typically occurs via progenesis, i.e., early maturation, in which eggs are produced by self-fertilization within the intermediate host (Poulin, 2001; Poulin and Cribb, 2002). When transmission rates to definitive hosts are low, progenesis should be favored and is viewed as a form of reproductive insurance, i.e., the ability to produce eggs without the risk of finding a mate in an eel's intestine, since eggs should still be released if the progenetic worm is ingested by a definitive host or even a non-host predator (Poulin, 2001; Wang and Thomas, 2002; Lefebvre and Poulin, 2005b).

Progenesis in the trematode *Stegodexamene anguillae* is facultative, with individuals from the same population adopting either 1 of 2 life cycle strategies. Eggs of *S. anguillae* hatch in the aquatic environment and infect freshwater snails, *Potamopyrgus antipodarum*, as first intermediate hosts. Asexual reproduction occurs within the snail host, producing numerous cercariae that leave the snail in search for the second intermediate host, small freshwater fish, mostly *Gobiomorphus* and *Galaxias* spp. (Macfarlane, 1951, 1952). Cercariae actively penetrate the fish and encyst as metacercariae within host tissues, where they await ingestion by a definitive host, either *Anguilla dieffenbachii* (New Zealand longfin eel) or *Anguilla australis* (short-finned eel). Alternatively, some metacercariae grow to larger sizes, mature, and produce eggs through self-fertilization while still within the second intermediate fish host. These eggs, contained inside the parasite's cyst, are released into the environment when the intermediate fish host dies or are expelled with the fish host's eggs when progenetic metacercariae are encysted in the host's gonads (Poulin and Lefebvre, 2006; Herrmann and Poulin, 2011a). Thus, the need for transmission to a definitive host is bypassed in parasites adopting progenesis.

If progenesis is phenotypically plastic, then the frequency of progenesis should be related to the probability of transmission to the definitive host. Several environmental factors affect adoption of alternative transmission routes. *Stegodexamene anguillae* preferentially adopts progenesis based on encystment site within the fish intermediate host and the opportunity for eggs to be released into the environment during host spawning events (Poulin and Lefebvre, 2006; Herrmann and Poulin, 2011a) and in hosts exposed to stressful conditions, which could indicate reduced host longevity and thus lower transmission probability (Herrmann and Poulin, 2011b). Another trematode, *Coitocaecum parvum*, exhibits variation in progenesis depending on genetic relatedness with coinfecting parasites (Lagrue et al., 2009), length of time within the intermediate host (Lagrue and Poulin, 2009), and chemical cues conveying information on availability of definitive hosts (Poulin, 2003; Lagrue and Poulin, 2007).

Thus far, field studies and laboratory experiments on progenetic species have focused on individuals from a single population. However, plasticity of reproductive traits has been found to vary among populations of both free-living and parasitic organisms, especially among populations experiencing different environmental conditions (Seigel and Ford, 2001; Loot et al., 2008). This study investigates, for the first time, the variation in the frequency of progenesis among populations of *S. anguillae* in 1 of its second intermediate host species, *Gobiomorphus cotidianus* (common bully). Two questions are addressed. First, is there any geographic variation in the frequency of progenesis among

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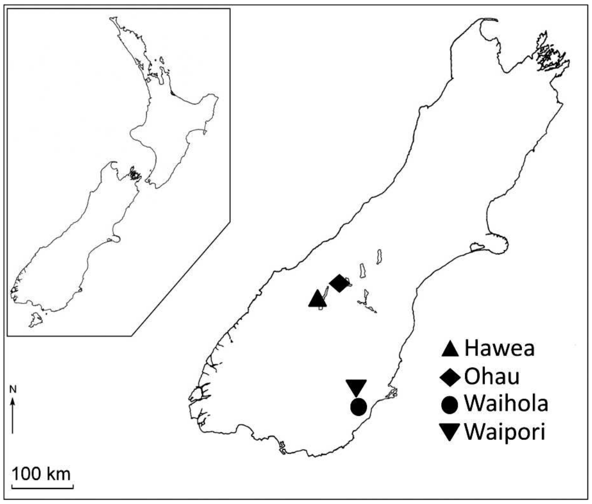

FIGURE 1. Map of the South Island, New Zealand, indicating the 4 sampling sites: Lakes Hawea, Ohau, Waihola, and Waipori.

populations? Second, do other individual- or population-level parameters, such as abundance of *S. anguillae*, worm size, and egg production, also vary among host populations? Altogether, this study is the first to compare the frequency of progenesis among parasite populations and provide insight into the real plasticity of life cycle abbreviation in natural populations.

MATERIALS AND METHODS

Study sites

Four lakes were selected as study sites, all on the South Island, New Zealand (Fig. 1). They were chosen based on published information on eel abundances, with relatively high eel abundances in Lakes Waihola and Waipori, low abundance in Lake Ohau, and intermediate abundance in Lake Hawea (Fig. 1) (Beentjes and Jellyman, 2003; Beentjes et al., 2006). Two lakes, Waihola and Waipori, are shallow, coastal, eutrophic lakes with slightly brackish water due to tidal inflow (Table I) (Schallenberg and Burns, 2003; Schallenberg et al., 2003). Lakes Hawea and Ohau are at higher elevation, have greater surface area, and are deep, oligotrophic lakes (Table I) (Beentjes et al., 1997; Beentjes and Jellyman, 2003). The common bully has been reported as a dominant species in these lakes (Jellyman, 1984; Jeppesen et al., 2000; Kattel and Closs, 2007) and is the main second intermediate host of *S. anguillae* in these lakes. Although 1 site per lake was sampled, similar infection levels have been observed throughout Lake Waihola (R. Poulin, unpubl. obs.); this past observation and the fact that only part of the shore of each lake is accessible justified sampling from a single site per lake.

Animal collection

All lakes were sampled within 1 mo (20 January to 20 February 2010). Relative eel abundance was measured using 2 fyke nets set overnight for 1 night and calculated as number of eels per trap (Chisnall and West, 1996; Jellyman and Graynoth, 2005). Common bullies were captured using 16 unbaited, weighted minnow traps set overnight, with 8 set in a row 1.5–2.0 m from shore, 2 m apart, at an approximate depth of 0.5 m, and 8 set 4.0–4.5 m from shore, 2 m apart, at an approximate depth of 1.0 m. Relative abundance of common bullies was calculated as the number of bullies per trap per hour (He and Lodge, 1990). Fyke nets and minnow traps were set following the same protocol, i.e., same formation in similar habitat, in all 4 lakes to reduce variation in sampling effort among sites. After capture, fish were counted to determine relative abundance among sites, and common bullies longer than 3.2 cm were kept, while others were released. When fewer than 20 bullies were caught in the traps, an electric fishing machine, a seine net, and/or push nets (mesh size 5 mm) were used to obtain a total of 20 fish of the minimum required size. Bullies retained for dissection were killed by an overdose of tricaine methanesulfonate (MS-222) and frozen until dissection. Water temperature was also recorded on each collection.

Measures and statistical analyses

Total length, weight, and sex of each fish were recorded. Fish body condition was determined as W/L^3, where W and L are the weight and

TABLE I. Lake parameters and measurements of hosts and *Stegodexamene anguillae* for the 4 lakes (lake information from Irwin, 1978; Beentjes and Jellyman, 2003; Schallenberg and Burns, 2003; Schallenberg et al., 2003).

	Hawea	Ohau	Waihola	Waipori
Latitude, longitude	44°26′S, 169°12′E	44°10′S, 169°49′E	46°00′S, 170°06′E	45°58′S, 170°07′E
Surface area (km^2)	141	63	6.4	2.2
Mean depth (m)	192	74	1.3	0.5
Max depth (m)	384	129	2.2	1.1
Surface elevation (m)	348	520	16	0
Relative eel abundance	0.5	0	7.5	4.5
Relative bully abundance	0.563	0.012	0.077	0.029
Mean bully length ± SE (cm) (range)	4.8 ± 0.14 (3.6–6.2)	4.3 ± 0.15 (3.2–6.0)	4.9 ± 0.10 (3.9–5.5)	4.5 ± 0.09 (4.0–5.3)
Bully sex ratio (males/females)	1.50	0.82	0.82	2.33
No. *S. anguillae*	1125	544	400	292
S. anguillae mean abundance ± SE (range)	56.3 ± 9.69 (6–162)	27.2 ± 4.07 (2–68)	20.0 ± 4.21 (4–89)	14.6 ± 3.01 (2–50)
S. anguillae mean abundance in gonads ± SE	2.2 ± 0.48	4.5 ± 1.14	5.3 ± 0.79	2.0 ± 0.71
Mean % progenetic ± SE (range)	1.6 ± 0.55 (0–10.0)	5.0 ± 1.72 (0–30.9)	17.1 ± 3.33 (0–50.0)	11.5 ± 2.94 (0–40.0)
Mean worm size (m^2) ± SE (range)	0.15 ± 0.007 (0.01–2.80)	0.41 ± 0.026 (0.01–5.16)	0.43 ± 0.027 (0.01–2.87)	0.31 ± 0.027 (0.01–2.51)
Mean number of eggs ± SE (range)	138.2 ± 33.2 (0–470)	339.5 ± 53.14 (0–1130)	131.2 ± 22.74 (0–560)	176.2 ± 33.89 (0–610)
Mean egg volume (m^3) ± SE	1.2e–04 ± 4.1e–06	1.4e–04 ± 4.5e–06	1.1e–04 ± 3.5e–06	9.9e–05 ± 3.6e–06

TABLE II. The predictor variables included in the global model used for model selection of each response variable. A check mark indicates inclusion in the global model.

Predictor variables	Progenesis	Worm size	No. of eggs	Egg volume
Eel abundance	✓	✓	✓	✓
Bully abundance	✓	✓	✓	✓
Water temperature	✓	✓	✓	✓
Host body condition	✓	✓	✓	✓
Host length	✓	✓	✓	✓
Host sex	✓	✓	✓	✓
Encystment site	✓	✓	✓	✓
Abundance of conspecifics	✓	✓		
Abundance of *Telogaster opisthorchis*	✓	✓		
Abundance of *Apatemon* sp.	✓	✓		
Developmental strategy		✓		
Worm size			✓	✓
No. of eggs expelled				✓

total length (Bolger and Connolly, 1989). Fish were dissected, and all tissues, except the brain and the lumen of the gastrointestinal tract (where metacercariae of *S. anguillae* are never found), were examined for *S. anguillae* as well as other parasite species. All *S. anguillae* metacercariae were individually removed from their cysts and classified as progenetic (eggs present), non-progenetic (no eggs present), or non-progenetic, but with visible vitellaria (no eggs present, but yolk-producing glands developed). Body surface of each worm was calculated as a surrogate for body size using the formula of an ellipsoid, (πLW)/4, where L and W are the length and width of the parasite; the latter measurements were taken using a dissecting microscope (×80). Eggs of progenetic worms expelled from the worm and free within the cyst were counted. Length (L) and width (W) of a sub-sample of 10 eggs from each progenetic worm were measured, and, assuming a regular ellipsoid shape, egg volume was calculated as (πLW^2)/6.

Differences among lakes in relative eel abundance, relative bully abundance, and total length of bullies sampled were assessed with ANOVAs, while a chi-square test was used to assess differences in bully sex ratio among samples. Two generalized linear models (GLMs), each fitted with a quasipoisson distribution, were used to assess differences among lakes in mean abundance of *S. anguillae*, while accounting for variability due to bully host length, and in mean abundance of *S. anguillae* in the gonads only, while accounting for host sex. Three generalized linear mixed models (GLMMs) were used to assess differences among lakes in

TABLE III. The statistical results for mean abundance of *Stegodexamene anguillae*, progenesis, worm size, and number of eggs expelled comparing the 4 populations while accounting for any other significant predictor variables emerging from the model averaging analysis. Abundance was assessed with generalized linear models, while progenesis, worm size, and number of eggs were assessed with generalized linear mixed models. Parameter estimate, standard error (SE), and estimate/SE are reported. The significant main effects are in bold.

Response	Predictor variable	Estimate	SE	Estimate/SE	*P*
Abundance of *S. anguillae*	**Lake: Hawea vs. Ohau**	**−0.387**	**0.174**	**−2.22**	**$P \leq 0.05$**
	Lake: Hawea vs. Waihola	**−1.047**	**0.189**	**−5.54**	**$P \leq 0.001$**
	Lake: Hawea vs. Waipori	**−1.051**	**0.219**	**−4.79**	**$P \leq 0.001$**
	Bully host length	**0.798**	**0.110**	**7.29**	**$P \leq 0.001$**
Abundance of *S. anguillae* in gonads only	Lake: Hawea vs. Ohau	0.687	0.369	1.86	$P > 0.05$
	Lake: Hawea vs. Waihola	**0.862**	**0.359**	**2.40**	**$P \leq 0.05$**
	Lake: Hawea vs. Waipori	−0.070	0.438	−0.16	$P > 0.05$
	Bully host sex	−0.268	0.244	−1.10	$P > 0.05$
Progenesis	**Lake: Hawea vs. Ohau**	**1.106**	**0.533**	**2.08**	**$P \leq 0.05$**
	Lake: Hawea vs. Waihola	**1.502**	**0.487**	**3.08**	**$P \leq 0.01$**
	Lake: Hawea vs. Waipori	**1.868**	**0.541**	**3.45**	**$P \leq 0.001$**
	Bully host length	**0.959**	**0.311**	**3.09**	**$P \leq 0.01$**
	Site: muscle vs. head	**1.087**	**0.451**	**2.41**	**$P \leq 0.05$**
	Site: muscle vs. body cavity	**2.692**	**0.413**	**6.53**	**$P \leq 0.001$**
	Site: muscle vs. gonads	**4.173**	**0.418**	**9.99**	**$P \leq 0.001$**
Worm size	**Lake: Hawea vs. Ohau**	**0.021**	**0.009**	**2.40**	**$P \leq 0.05$**
	Lake: Hawea vs. Waihola	**0.024**	**0.009**	**2.71**	**$P \leq 0.05$**
	Lake: Hawea vs. Waipori	0.003	0.009	0.29	$P > 0.05$
	Develop: non-progenetic vs. vitellaria	**0.176**	**0.006**	**29.15**	**$P \leq 0.001$**
	Develop: non-progenetic vs. progenetic	**0.286**	**0.006**	**45.61**	**$P \leq 0.001$**
	Site: muscle vs. head	0.005	0.003	1.40	$P > 0.05$
	Site: muscle vs. body cavity	**0.042**	**0.004**	**10.63**	**$P \leq 0.001$**
	Site: muscle vs. gonads	**0.072**	**0.005**	**14.80**	**$P \leq 0.001$**
No. of eggs	Lake: Hawea vs. Ohau	−0.991	27.347	−0.04	$P > 0.05$
	Lake: Hawea vs. Waihola	−0.383	24.332	−0.02	$P > 0.05$
	Lake: Hawea vs. Waipori	−0.017	25.932	0.00	$P > 0.05$

TABLE IV. The top-ranked candidate models for each response variable. If more than 1 model within 2 $\mathrm{AIC_C}$ of the top model emerged, then models were sorted by corrected Akaike information criteria ($\mathrm{AIC_C}$ or $\mathrm{QAIC_C}$), with model deviance, $\mathrm{AIC_C}$ or $\mathrm{QAIC_C}$, difference in $\mathrm{AIC_C}$ from the best model ($\Delta\mathrm{AIC_C}$), and weight ($\mathrm{AIC_W}$) values given for each model.

Response	Model	Deviance	$\mathrm{AIC_C}$	$\Delta\mathrm{AIC_C}$	$\mathrm{AIC_W}$
Progenesis	Bully abundance + site + host length + *Stegodexamene anguillae*	680.96	699.04	—	0.14
	Bully abundance + site + host length + *S. anguillae* + *Telogaster opisthorchis*	680.10	700.19	1.15	0.08
	Eel abundance + site + host length + *S. anguillae* + temperature	680.19	700.28	1.25	0.07
	Bully abundance + site + host length	684.25	700.31	1.27	0.07
	Bully abundance + site + host length + *T. opisthorchis*	682.26	700.34	1.30	0.07
	Bully abundance + eel abundance + site + host length	682.29	700.37	1.34	0.07
	Bully abundance + eel abundance + site + host length + *S. anguillae*	680.52	700.61	1.57	0.06
	Site + host length + *S. anguillae*	684.61	700.67	1.64	0.06
	Site + host length + *S. anguillae* + *T. opisthorchis*	682.73	700.81	1.77	0.06
	Bully abundance + site + host length + *S. anguillae* + temperature	680.74	700.84	1.80	0.06
	Bully abundance + site + host length + temperature	682.80	700.88	1.84	0.05
	Bully abundance + *Apatemon* + site + host length + *S. anguillae*	680.91	701.00	1.97	0.05
	Bully abundance + site + *Apatemon* + host length + *S. anguillae*	680.92	701.01	1.97	0.05
	Bully abundance + body condition + site + host length + *S. anguillae*	680.93	701.02	1.98	0.05
	Eel abundance + site + host length + temperature	682.96	701.03	2.00	0.05
Worm size	Body condition + development + site	−6248.16	−6228.07	—	0.70
	Development + site	−6244.41	−6226.33	1.73	0.30
No. of eggs	Intercept only	8598.05	23.20	—	0.71
	Worm size	8596.65	24.95	1.75	0.29
Egg volume	Intercept only	−1618.00	−1588.00	—	1.00

progenesis (with each worm classified as either progenetic, or not), log-transformed worm size, and number of eggs produced per progenetic worm. Individual fish identity was added as a random factor to account for many *S. anguillae* sharing the same host individual. The progenesis model was fitted with a binomial error structure, the worm size model was fitted with the Gaussian (normal) distribution, and the egg model was fitted with a quasipoisson distribution. In the GLMM on progenesis, host length and encystment site (muscle, head, body cavity, or gonads) were also included as factors, whereas developmental stage and encystment site were added to the GLMM on worm size. These variables were deemed as important predictors in the model averaging analyses described below. However, all the above analyses are designed solely to identify differences among lakes, and, therefore, lake identity is the main factor in all of them.

Subsequently, a separate series of analyses was performed to determine which parameters affect *S. anguillae* life history traits regardless of study site, i.e., lake. In these analyses, 4 response variables were assessed using a GLMM within an Akaike information criterion (AIC) and model averaging framework (Burnham and Anderson, 2002; see Table II). First, progenesis was the response variable in a GLMM fitted with a binomial error structure. Factors possibly influencing whether the parasite becomes progenetic or not were included in the GLMM to determine the effect of relative eel abundance, relative bully abundance, water temperature, host body condition, host length, host sex, encystment site (muscle, head, body cavity, or gonads), mean abundance of conspecifics, and mean abundance of 2 other common species of trematode metacercariae (*Telogaster opisthorchis* and *Apatemon* sp.). Lake and individual fish identity were added as random factors. The interaction between host sex and encystment site was included preliminarily; however, inclusion of this interaction resulted in similar model averaging and thus was not retained in order to achieve a simpler global model. This set of variables was used in the following analyses in addition to any specified (Table II). Second, worm size data were log-transformed to approach normality and used as response variable in a GLMM fitted with the Gaussian (normal) distribution. The same predictors as in the progenesis GLMM were included with the addition of developmental strategy (non-progenetic, vitellaria-present, and progenetic). Third, those same predictor variables were included in a GLMM, fitted with a quasipoisson distribution, on number of eggs expelled per progenetic worm as the response variable with the addition of worm size as an extra factor. Finally, a last GLMM with mean egg volume per progenetic worm as response variable and fitted with the Gaussian (normal) distribution included the additional factors of worm size and number of eggs expelled. The GLMMs on number of eggs and mean egg volume were performed to consider the possibility that some predictor variables might have more subtle effects on parasite biology than just influencing whether or not they become progenetic.

Global models were fitted using the package lme4 (Bates and Maechler, 2009) in the program R (R Development Core Team, 2009). The global model was then used to generate a model set of all possible models, with functions from the R package MuMIn (Bartoń, 2009). Each model in the set was ranked by $\mathrm{AIC_C}$, or $\mathrm{QAIC_C}$ for the model fitted with a quasipoisson distribution. Model averaging, using MuMIn and the natural averaging method, was performed on all models within 2 $\mathrm{AIC_C}$ (or $\mathrm{QAIC_C}$) of the best model. The predictor variables in the top models are reported with their relative importance weights, model-averaged parameter estimates, unconditional standard error, and 95% confidence intervals. When only 1 top model emerged, that model is reported.

TABLE V. Predictor variables from top models for each response variable. Relative importance weights ($w_+(i)$), coefficient estimates, their unconditional standard error (SE), and 95% confidence interval (CI) after model averaging are shown for each variable. Values from top model reported for response variables with only 1 top model. Variables in bold have a 95% confidence interval bounded away from zero.

Response	Predictor variable	$w_+(i)$	Estimate	SE	95% CI
Progenesis	Intercept	—	−8.010	5.100	−18.000 to 1.990
	Site: muscle vs. head	**1.00**	**1.100**	**0.452**	**0.2100 to 1.980**
	Site: muscle vs. body cavity	**1.00**	**2.690**	**0.413**	**1.880 to 3.500**
	Site: muscle vs. gonads	**1.00**	**4.130**	**0.417**	**3.310 to 4.950**
	Host length	**1.00**	**1.140**	**0.393**	**0.371 to 1.910**
	Relative bully abundance	**0.76**	**−2.020**	**1.020**	**−4.020 to −0.019**
	No. of *Stegodexamene anguillae*	0.68	−0.013	0.008	−0.028 to 0.002
	Relative eel abundance	0.26	0.359	0.371	−0.367 to 1.090
	Temperature	0.24	−0.676	0.885	−2.410 to 1.060
	No. of *Telogaster opisthorchis*	0.21	0.008	0.007	−0.005 to 0.021
	Host sex	0.05	−0.073	0.313	−0.686 to 0.541
	No. of *Apatemon* sp.	0.05	0.000	0.002	−0.003 to 0.004
	Host body condition	0.05	−23.800	131.000	−281.000 to 233.000
Worm size	Intercept	—	0.056	0.021	0.014 to 0.098
	Develop: non-pro vs. vitellaria	**1.00**	**0.176**	**0.006**	**0.165 to 0.188**
	Develop: non-pro vs. progenetic	**1.00**	**0.286**	**0.006**	**0.274 to 0.298**
	Site: muscle vs. head	1.00	0.005	0.003	−0.002 to 0.011
	Site: muscle vs. body cavity	1.00	**0.042**	**0.004**	**0.034** to **0.050**
	Site: muscle vs. gonads	1.00	**0.073**	**0.005**	**0.063** to **0.082**
	Host body condition	0.70	−0.760	2.490	−5.640 to 4.120
No. of eggs	Intercept	—	4.236	9.131	−13.660 to 22.132
	Worm size	0.50	−0.001	0.083	−0.164 to 0.163
Egg volume	Intercept	—	1.2e–04	8.1e–06	1.0e–04 to 1.3e–04

RESULTS

Relative bully abundance varied among lakes (Table I; $F_{3,63} = 28.50$, $P < 0.001$). A post-hoc Tukey's HSD showed that Lake Hawea had higher relative bully abundance than all other lakes, with a 0.05 level of significance, with all other comparisons between lakes being non-significant. Of the 80 bullies sampled, total length varied between 3.2 (lower collection limit) and 6.2 cm, and mean total length was significantly different only between Lakes Ohau and Waihola (Table I; $F_{3,76} = 4.30$, $P = 0.007$, Tukey's HSD $= -0.56$, $P = 0.010$). There was no significant difference in sex ratio of bullies sampled among lakes ($\chi^2 = 3.64$, df = 3, $P = 0.30$). Even though lakes were chosen based on prior information suggesting varying eel abundance, no such difference was detected statistically ($F_{3,4} = 1.03$, $P = 0.469$).

The total number of *S. anguillae* sampled from 20 bullies from each lake also varied (Table I). While prevalence in bullies was 100% at all lakes, mean abundance of *S. anguillae* was greater at Lake Hawea than all other lakes (Tables I, III). However, considering only worms in the gonads, the mean abundance was greater at Lake Waihola than all other lakes (Table III).

Model analysis on progenesis resulted in 15 top models within 2 $\mathrm{AIC_C}$ of the best model (Table IV), and all explanatory variables considered in the global model were included in at least 1 model in the top model set. Encystment site and bully host length emerged as the most robust predictor variables, with a relative importance weight of 1.00 and a 95% confidence interval bounded away from zero (Tables IV, V). There were greater proportions of progenetic worms in host head, body cavity, and gonads than in muscle tissue (Fig. 2A). Progenesis also increased with increasing host length (Fig. 3). Bully abundance also had a confidence interval that did not include zero but had a lower relative importance weight (Table V). Bully abundance and frequency of progenesis showed a negative relationship (Table V), with Lake Hawea having the greatest bully abundance and lowest proportion of progenetic worms compared with the other lakes (Tables I, III; Fig. 4).

Host body condition, developmental strategy, and encystment site were the predictors of worm size in the 2 top models, although 95% confidence intervals of only developmental strategy and encystment site did not include zero (Tables IV, V). Worms grew larger as they developed from non-progenetic to having vitellaria to becoming progenetic. Worms in the body cavity and gonads grew to larger sizes than those in the head and muscle tissues (Fig. 2B). Inter-lake comparisons showed that worms at Lakes Ohau and Waihola achieved larger sizes than those at Lake Hawea (Tables I, III).

Two top models emerged from model analysis on egg production, the intercept only model and a model with worm size as the only predictor (Table IV). Confidence interval of worm size included zero (Table V). Egg production did not differ among populations (Tables I, III). Only 1 top model, the intercept only model, resulted from model analysis on mean egg volume (Table IV). No variable measured in this study explained egg size. Furthermore, mean egg volume was also similar among populations (n = 910; Table I).

DISCUSSION

The present study found both similarities and differences in *S. anguillae* infections and life history traits among 4 lake populations. Since we sampled only 1 site at each lake, within-lake spatial variation may account for part of these differences, though it is unlikely to eclipse inter-lake variation. Although

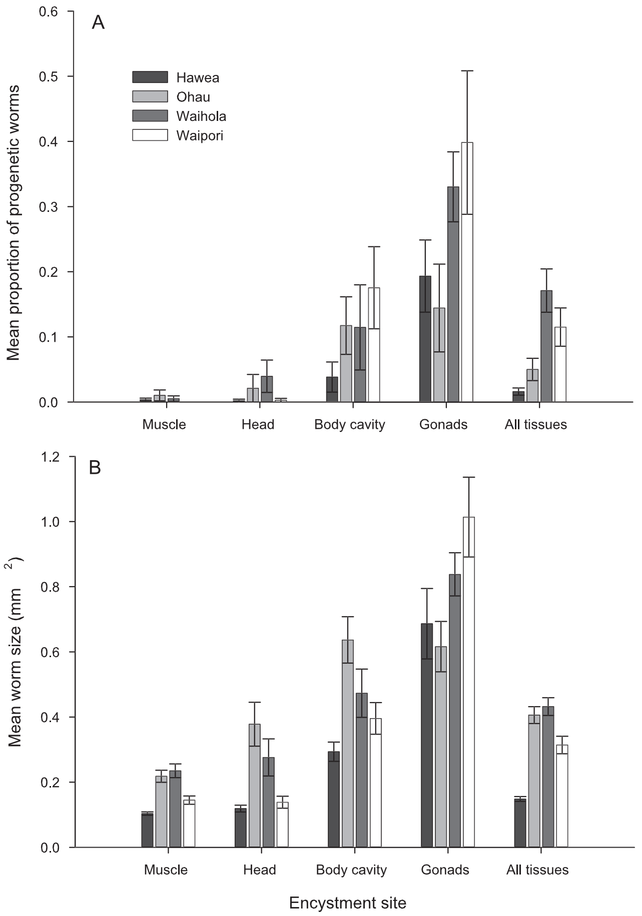

FIGURE 2. (**A**) Proportion of progenetic worms and (**B**) mean worm size (mm^2) at each lake as a function of encystment site. Error bars indicate the standard error of the mean.

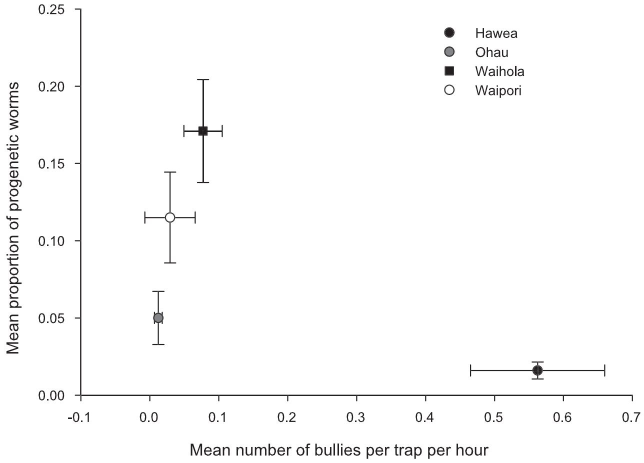

FIGURE 4. Mean proportion of progenetic *Stegodexamene anguillae* as a function of mean number of second intermediate hosts, the common bully, caught per trap per hour. Error bars indicate the standard error of the mean.

prevalence of *S. anguillae* metacercariae in bully intermediate hosts was 100% at all 4 lakes, abundance of *S. anguillae* varied among the lakes and was greatest at Lake Hawea. Relative abundance of the second intermediate host, common bully, was also substantially higher in Lake Hawea than in the other lakes studied. Since parasite abundance in an intermediate host is often positively correlated with definitive host abundance (Marcogliese et al., 2001; Smith, 2001; Latham and Poulin, 2003; Hechinger and Lafferty, 2005), the availability of suitable hosts must be adequate at all 4 lakes, but abundances of hosts may be best for transmission success at Lake Hawea. Further, abundance of *S. anguillae* also increased with increasing host length, since bullies probably acquire metacercariae continuously throughout their life (Barber and Crompton, 1997).

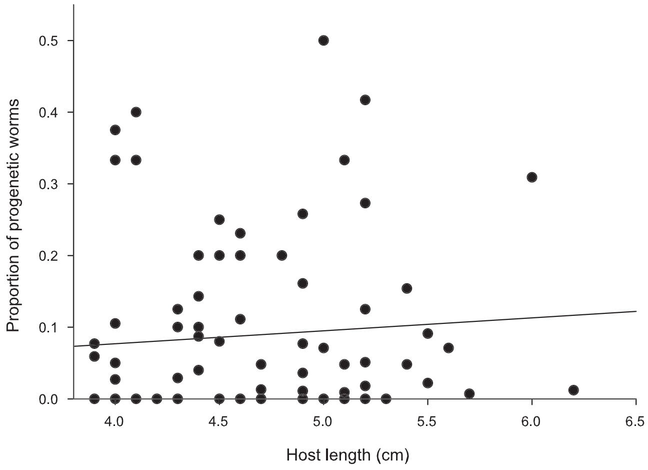

FIGURE 3. Proportion of progenetic worms as a function of host body length.

The frequency of progenesis was highest at Lake Waihola. This may be explained by the greater abundance of *S. anguillae* in the gonads of Lake Waihola bullies; worms encysted in the gonads are more likely to adopt progenesis. Host length was also an important predictor affecting progenesis. *Stegodexamene anguillae* are more likely to become progenetic in longer and, therefore, older, bully hosts. As an intermediate host ages, predation risk and the probability of transmission to a definitive host may decrease, and *S. anguillae* may thus respond to cues related to host aging and reproduce through progenesis before the intermediate host dies. This supports previous results in which an increase in progenesis occurrence was observed in bully hosts experimentally exposed to stressful conditions and experiencing reduced longevity (Herrmann and Poulin, 2011b). However, for some prey species, predation risk increases as the prey approaches senescence and thus the probability of transmission increases. Therefore, an alternative explanation of an increase in progenesis in longer fish may be that *S. anguillae* in older hosts could be older and may have an age-dependent strategy, as predicted by the developmental time hypothesis (Poulin and Cribb, 2002). The progenetic trematode, *C. parvum*, provides a good example, i.e., the longer it spends encysted within a second intermediate host, the more likely it is to mature and produce eggs (Lagrue and Poulin, 2009).

Transmission generally depends on host availability (Crossan et al., 2007). Low definitive host abundance is thought to be the main driving force behind the evolution of truncated life cycles (Poulin and Cribb, 2002). In spite of this, eel abundance did not significantly influence frequency of progenesis in this study. Although eel abundance was not addressed as an original objective, it is likely to be a possible source of variation in progenesis. However, too few lakes were sampled to adequately test this possibility. Additionally, the link between progenesis and eel abundance may be confounded by eel translocations into Lake Hawea. The lake's main outlet is the Clutha River, although Roxburgh and Clyde Dams have restricted eel recruitment into Lake Hawea since 1958 and 1992, respectively (Beentjes and Jellyman, 2003). In 1998, over 9,000 eels were transferred to Lake Hawea from high-density populations from branches of the Clutha River (Beentjes and Jellyman, 2003). These transfers, no doubt, also included *S. anguillae* within the eels. Intensive eel surveys in Lake Hawea prior to the transfer captured 3 eels each in 1995 and 1998 (Beentjes and Jellyman, 2003). Therefore, the majority of *S. anguillae* individuals in the current population at Lake Hawea are likely descendants of *S. anguillae* populations from the Clutha River. Progenesis of *S. anguillae* appears to be rare in river systems (I. Blasco-Costa, pers. comm.), which may explain the low incidence of progenesis in the Lake Hawea population compared with all other lakes.

Overall, there was a negative relationship between progenesis and bully abundance, with Lake Hawea having both the greatest abundance of bullies and the lowest prevalence of progenesis. Again, this relationship is highly likely to be confounded by the recent transfer of eels and *S. anguillae* into Lake Hawea from the Clutha River. The frequency of progenesis at Lake Hawea is likely to have been influenced by conditions experienced by the *S. anguillae* population from the Clutha River. The other 3 lakes had similar abundances of bullies but had different proportions of progenetic *S. anguillae*, suggesting that abundance of common bullies may not be an important factor in progenesis.

Worms were of smaller sizes in Lake Hawea than in Lakes Ohau and Waihola. Although Lake Hawea bullies harbored the greatest number of *S. anguillae*, abundance of *S. anguillae* did not affect individual worm size. Developmental stages (non-progenetic, vitellaria-present, or progenetic) and encystment site were the main predictors of worm size. As *S. anguillae* matured sexually, they also grew in size. Since the Lake Hawea population had the fewest progenetic individuals, its mean size would be expected to be smaller. Further, worms encysted in body cavities and gonads attained larger sizes than those in muscle tissue. Trematodes absorb monosaccharides across the tegument (Bibby and Rees, 1971; Erasmus, 1972), which may be more readily available in these tissues compared with muscle tissue.

Even though the proportion of progenetic individuals varied among lake populations, egg production was similar. Across the 4 lake populations, the mean ranged between 130 and 340 eggs per progenetic worm. A maximum of 1,130 eggs was produced by a worm from Lake Ohau. Egg production should be constrained in progenetic individuals inside a metacercaria cyst and relatively short-lived second intermediate host compared with those in the gut of a definitive host (Poulin and Cribb, 2002). Although fecundity of adults inside an eel definitive host is unknown, it is likely much higher than that of progenetic individuals. Egg volume did not vary among parasite populations and was not influenced by any other variable considered here, suggesting that this trait is not plastic and independent from factors influencing progenesis.

Overall, the present results indicate that progenesis in *S. anguillae* does vary among populations. Previous research, along with the present study, showed that encystment site and thus opportunity for releasing progenetic eggs into the environment (Poulin and Lefevbre, 2006; Herrmann and Poulin, 2011a), as well as longevity of the second intermediate host (Herrmann and Poulin, 2011b), are strong selective forces acting on early maturation and reproduction in *S. anguillae*. Progenesis may be a plastic trait responding to a variety of factors; however, abundance of definitive eel hosts does not seem to have measurable impacts on rates of progenesis in natural populations of *S. anguillae*.

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