

Phenotypic and community consequences of captive propagation in mosquitofish

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Abstract

1. Captive propagation can lead to phenotypic change in fish populations, but the broader community-level consequences of captive phenotypes remain largely unknown.
2. We investigate the degree to which captive propagation alters the phenotypes and ecological roles of fish stocked into wild communities. We focus on captive propagation of western mosquitofish (*Gambusia affinis*) for biocontrol, which represents one of the largest scale production efforts for any fish released into the wild.
3. Captive propagation in mosquitofish consistently generated novel mixtures of morphological and behavioural traits that deviate from those of wild populations.
4. A mesocosm experiment showed that mosquitofish from captive propagation facilities differ from wild fish in their effects on aquatic community structure by shifting their consumption to less-mobile, benthic prey.
5. *Synthesis and applications.* Captive-propagated and translocated wild fish stocks not only differ in phenotype, but can have substantially different ecological effects on the communities into which they are introduced. Therefore, captive propagation programmes involving continual release should expand their concerns beyond altered phenotypes and fitness to include whether propagated fish actually provide the intended ecological roles and services associated with their wild counterparts. Infusions of wild alleles and captive environments that mimic wild conditions are recommended strategies to retain the desired ecological role of captive-propagated fish.

KEYWORDS

antipredator evolution, biological control, captive propagation, domestication, fish introductions, mosquitofish, trophic cascades

1 | INTRODUCTION

Captive propagation and stocking of fish constitutes a massive human intervention in many wild ecosystems. Hundreds of species are currently reared at least partially in captive environments (e.g., hatcheries), with limited genetic input from wild populations

(Bilio, 2007; Teletchea & Fontaine, 2012). Captive propagation and release programmes are commonly operated with the intent to bolster declining wild populations (Araki & Schmid, 2010; Brown & Day, 2002), support commercial or sport-fishing activities (Halverson, 2008) or produce fish for biological control of pest species (Chandra, Bhattacharjee, Chatterjee, & Ghosh, 2008; Swanson, Cech, &

Piedrahita, 1996). Growing focus has been given to whether captive-propagated fish provide the socioeconomic or ecological services associated with wild fish (Ham & Pearsons, 2001; Pearsons & Hopley, 1999; Pister, 2001). Although captive-propagated fish can fill some socioeconomic roles of wild fish—providing food or recreation—we know much less about the extent to which captive-propagated fish serve as true ecological surrogates for wild fish. Recent evidence suggests that divergent phenotypes of fish and other organisms can lead to markedly different ecological conditions (Des Roches et al., 2018). Here we test the extent to which phenotypic (plastic and genetic) divergence of captive-propagated and wild fish may change the functional traits and ecological roles of captive lines in ways that alter aquatic community structure and ecosystem function following stocking.

Multi-generational captive rearing is widely associated with marked divergence from wild sources in morphology, life history and behaviour. Captive-propagated fish are often larger and have different fin placement and body shapes than wild fish (Pulcini, Wheeler, Cataudella, Russo, & Thorgaard, 2013). Propagated fish also tend to grow and mature more rapidly (Lorenzen, Beveridge, & Mangel, 2012; Vøllestad, Peterson, & Quinn, 2004). Behaviourally, propagated fish are generally less aware of predators, worse at identifying profitable food sources and have inappropriate levels of aggression towards conspecifics (Fenderson & Carpenter, 1971; Huntingford, 2004; Swain & Riddell, 1990). Such phenotypic change can markedly decrease survival and reproduction in the wild (Araki, Berejikian, Ford, & Blouin, 2008; Araki, Cooper, & Blouin, 2007; Bowlby & Gibson, 2011; Christie, Ford, & Blouin, 2014; Milot, Perrier, Papillon, Dodson, & Bernatchez, 2013). However, such a focus on reduced fitness does not fully address the extent to which captive-propagated fish fill the same ecological roles as wild fish.

While little work has directly examined the ecological role of captive-propagated fish in wild environments, suspected changes in the functional traits of propagated fish hint at important consequences for communities and ecosystems. Divergence in morphological traits that affect feeding mode and efficiency—that is head shape and body streamlining (Albertson, Streebman, & Kocher, 2003; Domenici, Turesson, Brodersen, & Brönmark, 2008; Langerhans, 2009)—are especially likely to have strong community impacts by determining the type and quantity of prey consumed and ability to avoid predators. Divergence in behavioural traits may also be important, including traits associated with habitat use, risk avoidance and foraging patterns (Schluter, 1993; Werner, Gilliam, Hall, & Mittelbach, 1983).

Here we assess phenotypic divergence and resulting ecological consequences around introductions of captive-propagated versus wild western mosquitofish (*Gambusia affinis*). Mosquitofish are the most commonly used form of mosquito biocontrol in the world (Swanson et al., 1996). We evaluate two hypothetical mechanisms for how captive propagation might shape the traits and community effects of propagated mosquitofish relative to wild-sourced fish:

1. A main goal of captive propagation is to increase survival by removing predation. Therefore, captive propagation may produce functional traits and ecological consequences similar to those of wild, predator-naïve populations.
2. Additionally, captive environments may differ from wild environments—not only through predator absence but also in a host of other important ways (e.g. higher densities, artificial feeding, simplified environments). Therefore, captive propagation may produce novel combinations of functional traits, which lead captive-propagated fish to have unique ecological consequences when released into the wild.

We examined behavioural and morphological traits across multiple captive-propagated and wild mosquitofish populations. We also used replicated pond mesocosms to assess cascading community effects of stocking captive-propagated versus wild-translocated fish. By comparing the community-level effects of mosquitofish from mosquito control propagation facilities with those caused by mosquitofish from wild populations, we assess the ecological implications of stocking captive-propagated fish versus the alternative of translocating wild fish. As both methods are widely employed by mosquito control districts (Swanson et al., 1996), this comparison not only provides novel insights into ecological consequences of captive propagation, but also illuminates yet unknown environmental impacts of these alternative biocontrol approaches.

2 | MATERIALS AND METHODS

We studied 11 populations of western mosquitofish (*G. affinis*) from central California, USA (Figure S1, Table S1) representing three different source-types: (a) mosquitofish produced for biocontrol in captive propagation facilities, (b) wild mosquitofish from low-predation ponds lacking largemouth bass (*Micropterus salmoides*) and (c) wild fish from high-predation ponds with largemouth bass present. Largemouth bass are a dominant predator of mosquitofish and have been shown to play a strong role in shaping the functional traits of mosquitofish populations (Langerhans, 2009; Langerhans, Layman, Shokrollahi, & DeWitt, 2004).

Western mosquitofish were introduced to California in the 1920s for mosquito control (Lenert, 1923). Although detailed stocking records and population genetic surveys are lacking these original fish were widely stocked and translocated throughout the region over a period of decades. As such, any differences among wild populations are presumed to reflect a combination of recent local divergence (through genetic adaptation and genetic drift) and phenotypic plasticity.

In central California, millions of mosquitofish are stocked annually with the intent to control mosquito borne diseases (Contra Costa Mosquito Vector Control, 2016; Sacramento-Yolo Mosquito & Vector Control, 2016). The potential for ecologically-relevant phenotypic change in captive-propagated mosquitofish is high due to their capacity for contemporary adaptation (Langerhans, 2009;

Langerhans et al., 2004; Stearns, 1983a; Stockwell & Weeks, 1999). The widespread introduction of mosquitofish, despite their strong, often harmful ecological effects on aquatic communities (Hurlbert & Mulla, 1981; Hurlbert, Zedler, & Fairbanks, 1972; Pyke, 2008) makes it particularly important to assess how captive propagation might shape these effects. In mosquitofish propagation facilities, fish breed volitionally in indoor tanks or in covered outdoor ponds where they are surface fed a powdered diet of fish meal. A subset of fish are periodically netted for stocking.

We compared the following traits and ecological effects among captive-propagated wild high-predation, and wild low-predation mosquitofish populations: (a) morphology: 10 populations (two captive-propagated, five wild low-predation and three wild high-predation); (b) exploratory behaviour: 10 populations (three captive-propagated, four wild low-predation and three wild high-predation); (c) boldness and activity behaviour: three populations (one captive-propagated, one wild low-predation, one wild high-predation); (d) ecological effects: three populations (the same as [c]). Differences in the number of population sources for each response were due to differences in availability of fish sources at the time of each study and infrastructure requirements (small tanks versus large mesocosms). For wild sources, we collected mosquitofish using a mixture of seine- and hand-netting; for captive sources, we used hand-nets, only. The predation regime of each pond was determined by performing repeated fish surveys over multiple dates using beach seines.

2.1 | Morphology

For morphological analyses, we used adult mosquitofish collected in July and August 2015. We euthanized all fish on-site and froze them for later morphometric analyses. We also supplemented our morphology dataset with individuals from the populations that were used in the subsequent mesocosm experiment (see below).

2.2 | Exploratory behaviour

To assay exploratory behaviour, we collected adults in June, July and August 2016. We held these fish at the University of California-Santa Cruz, Coastal Science Campus for 18–24 hr to acclimate without food prior to experimentation.

We assayed mosquitofish exploratory behaviour within a social context by measuring the latency time it took male–female pairs of the same population source to exit a refuge. We assessed exploratory behaviour in pairs because mosquitofish are extensively social, and males are almost always found in close company of females. Here we define exploratory behaviour as “willingness to investigate novel environments” (Conrad, Weinersmith, Brodin, Saltz, & Sih, 2011). We used an experimental arena consisting of an opaque plastic tank (49 cm × 34 cm × 21.5 cm) with a cylindrical PVC refuge (20.5 cm tall, 11 cm diameter) secured to the inside wall of the tank. The PVC cylinder (refuge) contained a remotely operated door that could be opened or closed by rotating the cylinder. We placed

cardboard around each trial enclosure to minimize exposure of the fish to movement outside the tank and observed fish through a small hole.

For each trial, we placed one female and one male fish inside the PVC refuge and allowed them to acclimate for 5 min. After allowing the fish to acclimate, we opened the refuge door and recorded the time each fish remained in the refuge before exiting, with a maximum trial time of 10 min. After each trial, we measured total length (including caudal fin) of each fish.

We calculated individual latency to exit the refuge as the proportion of the 600-s trial spent inside the starting refuge by each fish. We arcsine-square-root transformed these proportions for normality, then calculated the mean transformed latency of each pair of fish. We analysed mean transformed latency of each pair, rather than individuals, as latency times of individuals within a pair were correlated (Figure S2) (Arrington, Tharnan, Rettig, & Smith, 2009).

2.3 | In-mesocosm boldness and activity behaviour

We examined predation/propagation source-type differences in mosquitofish boldness and activity level using in-mesocosm behavioural assays (see mesocosm setup below) on day 18 after mosquitofish introduction. Here we define boldness as “reaction to a situation perceived as dangerous” and activity as degree of movement in the same situation (Conrad et al., 2011; Réale, Reader, Sol, McDougall, & Dingemanse, 2007). Mosquitofish tended to associate in tight shoals within our mesocosms. The same (treatment-blind) observer stood motionless next to each mesocosm and observed the shoal of mosquitofish for 150 s. At 30 s intervals, after a 30 s waiting period, the observer noted depth, distance from the observer and activity level of the shoal, all on a scale of 1–4. We calculated depth and distance by visually dividing the mesocosms into four equal thickness zones (perpendicular to the observer), then recording which zone the majority of the shoal occupied at the time of recording. Activity level ranks were based on type of shoal movement: 1—no movement; 2—slow, steady movement; 3—exploring, foraging; 4—burst-swimming, aggressive interactions.

2.4 | Ecological consequences

To assess ecological consequences of mosquitofish introduction and trait divergence, we used fish collected in May 2016. Our captive line was provided by Contra Costa Vector Control in Concord, California. This lineage has been reared in captivity with very limited genetic input for over 10 years, or roughly 30 mosquitofish generations (C. Miller, pers. comm.). Our wild low-predation line for this experiment (Table S1) was taken from the primary wild source location used to establish the Contra Costa captive-propagated population (C. Miller, pers. comm.). These three populations exhibited morphological and behavioural traits distributions that mirrored those of other populations from their respective source-type (captive-propagated, wild high, wild low; Figures S3–S6). We held all three

populations in outdoor 330 L Rubbermaid cattle tanks for a week before experimentation.

We established 48 1,100 L mesocosms in Santa Cruz, California, which we seeded with benthic and pelagic components of local pond ecosystems. We added unfiltered water (4 L total) equally from West Lake (N 36.976083°, W 122.045683°) and Antonelli Pond (N 36.955566°, W 122.060489°), both in Santa Cruz, to foster colonization by a diverse pelagic community. We added 20 L air-dried sediment and 1 L active sediment from West Lake, Santa Cruz. We added equal aliquots of zooplankton (>80 µm) from tows taken at both West Lake and Antonelli Pond to all mesocosms. We allowed mesocosms to settle and develop for 5 days before fish addition. We added dechlorinated city water to the mesocosms halfway through the experiment to compensate for evaporation.

We established four mesocosm treatments, one for each mosquitofish background (captive-propagated, wild low-predation, wild high-predation), plus a fish-free control. Each mesocosm, except those in the control treatment, received six fish, which were a hap-hazard mixture of mature males and females. Fish remained in each mesocosm for 3 weeks. Three-week duration of this experiment is similar to that of other mosquitofish mesocosm experiments, which documented consistent ecological consequences of mosquitofish phenotype (Fryxell & Palkovacs, 2017), and was long-enough for us to observe consistent ecological effects of mosquitofish presence and phenotype (see section 3).

We sampled common mosquitofish prey (zooplankton and benthic chironomid larvae) and primary producers to examine cascading ecological effects of mosquitofish presence and phenotypic divergence. Starting on the day of fish addition, we collected zooplankton weekly from 4 L water samples on 80 µm mesh and phytoplankton from 1 L water samples on a 0.7 µm filter. We later identified zooplankton to common taxonomic clades (cladocerans and copepods [adult and nauplii]) under a dissecting microscope. We estimated phytoplankton abundance as chlorophyll-*a* concentration measured fluorometrically (Turner Designs, Trilogy Module CHL-NA). We measured 24-hr gross primary production (GPP) using three dissolved O₂ measurements over a 24-hr period (dawn, dusk and dawn) 1 and 2.5 weeks after fish addition. We calculated GPP as the amount of oxygen produced during one day plus the amount of oxygen consumed during the following night (Harmon et al., 2009). We added plastic tiles (28 cm² surface area) on the day of fish addition. These were removed 2 and 3 weeks after fish addition to measure benthic chlorophyll *a* and benthic chironomid larva abundance. At the end of the experiment, we measured total adult fish dry biomass, adult sex ratio and counted the number of fry present in each mesocosm.

2.5 | Statistical analyses

We used R software (R Core Team, 2016) for all statistical analyses. All general and generalized linear mixed models were fit with the functions *lmer* and *glmer*, respectively, in the *lme4* package (Bates, Mächler, Bolker, & Walker, 2015). We conducted likelihood ratio tests on the components of all models with the default *anova(glmer*

or *lmer*) functions. We also categorized source-type level differences within all models (except exploratory behaviour) using post hoc multiple comparison tests with the function *glht* in the *multcomp* package (Hothorn, Bretz, & Westfall, 2008).

We used allometric models to examine differences in mosquitofish morphology across captive propagation and wild source-types. We used Image J (Schneider, Rasband, & Eliceiri, 2012) to measure several morphometric distances on each adult mosquitofish: snout–posterior edge of eye, snout–dorsal fin, snout–anal fin, minimum caudal peduncle depth, and total body length (excluding caudal fin). We fit the following allometric model for each morphometric variable:

$$\ln(Y) = a \cdot S + b \cdot \ln(L) + P. \quad (1)$$

Y is a morphometric variable, S is source-type, L is body length, P is a random effect term for population within source-type and a and b are model coefficients. We fit models using ln-ln-transformed data, separately for each sex.

To analyse the effects of source type, body length and the interaction thereof on pair exploration latency, we fit the following general linear mixed model:

$$E_{\text{pair}} = a \times S + b_1 \times S \times L_f + b_2 \times S \times L_m + P. \quad (2)$$

E_{pair} is pair mean transformed exploration latency, S is source type, L_f and L_m are female and male length, respectively, P is a random effect term for population within source-type and a , b_1 and b_2 are model coefficients.

We tested for source-type differences in shoal distance from observer and depth using generalized linear mixed models:

$$D = a \times S + M + T. \quad (3)$$

D is distance or depth, S is source-type, M is a random effect term for mesocosm identity within source-type, T is a random effect term for time since the start of observation and a is a model coefficient.

We tested for predation/hatchery source differences in activity level using two binary activity metrics: activity >1 (any movement) and activity >2 (any foraging, fast-swimming or aggressive behaviour). We used a generalized linear mixed model with a binomial distribution and a logit link function to predict activity:

$$A = \frac{e^x}{1 + (e^x)}. \quad (4)$$

$$X = a \times S + M + T. \quad (5)$$

A is activity, S is source-type, M is a random effect term for mesocosm identity within source-type, T is a random effect term for time since the start of observation and a is a model coefficient.

To test for fish source effects on community composition, we built models that predicted each producer or consumer metric:

$$N_{\text{producer}} = a \times S + b_1 \times B + b_2 \times R + b_3 \times F. \quad (6)$$

$$N_{\text{consumer}} = \exp(a \times S + b_1 \times B + b_2 \times R + b_3 \times F). \quad (7)$$

N is abundance, S is source-type, B is adult fish biomass, R is adult sex ratio (males/total), F is number of fry and a , b_1 , b_2 and b_3 are model coefficients. We used only mesocosms that contained

fish for these models. We used a general linear model for each producer metric, and a generalized linear model with a log link function and a Poisson distribution for each consumer metric.

3 | RESULTS

We found significant differences among population sources (captive-propagated, wild high-predation, wild low-predation) in morphology, behaviour and community effects. Captive-propagated fish did not simply resemble low-predation fish; they showed traits and community effects that differed from both wild source-types. All model coefficient estimates and likelihood ratio test outputs can be found in Appendix S1.

3.1 | Morphology

There was significant variation in mosquitofish morphology across source-types, with the largest differences between captive-propagated and wild sources (Figure 1, Table S2). Captive-propagated mosquitofish had more posterior eyes (larger heads) than fish from wild populations (likelihood ratio test for source-type effect: $\chi^2 > 10$, $df = 2$, $p < 0.01$ for both males and females; Figure 1; Table S2). Captive-propagated and wild high-predation male mosquitofish

both had deeper caudal peduncles than male wild low-predation fish (likelihood ratio test for source-type effect: $\chi^2 = 11.0$, $df = 2$, $p < 0.01$; Figure 1; Table S2).

3.2 | Exploration latency

The slope and direction of the size-latency relationship varied across source-types and sexes (likelihood ratio test for source-type \times male length: $\chi^2 = 9.36$, $df = 2$, $p < 0.01$; likelihood ratio test for source-type \times female length: $\chi^2 = 9.03$, $df = 2$, $p = 0.011$; Figure 2, Table S3). Captive-propagated females had similar exploration patterns to wild high-predation females, whereas captive-propagated males had similar exploration patterns to wild low-predation males. Specifically, pair latency increased (exploration decreased) with female size in both captive-propagated and wild high-predation populations; whereas, pair latency decreased (exploration increased) with larger female size in low-predation populations (Figure 2). Both the captive-propagated and wild low-predation pairs showed increased pair latency (decreased exploration) with increased male size, whereas wild high-predation pairs showed a weak negative relationship between latency (positive with exploration) and male length (Figure 2).

3.3 | In-mesocosm boldness and activity behaviour

Captive-propagated mosquitofish had similar in-mesocosm boldness and activity behaviour to low-predation wild fish. Captive-propagated and low-predation wild mosquitofish stayed farther from the observer and deeper in the water column than high-predation wild fish (Likelihood ratio test on source-type effect: $\chi^2 > 10$, $df = 2$, $p < 0.01$ for distance; $\chi^2 = 6.32$, $df = 2$, $p = 0.042$ for depth; Figure 3; Table S6). Captive-propagated and low-predation wild fish were also less active than high-predation wild fish during observation (Likelihood ratio test on source-type effect: $\chi^2 > 10$, $df = 2$, $p < 0.01$; Figure 4; Table S6).

3.4 | Ecological consequences

Fish additions resulted in a trophic cascade, as evident in the generally lower zooplankton and higher producer abundances in mesocosm with fish, compared to fishless control mesocosms (Figure 5). We observed source-type differences in the impact of mosquitofish on all measured consumers, but none of our producer metrics (likelihood ratio test for source-type effect on each measured consumer: $\chi^2 > 10$, $df = 2$, $p < 0.01$; Figure 5; Tables S4 and S5). Compared to our two wild populations, captive-propagated fish led to reductions in the number of benthic chironomid larvae and increases in the number of copepod nauplii (Figure 5). Compared to low-predation wild fish, high-predation wild fish generated decreases in every pelagic consumer and increases in benthic chironomid larvae, which were most abundant in the high-predation source mesocosms (Figure 5).

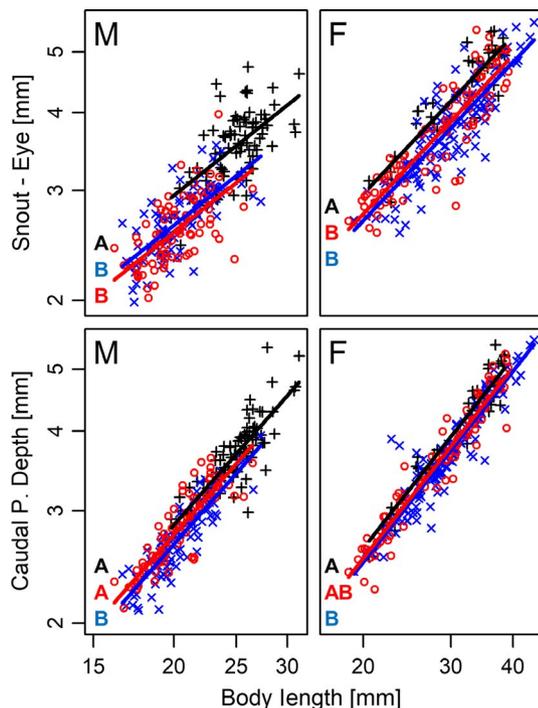


FIGURE 1 Morphology measurements for *Gambusia affinis* from three source-types: captive-propagated (black +), high-predation wild (red o) and low-predation wild (blue x), with population-level variation within source types removed. Captive-propagated *G. affinis* had more posterior eyes and deeper caudal peduncles than wild fish. Lines show predictions from general linear mixed models. Note the log-scaled axes. Letters show groupings based on Tukey post-hoc tests

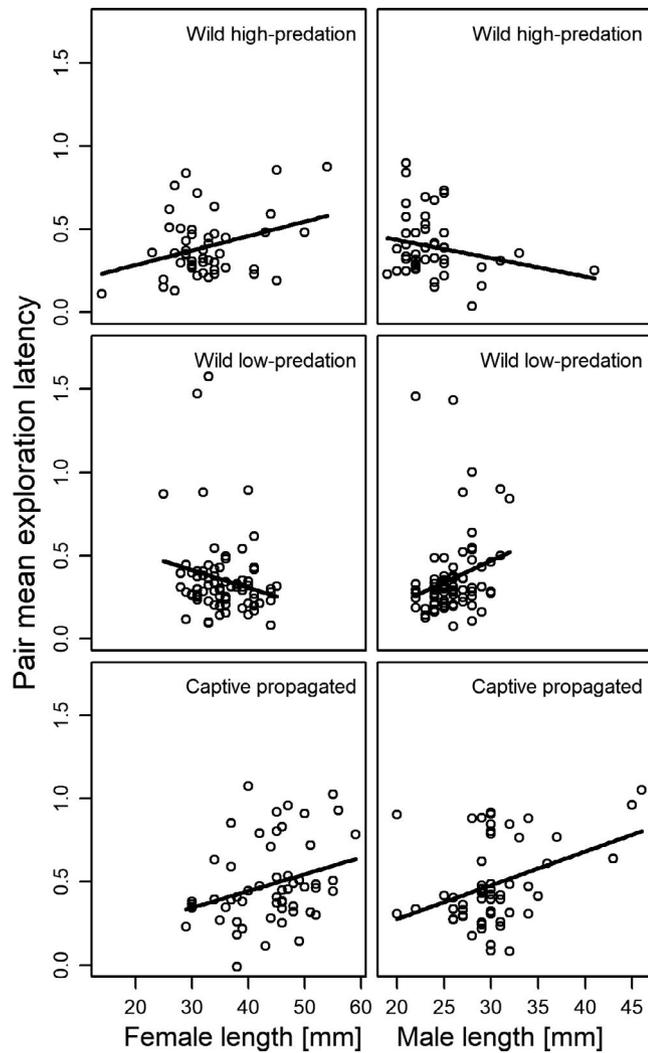


FIGURE 2 Exploration latency for pairs (male–female) of western mosquitofish (*Gambusia affinis*) based on source-type and individual body length, with male and female contributions to pair latency shown separately. Vertical axis data are arcsine-square root transformed proportions of a 600-s trial spent in an initial refuge before exploring, with variation from non-focal fish length (i.e., male length in the female length panels, etc.) and population within source-type removed. Lines show predictions from master model (Equation 2). Pair latency was analysed, rather than individual latency, as individuals within a pair had correlated leave times (Figure S2)

4 | DISCUSSION

4.1 | Captive propagation breaks wild trait patterns

Multiple populations of captive-propagated mosquitofish consistently demonstrated combinations of morphological and behavioural traits that deviated from typical suites of high- or low-predation wild traits. This result suggests that captive rearing conditions are not merely equivalent to other low-predation environments. Captive environments have high densities and few predators—much like low-predation wild environments—but also have abundant food and periodic removal of individuals—much like high-predation wild

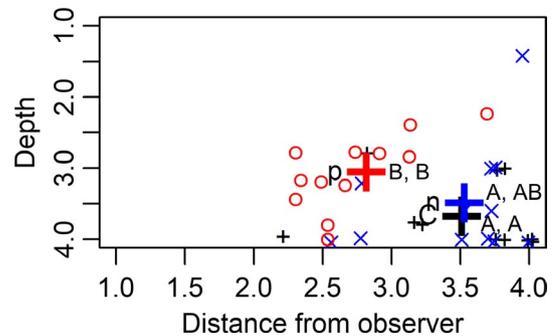


FIGURE 3 *Gambusia affinis* from a high-predation wild source (red o, p) lingered closer to a human observer and higher in the water column than captive-propagated (black +, C) or wild low-predation (blue x, n) fish during 150 s of observation. Source-type means indicated with bold +. Average distances and depths based on repeated measurements within each mesocosm are shown as single jittered points. Letters show categorization of distance and depth, respectively, based on Tukey post hoc tests

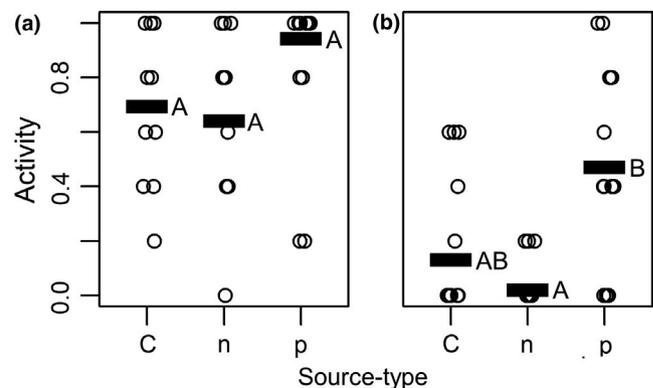


FIGURE 4 Wild *Gambusia affinis* shoals from a high-predation source (p) were more active than captive-propagated (C) or wild low-predation (n) fish during 150 s of observation. (a) Average frequency of behaviour > rank 1 (see text); (b) Average frequency of behaviour > rank 2. Thick bars show logit means for each source-type. Average activity values based on repeated measurements within each mesocosm are shown as single points. Letters show categorizations based on Tukey post-hoc tests

environments. Fitting with this unique combination of traits, we found evidence that captive-propagated phenotypes had cascading effects on pond communities unlike those from either wild type.

Multiple lines of captive-propagated mosquitofish had larger heads and caudle peduncles than wild fish (Figure 1), which is the opposite trend reported in the bulk of hatchery fish studies (which mostly cover salmonids) (Fleming & Einum, 1997; Fleming, Jonsson, & Gross, 1994; Swain, Riddell, & Murray, 1991), but see (Von Cramon-Taubadel, Ling, Cotter, & Wilkins, 2005). Larger tails have been associated with high-predation in wild mosquitofish (Langerhans, 2009; Langerhans et al., 2004) and other poeciliids (Magurran, Seghers, Carvalho, & Shaw, 1992; Palkovacs, Wasserman, & Kinnison, 2011; Reznick & Endler, 1982), but head size changes are reportedly variable in direction (Langerhans, 2009; Langerhans et al., 2004; Magurran et al., 1992; Palkovacs et al., 2011; Reznick & Endler,

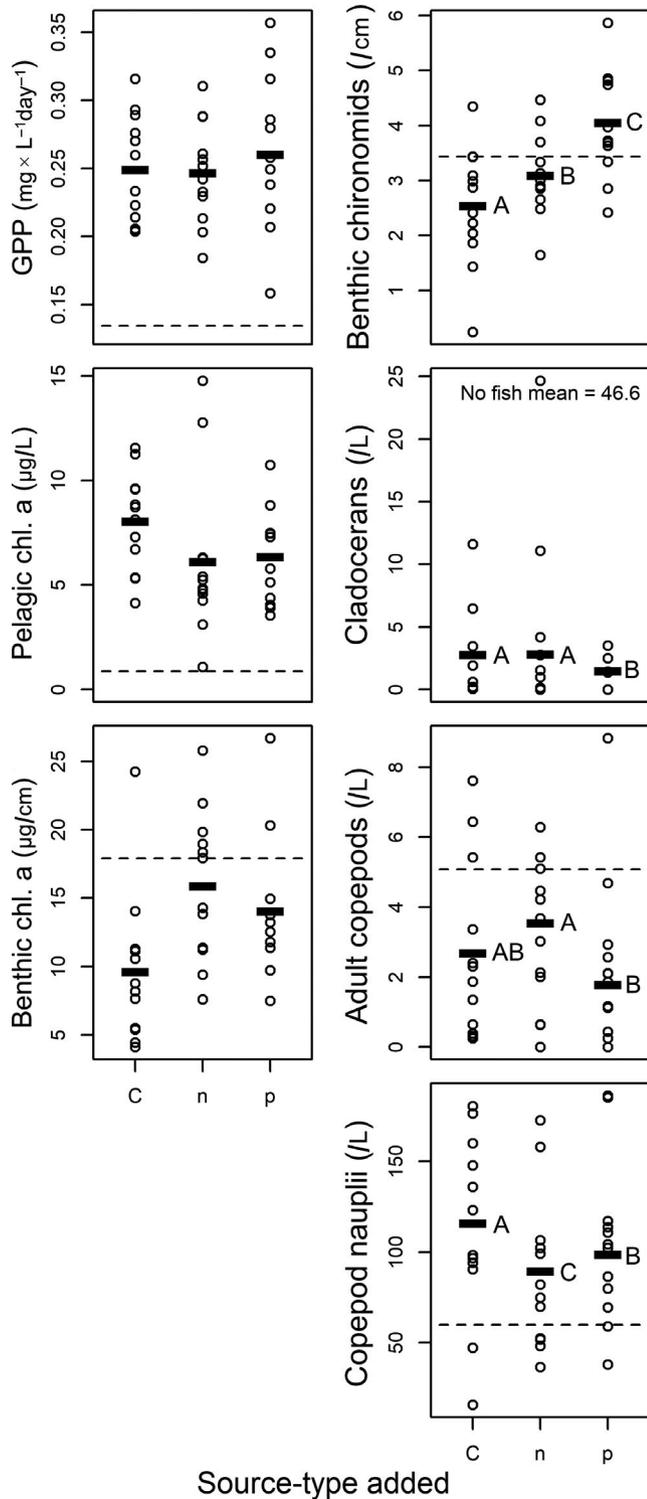


FIGURE 5 Mesocosm community responses to different *Gambusia affinis* source-types: captive-propagated fish (C), low-predation wild fish (n) and high-predation wild fish, with variation from fish biomass, sex ratio and fry count removed. Dashed lines show means from fishless control mesocosms. Fish presence caused a trophic cascade in almost all community variables. Fish source-type had little effect on producers (Table S4), but captive-propagated fish caused a consumer shift that strongly favoured copepod nauplii and cladocerans and lowered benthic chironomid abundance (Table S5). All responses above were measured 3 weeks after fish introduction, but are largely consistent with trends observed earlier in experimentation (Figure S6). Letters represent significant differences among fish population sources based on Tukey post-hoc tests

Female captive-propagated and wild high-predation mosquitofish both exhibited negative size-exploration relationships, whereas wild low-predation females drove positive size-exploration relationships (Figure 2). Decreased exploration with size may be a signature of selection against exploratory individuals more easily detected by largemouth bass (which are not gape limited when feeding on mosquitofish) in high-predation wild females (Blake & Gabor, 2014) and more easily captured by nets for stocking-out in captive-propagated females (van Wijk et al., 2013). In males, captive-propagated mosquitofish and wild low-predation mosquitofish both showed decreased exploration tendency with larger size. Our observed trend may indicate an energetic trade-off driven by determinate growth in males, in which smaller, more sexually aggressive (Hughes, 1985), exploratory males allocate fewer energetic and material resources to growth. As we observed, this trade-off may be stronger in captive propagation facilities and wild low-predation ponds compared to wild high-predation ponds due to more intense competition.

During exposure to an observer, captive-propagated and wild low-predation mosquitofish were less active than high-predation wild mosquitofish and remained farther in lateral distance and depth from the observer (Figures 3 and 4). Studies of other poeciliids (Archard & Braithwaite, 2011; Brown, Jones, & Braithwaite, 2005; Magurran et al., 1992) and of European minnows (*Phoxinus phoxinus*) (Magurran, 1990) show increased inspection activity and decreased inspection distance in high-predation fish. Such behaviour suggests that efficient risk-perception can be a component of antipredator adaptation, and as such high-predation individuals may take better advantage of times when predators are not nearby.

4.2 | Captive propagation alters communities

Captive-propagated mosquitofish significantly rearranged consumer communities. Relative to both wild source-types, captive-propagated mosquitofish reduced the abundance of benthic invertebrates (chironomids) and increased the abundance of pelagic invertebrates (zooplankton) (Figure 5). This community change suggests a substantial shift in captive fish foraging niche and/or reduced ability to capture smaller, more mobile prey. The more posterior eyes

1982). While fish in most captive propagation systems are free from interspecific predation, the enhanced burst-swimming ability conferred by a larger caudle peduncle (Langerhans, 2009) may also aid fish in frenzied food capture, net evasion (van Wijk et al., 2013) or escape from cannibalism—which can be intense in dense populations of captive-propagated mosquitofish (Dionne, 1985). Furthermore, the larger head sizes we observed in captive-propagated mosquitofish may increase perceptive ability, aiding in all of the above as well.

of captive-propagated fish (Figure 1) may decrease recognition and capture of small, mobile prey. Captive lines that become adapted or habituated to food that settles to the bottom of tanks might maintain these benthic feeding habits in the wild. Furthermore, the behavioural changes in captive-propagated fish—which may be due to avoidance of human “predators” (see above)—may shift the preferred habitat of captive-propagated mosquitofish to benthic areas away from possible net capture. Indeed, changes in feeding style or efficiency have been noted for captive populations of other species (Huntingford, 2004), including masu salmon (*Oncorhynchus masou*) (Reinhardt, 2001), rainbow trout (*Oncorhynchus mykiss*) (Lucas, Drew, Wheeler, Verrell, & Thorgaard, 2004), Atlantic salmon (Einum & Fleming, 1997) and zebra danio (Robison & Rowland, 2005). These prior studies did not examine the effects of feeding differences on food webs, but widespread observations of feeding changes caused by captive propagation suggest that broader ecological effects, as shown here, could be common. Although rarely considered, such a niche shift—as opposed to some general reduction in vigour—may be at least partly responsible for observations of low fitness of captive fish lines stocked into wild environments. Likewise, niche shifts might partly explain why captive-propagated fish sometimes fail to achieve biocontrol goals (Blaustein, 1992).

While mosquitofish presence significantly altered pelagic production through a trophic cascade (Figure 5), differences among mosquitofish source-types in invertebrate community structure did not overtly extend to primary producers. Cascading effects of captive propagation on producers could have occurred on longer or shorter time-scales than our sampling schedule, or could have been missed by our particular producer metrics. Community compensation in the producer or consumer trophic levels could also dampen the effect of mosquitofish phenotype on producers (Pace, Cole, Carpenter, & Kitchell, 1999) and could be missed by measures like total chlorophyll-*a* and GPP (i.e., cryptic eco-evolutionary trophic cascades, Kinnison, Hairston, & Hendry, 2015). In another model system for evo-to-eco effects, evolutionary divergence in stickleback (*Gasterosteus aculeatus*) feeding modes led to consumer community divergence, but this consumer restructuring did not always cascade down to the producer level (Des Roches, Shurin, Schluter, & Harmon, 2013).

In the ecological frame, a shifting niche in captive fish lines has potentially broad ecosystem implications. Phenotypic divergence leading to shifts from pelagic to benthic feeding, as we observed in captive-propagated sources, has the potential to alter food web interactions and nutrient pathways (Tuckett, Simon, & Kinnison, 2017) potentially leading to a range of unintended ecological consequences, from simple community composition shifts to full ecosystem regime shifts (Evans & Loftus, 1987; Jackson et al., 2014; Tuckett et al., 2017). Given that much fish stocking occurs into already stressed ecosystems, the scope and consequences of such divergence deserves much broader consideration.

The consistent morphological and behavioural differences between replicate populations of captive and wild mosquitofish suggest that captive propagation has an identifiable phenotypic and

ecological signature in mosquitofish. While we focused on mosquitofish taken directly from their respective sources to reflect the reality of stocking and translocation programmes (i.e., instead of using common garden rearing), there is widespread evidence for genetic local adaptation in *Gambusia* spp. (Brown, 1985; Meffe, Weeks, Mulvey, & Kandl, 1995; Stearns, 1983b), suggesting that at least some of the trait variation we observed has a genetic basis. Thus, the community changes wrought by captive-propagated mosquitofish suggest that the syndrome of captive propagation extends to the ecological role of fish after release. This syndrome may eventually be reversed through plastic and genetic re-adaptation to the wild (i.e., feralization (Daniels & Bekoff, 1989; Stringwell et al., 2014)), dampening the environmental impact of one-time fish introductions. However, continued introduction of captive-propagated fish to the same area (e.g., supplementation) is likely to sustain the persistence and ecological impacts of captive phenotypes. Based on the high frequency of continued intentional (Pister, 2001) or unintentional (Naylor et al., 2005) releases of captive-propagated organisms into the wild, the degree to which captive propagation alters the ecological role and ecosystem services of fish demands greater attention.

5 | CONCLUSIONS

A unique combination of environmental conditions and selective processes—likely including competition, harvest and cannibalism—creates unique combinations of morphological and behavioural traits in captive-propagated mosquitofish. Such trait change also appears to shift the foraging niche of captive bred mosquitofish to favour consumption of relatively immobile, benthic food resources. This change in feeding niche altered aquatic prey community outcomes of fish introduction. Despite the potential negative environmental consequences of mosquitofish introductions (Pyke, 2008), mosquitofish remain a widespread tool for biocontrol and large-scale introduction is likely to continue (Swanson et al., 1996). We suggest that the choice of stocking from wild translocations or captive sources should be a conscious decision that weighs the potential broader ecological effects and services afforded by different phenotypes. Infusions of wild fish into captive programmes, and captive environments that more closely mimic wild conditions are common recommendations to slow inadvertent domestication (Hutchings & Fraser, 2008). Our results suggest that these tools may also have broader roles in achieving some ecosystem service goals of stocking.

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AUTHORS' CONTRIBUTIONS

M.T.K., Z.T.W. and E.P.P. conceived the project. Z.T.W., R.R.R., E.P.P. and M.T.K. designed experiments. Z.T.W., M.T.K. and R.R.R. collected fish. Z.T.W. and M.T.K. established mesocosms. R.R.R. conducted exploration behaviour trials. Z.T.W. conducted boldness and activity behavioural trials. Z.T.W. and D.C.F. conducted ecological sampling. Z.T.W. analysed the data and created the figures. Z.T.W., D.C.F., R.R.R., E.P.P. and M.T.K. wrote the manuscript.

DATA ACCESSIBILITY

Data available via the Dryad Digital Repository <https://doi.org/10.5061/dryad.0jh0f94> (Wood, Fryxell, Robinson, Palkovacs, & Kinnison, 2019).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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