Can separation along the temperature niche axis promote coexistence between native and invasive species?

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\textbf{ABSTRACT}

\textbf{Aim} Western mosquitofish (\textit{Gambusia affinis}) have been linked with the decline of native fish and amphibians throughout the world. Separation along the temperature niche axis may promote the long-term coexistence of introduced western mosquitofish, with native species in temperate regions. Recent research has shown that western mosquitofish can reduce the recruitment of native least chub (\textit{Iothichthys phlegethontis}) endemic to the Bonneville Basin. We tested the hypotheses that cold temperatures ($\leq$ 15 °C in the summer, freezing winters) would: (1) reduce the aggressive and predatory effects of western mosquitofish on least chub, and (2) eliminate the overwinter survival and recruitment of western mosquitofish while having little effect on least chub recruitment.

\textbf{Location} Bonneville Basin of Utah, USA.

\textbf{Methods} We used short-term tests in the laboratory at the level of individuals and manipulated temperature (warm, cold and seasonal treatments) in long-term experiments using mesocosms at the population level.

\textbf{Results} Cold temperatures ($\leq$ 15 °C) reduced the aggression and predation of western mosquitofish on least chub at the level of individuals. At the population level, however, cool summers ($\leq$ 15 °C) eliminated recruitment in both species because they required warm summers (c. 20–30 °C) to survive freezing winters. Although least chub had an overwinter advantage in survival (75\% least chub, 45\% western mosquitofish), it was overwhelmed by the rapid reproduction of western mosquitofish as temperatures increased in the summer.

\textbf{Main conclusions} Studies at the level of populations are necessary to understand the ultimate effects of introduced species on native taxa. Separation along the temperature niche axis was not sufficient to promote coexistence between these species in habitats with warm summers (c. 30 °C). Although coexistence may be possible in habitats with cool summers ($\leq$ 20 °C) and freezing winters, the ability of niche separation to promote long-term coexistence between native and introduced species may ultimately depend on their respective rates of evolution. Long-term coexistence may not be possible if introduced species can adapt to new environmental conditions faster than native species can evolve mechanisms to reduce their harmful effects.

\textbf{Keywords} Biological invasions, evolutionary race, invasive species, least chub, long-term experiments, niche separation, western mosquitofish.
INTRODUCTION

Introduced species can cause the decline or local extirpation of native species because of unstable direct and indirect biotic interactions (Barel et al., 1985; Coblentz, 1990; Hobbs & Mooney, 1998). When native species decline because of introduced taxa, the ultimate outcome (coexistence or extinction) may depend on the ability of native species to exploit a niche dimension unavailable to introduced species.

Traditional and current ecological theory suggests that competing species can coexist if their niche requirements are sufficiently different (MacArthur & Levins, 1967; Diamond, 1975; Chesson, 2000). Under the concept of the Grinnellian requirements, niche (Grinnell, 1917; Pulliam, 2000) sufficient differences among species can be determined by their response to environmental stress ($S^\ast$). For example, when two competing species are affected by the same stress (e.g. cold temperatures) the species that can tolerate the greatest level of stress (e.g. coldest temperatures) will persist (Chase & Leibold, 2003).

Mosquitofish are the most widely distributed freshwater fish in the world having been introduced as a mosquito control agent to every continent except Antarctica (Dawes, 1991; Pyke, 2005). The Global Invasive Species Database listed western mosquitofish as one of the world’s worst 100 invasive species (Lowe et al., 2000). Western mosquitofish have been linked with the decline and local extirpation of native fish and amphibians around the world (e.g. Courteney and Meffe, 1989; Hamer et al., 2002). They are live-bearing topminnows (Poeciliidae) capable of achieving high population densities within a single growing season (McKay, 1984; Courteney and Meffe, 1989).

Western mosquitofish are native to subtropical climates of the southern United States and the Mississippi River drainage (Courteney and Meffe, 1989). Western mosquitofish select habitats (Bacon et al., 1968; Winkler, 1979), and show maximum prey consumption rates (Chippa & Wahl, 2004) and growth rates (Wurtsbaugh & Cech, 1983; Vondracek et al., 1988) at temperatures near 30 °C inside and outside their native range (Pyke, 2005). However, the effect of freezing temperatures on the overwintering capacity of western mosquitofish has not been explored. They were introduced to Utah from Tennessee in the early 1900s, and have since spread throughout the state in a variety of habitats, including artesian springs of the Bonneville Basin (Rees, 1934; Otto, 1973).

Least chub are cyprinid minnows that were once widely distributed in a variety of habitats throughout the Bonneville Basin (e.g. Cope & Yarrow, 1875; Jordan, 1891). By 1979, habitat alterations and interactions with western mosquitofish reduced least chub to 11 small populations in artesian springs (Perkins et al., 1998).

Least chub are native to colder climates and appear to have a colder temperature tolerance than mosquitofish (Billman et al., 2006). Billman et al. (2006) found that the optimal temperature for growth of juvenile least chub was 22 °C, 8 °C lower than the optimal temperature for growth of western mosquitofish. Although the overwinter survival rates of least chub have not been investigated, they probably depend on summertime temperatures. The overwinter capabilities of small fish often depend on sufficiently high summer temperatures to permit the development of lipid stores which prevent starvation during the winter (Meffe & Snelson, 1993a,b). Least chub may find a refuge from western mosquitofish if they can store lipids at colder summertime temperatures. Laha & Mattingly (2006) suggested that 15 °C during the summer was a possible temperature refuge for Barrens topminnow (Fundulius julis) because at this temperature their growth was 2 times greater than western mosquitofish.

Our objective was to determine if separation along the temperature niche axis could promote coexistence between least chub and western mosquitofish. Our emphasis was on experimentally determining the overwintering capacity of western mosquitofish compared with native least chub. We tested two hypotheses at the level of individuals: (1) colder temperatures ($\leq 15$ °C) would reduce the aggressive behaviour and predatory effects of western mosquitofish on least chub, and (2) colder temperatures ($\leq 15$ °C) would reduce the non-lethal effects of western mosquitofish on the habitat use, activity and feeding of least chub. However, factors that alter the behaviour of individuals may not necessarily scale-up to affect recruitment at the population level (Werner, 1998). Thus, we tested two additional hypotheses: (3) recruitment of least chub in the presence of western mosquitofish would be greater at seasonally constant cold temperatures (summers $\leq 15$ °C and freezing winters) than at seasonally constant warm temperatures (e.g. summers reaching 30 °C with warm winters $> 15$ °C), and (4) normal seasonal variation in temperatures (warm summers, freezing winters) would improve the overwintering capacity of least chub while eliminating western mosquitofish.

CONCEPTUAL BACKGROUND

Figure 1 shows the hypothetical performance curves of least chub and western mosquitofish as a function of temperature. Peaks show the optimal temperatures for reproduction and growth, the tails show a decrease in performance with changes in temperature and bars show differences in cold tolerance or the temperature range required for winter survival. The shape of the curves at cold temperatures and the width of the bars are not known for both species but will be examined in this study. The top panel shows the predicted separation in the performance and overwinter ability of both species (Fig. 1a). It shows sufficient separation along the temperature niche axis to promote coexistence. Two outcomes would increase overlap along the temperature niche axis and decrease the probability of coexistence: (1) least chub may have a narrower performance curve and poorer overwinter capacity than expected and be unable to perform better than western mosquitofish at colder temperatures (Fig. 1b), and (2) introduced western mosquitofish may have a wider performance curve and better overwinter capacity than expected (Fig. 1c). The last
alternative would indicate that western mosquitofish intro-
duced to Utah have developed an increased tolerance to the
cold.

METHODS

Individual level: predation

We examined the predatory effects of western mosquitofish on
juvenile least chub at four temperatures: 10, 15, 20 and 25 °C.
Four adult female western mosquitofish (> 40 mm SL) and
four juvenile least chub (< 4 mm SL) were haphazardly netted
from their respective holding tanks (190 L) and placed in an
observation aquarium (20 L) at each temperature. Female
western mosquitofish were used because they are larger and
more aggressive than males. We obtained western mosquitofish
from the Davis County Mosquito Abatement District. These
fish are descendents of multiple wild populations introduced
to Utah around 70 years ago.

All western mosquitofish were deprived of food for 48 h
prior to a trial. All fish were acclimated in the observation
aquarium for 1 h before western mosquitofish were released
and the trial began. During the acclimation period, western
mosquitofish were kept in clear, plastic containers inside the
observation aquarium to prevent contact with least chub. Each
observation aquarium was supplied with cover from preda-
tion (artificial vegetation), and all fish were used in only one
trial.

We performed a total of thirty-one trials, eight at each
temperature except 25 °C, where we ran only seven trials. Four
trials at each of the four temperatures were run simultaneously.
Each trial was terminated independently when the number of
least chub was reduced by half or after 48 h, whichever came
first. All sides of the aquaria were covered with opaque plastic
to minimize the effects of humans on fish behaviour. One
panel of plastic was briefly removed to record the number of
surviving least chub every half hour for the first 2 h and every
hour thereafter. All trials began between 9:00 and 9:30 AM and
were performed in August 2006.

We controlled temperatures by placing the observation
aquaria inside a larger holding aquaria (190 L) equipped with
chillers or 100-W heaters. All fish were acclimated in separate
190-L aquaria to each of the four treatment temperatures for at
least 1 week before the trials began.

The effect of temperature on the survival of juvenile least
chub (response variable) in the presence of predatory western
mosquitofish was determined using a survival analysis (Kalb-
bleisch & Prentice, 2002). This analysis is based on censored
observations. Censored observations are categorical because
they occurred within time intervals and the precise time of
mortality was not known. An analysis of variance would
require the exact time of death, whereas nonparametric
procedures (e.g. a rank sum analysis) would be appropriate
but lack power to resolve differences in mortality between
temperature treatments. Survival analysis combines the power
of parametric statistics with categorical/censored data. The
survival time of individual fish in each treatment was modelled
using the Weibull distribution and the effects of temperature
on mortality were modelled using The Proportional Hazards
model (Kalbfleisch & Prentice, 2002). In this case, the hazard is
the probability of being eaten in the next time interval.
Product–limit curves were used to display the mortality data
(Kalbfleisch & Prentice, 2002).

Individual level: aggression

We used the same aquaria and set-up as in the predation study
to determine the effects of temperature on aggressive inter-
actions between least chub and western mosquitofish. This was a
2 x 4 factorial design with the presence or absence of western
mosquitofish crossed with each temperature (10, 15, 20 and
25 °C). This was a paired design because the behaviour of the
same individual fish (least chub) at one of the four temper-
atures was recorded in the presence (treatment) and absence
of western mosquitofish (control). We ran six trials at each
temperature and each trial spanned 2 days because we waited
24 h between running treatments with mosquitofish and
controls without mosquitofish. We randomly determined the
order of the control and treatment and all fish were deprived
of food for 24 h prior to each trial.

Four least chub, two large (30–40 mm SL) and two small
(20–30 mm SL), were haphazardly netted from a holding tank
and placed in an observation aquarium at the start of a trial.
We used small and large individuals of both species because

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interactions are often size dependent in fish. In treatments with western mosquitofish, four females, two large (30–40 mm SL) and two small (20–30 mm SL), were kept in a separate plastic container within the observation aquarium during the acclimation period (40 min). At the end of the acclimation period, flake food was placed in a food ring floating at the surface of the water, the western mosquitofish were released with a drawstring without exposure to humans and all interactions were continuously recorded with digital camcorders for 20 min. Four trials in four separate aquaria, one at each temperature, were recorded simultaneously. The amount of food was not sufficient to satiate and dampen the aggressiveness of western mosquitofish.

We analysed the video to measure the effect of temperature on habitat use, activity, feeding and aggression of least chub in the presence and absence of western mosquitofish. The front wall of the observation aquarium was divided into equal quadrants (top left, top right, bottom left and bottom right) and we randomly placed artificial vegetation in either the left or the right quadrant. Habitat use was the proportion of time spent in each of the quadrants, hereafter referred to as top open, bottom open, top cover and bottom cover. Activity was measured as the number of line crossings between quadrants. The number of aggressive interactions was recorded for each trial (biting, pushing, chasing, etc.). The species and size of the initiator, recipient and victor were noted for each interaction. An initiator was identified as a fish that directly and quickly swam towards another fish, and the victor was the fish that kept the space after the interaction (Mills et al., 2004).

We positioned a floating food ring (28.3 cm²) in the open quadrant to determine the feeding rate of least chub in the presence and absence of western mosquitofish and to maximize the probability that the two species would interact. Least chub could forage in the open and run the risk of encountering western mosquitofish or remain sheltered and forgo feeding. Previous observations have shown that least chub will readily feed at the surface, especially when they are hungry. Feeding was measured as the number of bites per trial.

We used a mixed regression model (PROC MIXED; SAS Institute, 1997) to determine the effects of temperature, size, presence or absence of western mosquitofish and all interactions of factors on habitat use, activity and feeding (the three dependent variables) in separate analyses. We used a natural log transformation of the activity, a square root transformation of feeding and a logit transformation of habitat use. We dropped non-significant interactions from the full model and re-ran the analysis. Aggressive interactions were analysed with a generalized linear mixed model (PROC GLIMMIX; SAS Institute, 1997) to determine the effects of temperature and fish size on the number of aggressive interactions (dependent variable).

Population level: recruitment

We examined the recruitment and population growth of least chub for 22 months (June 2006–March 2008) in the presence and absence of western mosquitofish at seasonally constant warm and cold temperatures (hypothesis 3). The cold treatment experimentally tested the overwintering capacity of least chub and western mosquitofish without the advantage of warm summer temperatures. We added ten adult least chub (five males and five females) to each of 20 mesocosms and randomly assigned ten adult western mosquitofish (five males and five females) to five mesocosms in each temperature treatment using a fully crossed design: seasonally constant cold and warm temperatures in the presence and absence of western mosquitofish.

Our mesocosms consisted of large (1136 L), circular livestock watering tanks fitted with a standing drain (20 cm) and a gravity-fed, flow-through plumbing system (Fig. 2). City water was pumped through a large charcoal filter leading to two lines. One line remained indoors and fed two holding tanks (1136 L each) located on an elevated platform (1.2 m in height), whereas the second line transported water to outdoor mesocosms. Chiller and heaters were used to cool water in the indoor holding tanks in the summer and warm it in the winter, respectively. Temperatures could be manipulated by adjusting the temperature setting on the Frigid Units and controlling the flow rate into each...
mesocosm. We also used air-conditioning indoors in the summer and freezing temperatures outdoors in the winter to maintain the cold treatment. Similarly, we kept fish in the warm treatment outdoors in the summer and indoors in the winter. We transported fish between the indoor and outdoor mesocosms in the spring and fall to maintain our temperature treatments. During the transfer process, the total number of fish in each mesocosm/replicate was counted and then randomly reassigned as a group to a new mesocosm within the same treatment either indoors or outdoors in September 2006, April 2007 and September 2007. Although the location of fish changed, they remained in the same replicate within the same treatment as a group throughout this experiment. Large windows exposed the indoor tanks to the same natural light cycle as the outdoor tanks.

Although this experiment ended in September 2007, the warm treatment was extended through the winter until March 2008. Both species in the warm treatment were subjected to normal winter temperatures in 2007–08 to test the hypothesis that normal summer temperatures would improve the over-wintering capacity of least chub while eliminating western mosquitofish (hypothesis 4). In September 2007, 61 adult (≥30 mm SL) and 97 juvenile (<30 mm SL) least chub from the warm treatment were placed in each of five outdoor tanks. At the same time, 100 adult (≥30 mm SL) and 400 juvenile (<30 mm SL) western mosquitofish were kept separate from least chub in five additional outdoor tanks. The surviving number of adult and juvenile least chub, and western mosquitofish were counted at the end of the winter (March 2008).

We used digital thermographs to record the temperature every 2 h in each tank for the duration of the warm, cold and seasonal treatments. We fed the fish in all mesocosms each day with a mixture of flake and granular food. Their diet was also periodically supplemented with zooplankton from Utah Lake. Least chub in three of the warm treatment tanks in the absence of western mosquitofish died from infection (Aeromonas spp.) during the first winter (2006). They were replaced in the spring of 2007.

The cold and warm treatments and the presence of western mosquitofish were our predictor variables for the population growth of least chub (dependent variable) in a general regression model (PROC GENMOD; SAS Institute, 1997). We transformed the dependent variable using the natural log function with a Poisson distribution, assuming extra Poisson variability. We also used a logistic regression analysis (PROC LOGISTIC; SAS Institute, 1997) to determine the percentage overwinter survival of least chub and western mosquitofish in the seasonal treatment based on three predictor variables: (1) fish size (juveniles vs. adults within species), (2) species (least chub vs. mosquitofish), and (3) treatment (seasonal overwintering survival vs. overwintering survival in the warm and cold treatments). We repeated this analysis deleting data from the least chub populations used to replace those that died of infection during the first year in the warm treatment without western mosquitofish to determine if this affected our results.

RESULTS

Individual level: predation

Colder temperatures reduced the predation of western mosquitofish on least chub (Fig. 3). Decreasing temperatures were positively correlated with a decline in the mortality of least chub ($\chi^2 = 49.30; d.f. = 3; P < 0.001$). The pair-wise comparison between 20 and 25 °C was the only non-significant comparison ($\chi^2 = 0.32; d.f. = 1; P = 0.572$), all others were significantly different ($\chi^2 = 10.73; d.f. = 1; P < 0.001$). The rate of survival was over 3× greater at 10 vs. 25 °C. Only five least chub were eaten in all trials at 10 °C.

Individual level: aggression

There was a positive relationship (Fig. 4a) between the number of aggressive interactions and temperature ($F_{2,17} = 7.83$; $P = 0.004$). There were no aggressive interactions at 15 °C and only three at 10 °C. There were 96 aggressive interactions summed across all temperatures. Of those, western mosquitofish initiated 62% and won 74%. There was only one instance where western mosquitofish initiated an aggressive interaction and failed to be the winner. Fish size (least chub or western mosquitofish) was not significantly correlated with the number of aggressive interactions ($F_{1,17} = 1.49; P = 0.239$).

The proportion of time that least chub spent in cover was not significantly correlated with temperature ($F_{3,20} = 1.33$, $P = 0.29$) or the size of least chub ($F_{1,16} = 1.56$, $P = 0.21$), but was affected by the presence of mosquitofish ($F_{1,23} = 25.96$, $P < 0.001$). Contrary to predictions and previous research (Mills et al., 2004), least chub in the presence of western mosquitofish spent less time in cover and more time in the open (Fig. 4b), were more active ($F_{1,23} = 37.64$, $P < 0.001$; Fig. 4c) and fed more frequently in the top open quadrants, especially at higher temperatures (Table 1; Fig. 4d). Least chub in this study were naive and did little to protect themselves from western mosquitofish predation and aggression. Instead, they tended to school with western mosquitofish leading to increases in least chub activity and feeding, and reducing least chub use of cover.

Figure 3 Cumulative percentage mortality of juvenile least chub in the presence of adult female western mosquitofish at four temperatures over 48 h. Vertical lines represent the time of death of one or more least chub.
As expected, feeding (Table 1) and activity ($F_{3,15} = 3.23; P = 0.05$) of least chub increased as temperature increased. Also, the size of least chub had a significant effect on feeding rates in the bottom open quadrants because large least chub spent more time than small least chub on the bottom, and large least chub fed more frequently than small least chub (Table 1). However, least chub of both size classes spent only 3% of the total time in all trials in the top quadrants.

### Population level: recruitment

Our experimental set-up created distinctly different temperature treatments. During the first year, fish in both the cold and warm treatments were kept at relatively constant cold or warm temperatures with little seasonal variation (Table 2). Temperatures in the cold treatment remained below 15 °C year round, with winter temperatures near freezing. Although ice formed on the surface of water in the cold treatment in the winter, there was always at least 15 cm of liquid water in each mesocosm. Temperatures in the warm treatment remained above 15 °C throughout the year, reaching over 30 °C in the summer.

Cold temperatures with little seasonal variation eliminated western mosquitofish recruitment and survival. Western mosquitofish numbers in the cold treatment were smaller than in the warm treatment in September 2006 (Fig. 5; $\chi^2 = 174.09; d.f. = 1; P < 0.001$) because there was no recruitment in the cold treatment during the summer of 2006. Western mosquitofish numbers also differed between the cold and warm treatments in May 2007 because none of the western mosquitofish in the cold treatment survived the winter of 2006 (Fig. 5). These data show that normal winter temperatures can eradicate western mosquitofish if preceded by cold spring/summer temperatures ($\leq 15 ^\circ C$). In contrast, western mosquitofish in the warm treatment reached high densities by the end of the first summer and maintained high densities through the winter and the following spring/summer (Fig. 5). Juveniles and adults of both species showed near 100% overwinter survival in the warm treatment (Fig. 6).

Least chub are better adapted to freezing winter conditions than western mosquitofish. Western mosquitofish were able to survive normal freezing winters if preceded by summer temperatures near 30 °C. Between 40 and 45% of western mosquitofish survived the winter in the seasonal treatment compared to 0% overwinter survival of western mosquitofish in the cold treatment (Fig. 6). Juvenile and adult least chub in the seasonal treatment ($\chi^2 = 0.01; d.f. = 1; P = 0.94$) showed c. 75% overwinter survival if preceded by warm summer temperatures (Fig. 6). In contrast to western mosquitofish, adult survival of least chub was the same (75%) in the cold and seasonal treatments ($\chi^2 = 0.13; d.f. = 2; P = 0.94$). Like western mosquitofish, however, none of the juvenile least chub survived the winter in the cold treatment (Fig. 6).

Western mosquitofish had no effect on the number of least chub in the cold treatment ($\chi^2 = 0.51; d.f. = 1; P = 0.476$), but the number of least chub was similar throughout the experiment because of the absence of recruitment (Fig. 7). Although juvenile least chub were born during the summer in the absence of western mosquitofish in the cold treatment (between 1 and 10 observed per mesocosm), none survived the winter. In contrast, western mosquitofish eradicated least chub in the warm treatment after the first year (Fig. 7; $\chi^2 = 4.15; d.f. = 1; P = 0.042$). Numbers declined during the first summer and only four least chub (all males) from all five replicates remained by the summer of 2007 (Fig. 7). However, a significant increase in least chub in the warm treatment in the absence of western mosquitofish (Fig. 7) was observed during the spring/summer of 2006 ($\chi^2 = 41.88; d.f. = 1; P < 0.001$) and 2007 ($\chi^2 = 58.88; d.f. = 1; P < 0.001$). This observation was not altered when we deleted data from the
three populations that died because of infection during 2006 ($\chi^2 = 26.83$; d.f. = 1; $P < 0.007$).

**DISCUSSION**

Warm summer (c. 30 °C) and winter (> 15 °C) temperatures produced dense populations of western mosquitofish capable of completely eradicating least chub from mesocosms in < 1 year. In the wild, western mosquitofish prey on and out-compete least chub (Mills *et al.*, 2004) because of spatial and temporal overlap during reproduction (Ayala *et al.*, 2007). Both species reproduce in shallow (< 30 cm), warm (20–30 °C) marshes near their respective optimal temperatures for growth (Pyke, 2005; Billman *et al.*, 2006). This interaction is undoubtedly an important cause for the decline of least chub (Ayala *et al.*, 2007).

Least chub may coexist with western mosquitofish if they can reproduce and grow at colder temperatures or if western mosquitofish are unable to survive freezing winter temperatures that have little effect on the survival of least chub. Laboratory experiments showed that cold temperatures (< 15 °C) reduced the predation and aggression of western mosquitofish on least chub. However, long-term experiments at the population level showed that a reduction in negative interactions between individuals was not sufficient to promote coexistence.

Our results support previous observations that the critical temperature for the onset of western mosquitofish reproduction is near 14–16 °C (Medlen, 1951; Koya & Kamiya, 2000). That is, western mosquitofish failed to reproduce or overwinter in the cold treatment. Annual temperatures that never exceed 15 °C can eradicate this species in the Bonneville Basin. However, seasonally constant cold temperatures (≤ 15 °C) did not constitute a refuge for least chub because least chub reproduction through the summer in the cold treatment was barely sufficient to offset the small amount of adult mortality.
and no juvenile least chub from the cold treatment survived the winter. Thus, least chub have a narrower performance curve and are less tolerant of cold temperatures than initially expected, consistent with Fig. 1(b).

Juveniles of both species, and adult western mosquitofish, required warm summer temperatures (c. 30 °C) to achieve sufficient size and energy reserves to successfully survive freezing winter temperatures. That is, 75% of least chub and 45% of western mosquitofish survived freezing temperatures in the seasonal treatment when previously exposed to normal summer temperatures. This advantage in overwinter survival of least chub over western mosquitofish was not sufficient to promote coexistence. Coexistence may require low reproduction and growth of western mosquitofish in the summer and nearly complete mortality in winter because of their high reproductive potential. Normal, warm summer temperatures prior to normal freezing conditions in the winter allowed western mosquitofish to increase from 10 to an average of 500–600 hundred individuals per mesocosm by the end of the first summer.

The seasonal treatment confirmed previous observations that cold-adapted western mosquitofish can survive freezing winter temperatures (Krumholz, 1948; Pyke, 2005). Western mosquitofish have a broader performance curve and were more tolerant of cold temperatures than initially expected, consistent with Fig. 1(c). Their overwinter survival, however, is dependent on warm summer temperatures (c. 30 °C), which has a positive effect on the amount of energy stored prior to the onset of winter. This is an important caveat because summer temperatures in artesian springs of the Bonneville Basin are between 25 and 32 °C and winter temperatures at the inflow are ≥ 9 °C (Keleher & Rader, 2008). Thus, most artesian springs provide insufficient separation along the temperature niche axis to permit coexistence between these species because of warm summer and warm winter temperatures.

Separation along the temperature niche axis between least chub and western mosquitofish was smaller than initially hypothesized (Fig. 1a) because least chub performed worse (Fig. 1b) and western mosquitofish performed better than expected at cold temperatures (Fig. 1c). There may be a narrow window around 20 °C that would permit coexistence by reducing the recruitment of western mosquitofish while sustaining least chub. Twenty degrees centigrade is near the optimal temperature for growth of least chub, but it is 10 °C below the optimal temperature for the growth of western mosquitofish. At 20 °C, least chub may succeed at storing sufficient energy reserves to overwinter, whereas western mosquitofish may fail. Reintroducing least chub to Rocky Mountain streams surrounding the Bonneville Basin, which was part of their historic range, may provide a refuge from western mosquitofish. Summer temperatures near 20 °C combined with freezing winters are common in most Rocky Mountain streams.

Determining the overwintering capacity of western mosquitofish in Utah is an intriguing question because they are capable of rapid genetically based evolution (Stockwell & Weeks, 1999). Western mosquitofish introduced to northern climates appear to eventually develop a lower temperature tolerance than in their home range (Rees, 1934; Krumholz, 1944; Otto, 1973).

In 1927, the Salt Lake City Mosquito Abatement District translocated 50,000 western mosquitofish from southern California to various non-thermal ponds throughout the city. None survived the first winter (Rees, 1934). In 1945, western mosquitofish translocated 10 years earlier from Tennessee to Utah could only survive the winter in warm artesian springs. Over the next 50 years, these fish were repeatedly introduced and re-introduced to a variety of shallow, non-thermal habitats for mosquito control. By 2001, 20–40% of these western mosquitofish, originally from Tennessee, could overwinter in non-thermal rearing ponds with a layer of ice for 3–4 months (Davis County Mosquito Abatement, pers. comm.). Thus, introduced western mosquitofish appear to have evolved an increased tolerance to freezing winter conditions. This may be a genetically based adaptation, rather than cold acclimation attributed to plasticity because the increased tolerance to freezing was acquired over several generations. However, we cannot, without appropriate experiments, exclude the possibility that increased cold tolerance is a plastic trait (e.g. Rader et al., 2005). Such experiments were beyond the scope of this study.

The ability of niche separation to promote long-term coexistence between native and introduced species may ultimately depend on their respective rates of evolution. Long-term coexistence may not be possible if introduced species can adapt to new conditions outside their home range (e.g. freezing temperatures) faster than native species can evolve mechanisms that reduce their harmful effects (Whitney & Gabler, 2008).

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REFERENCES


Winkler, P. (1979) Thermal preference of *Gambusia affinis affinis* as determined under field and laboratory conditions. *Copeia*, 1979, 60–64.


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