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Niche Separation Along Environmental Gradients as a Mechanism to
Promote the Coexistence of Native and Invasive Species

by

Edmund R. Priddis

A thesis submitted to the faculty of

Brigham Young University

in partial fulfillment of the requirements for the degree of

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Department of Biology

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BRIGHAM YOUNG UNIVERSITY

GRADUATE COMMITTEE APPROVAL

of a thesis submitted by

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As chair of the candidate's graduate committee, I have read the thesis of Edmund R. Priddis in its final form and have found that (1) its format, citations, and bibliographical style are consistent and acceptable and fulfill university and department style requirements; (2) its illustrative materials including figures, tables, and charts are in place; and (3) the final manuscript is satisfactory to the graduate committee and is ready for submission to the university library.

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ABSTRACT

Niche Separation Along Environmental Gradients as a Mechanism to Promote the Coexistence of Native and Invasive Species

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Department of Biology

Master of Science

Niche separation may be the key to promoting the long-term coexistence of introduced and native species. Physical alterations to the environment (habitat manipulation) or re-introducing native species to former habitats can exploit the maladapted traits of introduced species to create a refuge for native species. No two species have identical niches because evolutionary constraints differ between species with different evolutionary histories. Our objectives were to determine if cold temperatures could promote coexistence between native least chub and introduced western mosquitofish. We used individual scale and population scale experiments to test four hypotheses: 1) colder temperatures would reduce the aggressive behavior and predatory effects of western mosquitofish on least chub, 2) colder temperatures would reduce the effect of western mosquitofish on the habitat use, activity, and feeding of least chub, 3) western mosquitofish would not be able to overwinter without warm refuges,

and 4) western mosquitofish reproduction would be delayed or absent at colder temperatures, whereas colder temperatures would not inhibit least chub recruitment. At the individual scale cold temperatures reduced the aggression and predation of western mosquitofish on least chub. However at the population scale there was little recruitment in the cold treatment and juvenile least chub did not survive the winter in the cold treatment. Adult least chub successfully overwintered at freezing temperatures whereas western mosquitofish had no recruitment in the cold treatment during the summer and no western mosquitofish survived the winter. There is adequate niche separation among the adults to promote coexistence but the juveniles of both species require warm habitat in the spring and summer to survive freezing winter temperatures. Habitat manipulation may reduce the availability of warm winter refuges for western mosquitofish while leaving warm habitats during the spring for least chub spawning and recruitment. Transplanting least chub to former cold habitats could eliminate western mosquitofish because of niche separation between the species along a temperature gradient. We suggest that the niche separation hypothesis has general application for the restoration of a variety of threatened native species.

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“Nature...is a unity in diversity of phenomena; a harmony, blending together all created things, however dissimilar in form and attributes; one great whole animated by the breath of life.”

Alexander von Humboldt, 1849

INTRODUCTION

Alexander von Humboldt (1849) described a world in harmony where coexistence and order emerged from the chaos of conflict. Darwin ([1859](#)) described a process that could reduce the extraordinary harm of one species on another. That is, nature can select for individual traits that tend to reduce niche overlap and thus promote the long-term coexistence of species ([Tilman 1982](#), [Chesson 2000](#)). The effects of invasive species often include the decline and local extirpation of native taxa ([Taylor et al. 1984](#), [Barel et al. 1985](#), [Miller et al. 1989](#), [Fritts and Rodda 1998](#), [Hobbs and Mooney 1998](#)). The introduction of species outside their historic range and the subsequent decline of native taxa sometimes occur faster than traits and mechanisms can evolve to promote coexistence ([Schoenherr 1981](#), [Arthington and Lloyd 1989](#), [Kupferberg 1997](#), [Mills et al. 2004](#)).

Western mosquitofish (*Gambusia affinis*) are one of the most widely introduced species around the world ([Courtney and Meffe 1989](#), [Dawes 1991](#)). They are live-bearing topminnows (Poeciliidae) with rapid reproductive potentials and the ability to achieve high population densities within a single growing season ([McKay 1984](#), [Courtney and Meffe 1989](#)). Western mosquitofish have been linked with the decline and local extirpation of native fish and amphibians throughout the Western United States ([Bay 1972](#), [Meffe et al. 1983](#), [Moyle et al. 1986](#), [Courtney and Meffe 1989](#)). Western

mosquitofish were introduced to Utah 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 (*Iotichthys phlegethontis*) are cyprinid minnows endemic to the Bonneville Basin. Historically, least chub were common throughout the basin but have recently declined to a few populations restricted to artesian springs ([Perkins et al. 1998](#)). Habitat degradation and interactions with western mosquitofish are the primary reasons for their decline ([Perkins et al. 1998](#)). Previous research in our lab has shown that western mosquitofish can out-compete least chub and that adult western mosquitofish prey on juvenile least chub ([Mills et al. 2004](#)). Field studies subsequently showed that adult western mosquitofish co-occurred with juvenile least chub when both species utilized the same warm, shallow marshes for spawning and rearing ([Ayala et al. 2007](#)). Thus, decreases in least chub recruitment are attributed to predation by adult western mosquitofish on juvenile least chub during spawning and rearing.

As with many invasive species, efforts to exterminate western mosquitofish (rotenone and trapping) even from small springs (< 0.5 km²) have been costly and unsuccessful (Utah Department of Wildlife Resources 2005, unpublished data). Because extermination is often not possible, we need to explore new ways of reducing the harmful effects of invasive species on native taxa. Coexistence among interacting species (competition and predation) is accomplished by niche separation ([Chesson 2000](#)). Habitat manipulation or transplanting native species to new habitats to re-establish declining native species should consider how niche separation (e.g. [Chesson 2000](#)) could promote coexistence between native and introduced species.

The importance of competition, niche overlap, and the theory of limiting similarity in determining the coexistence of species has a long and contentious history (e.g. [Gotelli and Graves 1996](#)). Hutchinson and MacArthur proposed that the number of species that could coexist in a local community was determined by their niche separation ([Hutchinson 1959](#), [MacArthur and Levins 1967](#)). New colonists could successfully invade a community if their niche requirements were sufficiently different from already established species (e.g. [Diamond 1975](#)). Although the ubiquitous importance of competition, niches, and the validity of limiting similarity has been questioned (e.g. [Simberloff 1978](#), [Simberloff and Boecklen 1981](#)), the niche concept and the relevance of niche separation in determining coexistence continues to play an important role in ecology (e.g. [Chesson 2000](#), [Chase and Leibold 2003](#)). In general, there may often be sufficient niche separation along important environmental gradients to promote the coexistence of invasive and native species. Efforts to try and eradicate or control invasive species might be complemented with equal efforts to try and promote coexistence.

We used the interaction between native least chub and introduced western mosquitofish to explore the niche separation hypothesis. For example, can physical alterations to the environment (habitat manipulation) exploit niche differences between introduced and native species to create a refuge for native species? No two species have identical niches because evolutionary constraints differ between species (e.g. [Stearns 1977](#), [Southwood 1988](#)). By definition, different species have different evolutionary histories (e.g. [Mallet 2006](#)). Exploiting niche differences may be most effective at

promoting coexistence between native and introduced species when they have evolved in different regions and under different climatic conditions.

Western mosquitofish are native to subtropical climates of the southern United States and the Mississippi River drainage ([Courtenay and Meffe 1989](#)). Growth and reproduction of western mosquitofish decrease as temperatures decrease ([Wurtsbaugh and Cech 1983](#), [Vondracek et al. 1988](#), [Pyke 2005](#)). In their native range, western mosquitofish prefer warmer temperatures close to 31° C and cannot tolerate extremely cold temperatures ([Pyke 2005](#)). But, western mosquitofish have been introduced to increasingly northern climates ([Krumholz 1944](#)) and once acclimated to the colder temperatures have a lower temperature tolerance ([Otto 1973](#)). Cold adapted western mosquitofish can survive temperatures as low as 1° C for very “brief periods” ([Pyke 2005](#)). Still, western mosquitofish populations often decline as temperatures decrease during the winter ([Krumholz 1944](#), [Woodling 1985](#), [Nelson and Keenan 1992](#)) and often do not survive the winter in colder climates ([Rees 1934](#)). We obtained western mosquitofish from the Davis County Mosquito Abatement District. These fish are descended from fish taken from wild populations in Utah and are assumed to be acclimated to this area.

Unlike western mosquitofish, least chub are native to colder climates and appear to have a broad temperature tolerance ([Billman et al. 2006](#)). Least chub may find a refuge from western mosquitofish if they can grow and reproduce at colder temperatures than western mosquitofish.

Our objectives were to determine if cold temperatures could promote coexistence between least chub and western mosquitofish. Although temperature may affect

interactions between species at the individual scale (lethal or sublethal), those interactions may not affect recruitment at the population scale. Thus we tested two hypotheses at the individual scale: 1) colder temperatures would reduce the aggressive behavior and predatory effects of western mosquitofish on least chub, and 2) colder temperatures would reduce the effect of western mosquitofish on the habitat use, activity, and feeding of least chub. We further tested two hypotheses at the population scale: 3) western mosquitofish reproduction would be delayed or absent at colder temperatures, whereas colder temperatures would not inhibit least chub recruitment, and 4) western mosquitofish would not be able to overwinter without warm refuges.

METHODS

Individual Scale: 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 liters) and placed in an observation aquarium (20 liters) at each temperature. Female western mosquitofish were used because they are larger and more aggressive than males. All western mosquitofish were deprived of food for 48 hours prior to a trial. Both least chub and western mosquitofish were allowed to acclimate in the observation aquarium for one hour before the western mosquitofish were released and the trial began. During the acclimation period, western mosquitofish were kept in a separate clear, plastic container inside the observation aquarium to prevent

contact with least chub. Each observation aquarium was supplied with artificial vegetation as a source of cover from predation, and all fish were used in only one trial.

We performed a total of thirty-one trials, eight at each temperature (only seven at 25° C). Four trials were run simultaneously, each with one of the four temperatures. Each trial was terminated independently when the number of least chub was reduced by half or after 48 hours, whichever came first. Brief observations were made by the investigators to record the number of surviving least chub every half hour for the first two hours and then every hour thereafter. All sides of the aquaria were covered with opaque plastic to minimize the effects of humans on fish behavior. All trials began between 9:00 and 9:30 a.m. and were performed in August 2006.

We controlled temperatures by placing the observation aquaria inside larger 190-l holding aquaria equipped with chillers (Frigid Units, Inc., Model D1-16) or 100W heaters (Visi-Therm, Model VTH-100). Western mosquitofish and least chub were acclimated in separate 190 liter aquaria to each of the four treatment temperatures for one week before the trials began.

The effect of temperature on the predation times for juvenile least chub (response variable) in the presence of predatory western mosquitofish was analyzed using a censored failure time analysis ([Kalbfleisch and Prentice 2002](#)). The censored data resulted from ending the trials after 48 hours. The predation times were modeled using the Weibull distribution and the proportional force of predation model.

Individual Scale: Aggression

We used the same aquaria and set-up as in the predation study to determine the effects of temperature on the aggressive behavior of western mosquitofish. This was a 2x4 factorial design with the presence or absence of western mosquitofish crossed with each temperature (10°, 15°, 20°, 25° C). This was a paired design because the behavior of the same fish (least chub) at one of the four temperatures was recorded in the presence (treatment) and absence of western mosquitofish (control). We randomly determined the order of the control and treatment in each trial and we waited 24 hours between treatments and controls so that all fish were deprived of food for 24 hours in the control and treatment. We ran six trials at each temperature and each trial spanned two days.

Four least chub, two large (30-40 mm SL) and two small (20-30 mm SL), were haphazardly netted from their respective holding tanks and placed in an observation aquarium at the start of a trial. In the western mosquitofish treatments, four female western mosquitofish, 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, TetraMin® Tropical Flakes were placed in a food ring (see below), the western mosquitofish were released, and all interactions were continuously recorded with video cameras for 20 minutes. Four trials in four separate aquaria, one at each temperature, were recorded simultaneously using digital camcorders to remove the effects of human observers.

We analyzed the video to measure the effect of temperature on habitat use, activity, feeding, and aggression of least chub (biting, pushing, chasing, etc.) in the presence and absence of western mosquitofish. The front of the observation aquarium

was split into equal quadrants (top left, top right, bottom left, bottom right) and we randomly placed artificial vegetation in either the top and bottom left or top and bottom right quadrants. 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. Also, the number of aggressive interactions was recorded for each trial. The species and size of the initiator, recipient, and victor were noted for each interaction. An initiator was identified as a fish that swam towards another fish quickly and directly 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. Least chub could forage in the open and run the risk of encountering western mosquitofish or remain sheltered and forgo feeding. Feeding was measured as the number of bites.

We used a mixed regression model (SAS PROC MIXED) 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 hierarchically dropped any non-significant interactions from the full model and reran the analysis. The aggressive interactions were analyzed with a generalized linear mixed model (SAS PROC GLIMMIX) to determine the effects of temperature and fish size on the number of aggressive interactions (dependent variable). We linked these data using the natural log function.

Population Scale: Recruitment

We examined the effects of western mosquitofish on the recruitment and population growth of least chub for 16 months (June 2006 to September 2007) at warm and cold temperatures using twenty mesocosms, ten for each temperature treatment. We added ten adult least chub (five males and five females) to each mesocosm and randomly assigned ten adult western mosquitofish (five males and five females) to five mesocosms in both temperature treatments using a fully crossed design: cold and warm temperatures in the presence and absence of western mosquitofish. Temperature and presence or absence of western mosquitofish were our predictor variables for the population growth (dependent variable) in a general regression model (SAS PROC GENMOD). We linked the dependent variable using the natural log function and used a Poisson distribution, assuming extra Poisson variability.

Our mesocosms consisted of large (1,136 liters), circular livestock watering ponds (Rubbermaid®) fitted with a standing drain (20 cm) and a gravity-fed, flow-through plumbing system ([Fig. 1](#)). Culinary water was pumped through a large charcoal filter (Aqua-netics filtration unit, Model 173) leading to two lines. One line remained indoors and fed two holding tanks (1,136 liters each) located on an elevated platform (1.2 m in height), whereas the second line transported water to the outdoor mesocosms. Chiller/heaters (Frigid Units model DQ15D, 2000W) were used to cool the water in the holding tanks in the summer and warm it in the winter. Temperatures could be manipulated by adjusting the temperature setting on the Frigid Units and controlling the flow rate into each mesocosm. However, 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. Indoor tanks were subjected to the same natural light cycle as the outdoor tank facilitated by windows located above the indoor tanks.

Our experimental set-up created distinctly different temperature treatments. The average summertime temperature was 15.5° C in the cold treatment and 23.5° C in the warm ([Fig. 2a](#)), whereas the average wintertime temperature was 8.4° C in the cold and 17.6° C in the warm ([Fig. 2b](#)). Although ice formed on the surface of the water in the cold treatment in the winter, there was always at least 15 cm of liquid water in each mesocosm.

We transported fish between the indoor and outdoor mesocosms in the spring and fall. When we switched the fish (September 2006, April 2007, and September 2007), we counted the total number in each mesocosm. Fish from each mesocosm were randomly assigned to new mesocosms during the switching process. Several least chub in the warm treatment in the absence of western mosquitofish died from infection during the winter (*Aeromonas spp.*). Because the illness was not due to the temperature manipulations we considered this an extraneous situation and therefore least chub, in the warm treatment in the absence of western mosquitofish, were replenished to their original numbers at the end of the first winter to act as a control for the least chub in the presence of western mosquitofish.

We used StowAway® thermographs (Onset Computer Corporation) to record the temperature every two hours in each tank for the duration of this study. We fed the fish in all mesocosms each day using a mixture of TetraMin® Tropical Flakes and New Life

Spectrum All Purpose Formula. Their diet was also periodically supplemented with zooplankton from Utah Lake.

RESULTS

Individual Scale: Predation

As predicted, colder temperatures reduced the predation times of western mosquitofish on least chub. Decreasing temperatures were positively correlated with the predation times ($\chi^2 = 49.30$; $p < 0.001$; [Fig. 3](#)). All pair-wise comparisons were significant except between 20° and 25° C ([Table 1](#)). There was only one trial at 10° C that was ended before the 48 hour limit and only five least chub were eaten in all of the trials at 10° C. There was also a significant date effect ($\chi^2 = 21.27$; $p < 0.001$). The general trend was identical across all dates but there were some dates when more least chub were eaten than on other dates.

Individual Scale: Aggression

The number of aggressive interactions decreased as temperature decreased ($F_{2,17} = 7.83$; $p = 0.004$; [Fig. 4a](#)) and fish size was not significantly correlated with the number of aggressive interactions ($F_{1,17} = 1.49$; $p = 0.239$). There were no aggressive interactions at 15° C and only three at 10° C. Although 38% of the 96 total aggressive interactions were initiated by least chub, they were only victors in 26%. There was only one instance where a small western mosquitofish initiated an aggressive interaction and failed to be

the winner. Large western mosquitofish were victors in every interaction that they initiated

Habitat use by least chub was not significantly correlated with temperature ([Table 2](#)). Also, the size of the least chub and all two-way interactions were not correlated with habitat utilization ([Table 2](#)). Least chub of both size classes only spent three percent of the total time in all trials in the top quadrants, which was not sufficient to analyze statistically. As expected, the activity ($F_{3,15} = 3.23$; $p = 0.052$) and feeding of least chub in both the top and bottom open quadrants ([Table 3](#)) increased with temperature. Size was also a significant indicator of feeding frequency in the bottom open quadrant with large least chub taking more bites than small least chub ([Table 3](#)). Surprisingly however, least chub in the presence of western mosquitofish spent more time in the open ([Table 3](#); [Fig. 4b](#)), less time in cover ([Table 3](#); [Fig. 4b](#)), were more active ($F_{1,23} = 37.64$; $p < 0.001$; [Fig. 4c](#)), and fed more frequently in the top open ([Table 4](#); [Fig. 4d](#)) than in the absence of western mosquitofish.

Population Scale: Recruitment

As predicted, cold temperatures had a devastating effect on western mosquitofish recruitment and survival. Western mosquitofish numbers in the cold treatment were lower than the warm in September 2006 ($\chi^2 = 174.09$; $p < 0.001$) because there was no recruitment in the cold treatment. Western mosquitofish numbers also differed between the cold and warm treatments in May 2007 because there were no overwintering survivors in the cold ([Fig. 5](#)). By 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 for the remainder of the study ([Fig. 5](#)). The maximum number of western mosquitofish per mesocosm was 740 individuals in the warm treatment by September 2007.

Western mosquitofish had no effect on the number of least chub in the cold treatment ($\chi^2 = 0.51$; $p < 0.476$), which did not change throughout the experiment ([Fig. 6a](#)). Although we observed juvenile least chub during the summer in the absence of western mosquitofish in the cold treatment (between 1 and 10 per mesocosm), none survived the winter. Similarly, about 20% of the adult least chub failed to overwinter. By contrast, western mosquitofish had a devastating effect on least chub in the warm treatment ($\chi^2 = 4.15$; $p = 0.042$, [Fig. 6b](#)). Numbers declined during the first summer and only four least chub in all five replicates remained after the first year ([Fig. 6b](#)). The four remaining least chub were all males. Least chub in the presence of western mosquitofish in the warm treatment were extinct by the summer of 2007. However, least chub in the warm treatment in the absence of western mosquitofish showed a significant increase during the summer of 2006 ($\chi^2 = 41.88$; $p < 0.001$) and 2007 ($\chi^2 = 58.88$; $p < 0.001$, [Fig. 6b](#)). The maximum number of least chub per mesocosm in the warm treatment was 183 individuals by September 2007.

DISCUSSION

We were surprised that least chub were more active, fed more frequently, and spent less time in cover in the presence of western mosquitofish because previous research has shown that least chub in the presence of western mosquitofish are less active, feed less, and spend more time in cover ([Mills et al. 2004](#)). Perhaps the difference

is attributed to experience. That is, Mills et al. ([2004](#)) used least chub that had previous contact with western mosquitofish. We observed, however, that naïve least chub do little to protect themselves from western mosquitofish. Instead they tend to school with western mosquitofish. Our observations support previous research suggesting bold/aggressive/active behavioral syndromes may be a common link among introduced species ([Sih et al. 2004](#)). We have noticed that when western mosquitofish are placed in a novel environment they quickly begin to explore and test their surroundings, are aggressive, and are more active. By contrast, least chub did not venture from cover habitat in aquaria or mesocosms until western mosquitofish were introduced.

Many vulnerable native fish may be timid, whereas many introduced fish may be bold. We suggest that this “Timid Hypothesis” may be caused by the effects of variable versus constant environmental conditions on fish behavior. Bold traits may be selected in variable environments because of the necessity to track changing abiotic and biotic conditions. Boldness has also been correlated with greater dispersal ability, and when coupled with aggressiveness and hyper-activity, introduced species are able to out-compete more timid native species ([Sih et al. 2004](#)). Western mosquitofish evolved in a variety of variable environmental types in the southeastern United States (e.g. from small riverine habitats to the Everglades). Current lineages of least chub, on the other hand, have evolved in springs, one of the most constant aquatic environments on Earth ([Rader and Keleher 2008](#)). As such, there may be no advantage to boldness. Future research should explore the timid hypothesis as it relates to the general ability of many introduced species to displace native species.

Our recruitment experiment confirmed previous suspicions that western mosquitofish cannot overwinter in temperate regions without a warm refuge ([Krumholz 1944](#), [Woodling 1985](#), [Nelson and Keenan 1992](#)). There was no western mosquitofish recruitment in the cold treatment during the summer and no western mosquitofish survived the winter. This supports the general assumption that introduced species are constrained by the environmental conditions under which they evolved (e.g. warm temperatures in the subtropics) and that western mosquitofish need warm winter refuges even when they are acclimated to temperate climates. Warm water refuges may consist of pockets or inflows of warm water or perhaps even burrowing into mud, a behavior that has been reported in western mosquitofish ([Pyke 2005](#)). Our experiments were not designed to identify the specific temperatures that constitute a warm winter refuge but temperature experiments on western mosquitofish have shown that cold acclimated fish can withstand temperatures as low as 3° C for 24 hours and may be able to survive a winter at 5° C ([Pyke 2005](#)). Unfortunately, the temperature at the inflow of most springs in the Bonneville Basin is $\geq 9^{\circ}$ C ([Keleher and Rader 2008a](#)).

Cold temperatures significantly reduced the predation and aggression of western mosquitofish on least chub at the individual scale. This is consistent with previous research showing that cooler temperatures disproportionately reduced western mosquitofish growth compared to native Barrens topminnows in Tennessee ([Laha and Mattingly 2006](#)). However, these results do not necessarily transfer to the population scale.

We found that least chub required warm temperatures for reproduction and recruitment even though cold temperatures reduced the harmful effects of western

mosquitofish at the individual scale. Unlike western mosquitofish, least chub adults successfully overwintered at freezing temperatures and they were able to reproduce at cold temperatures, but recruitment in the cold was minor when compared with the warm treatment. Least chub recruitment through the summer in the cold was barely sufficient to offset the small amount of adult mortality. More importantly, however, juvenile least in the cold treatment failed to survive the winter, presumably because of a reduced growth rate during the summer in cold temperatures. Billman et al. (2006) found that the optimal temperature for juvenile least chub growth was 22° C. Shallow marshes associated with artesian springs in the Bonneville Basin provide warm summer habitat near 22° C (Keleher and Rader 2008b). Unfortunately, both species can proliferate in marshes during the spring, which provides adult western mosquitofish the opportunity to prey on juvenile least chub.

Management Implications

Classical niche theory (MacArthur and Levins 1967) suggests that the ability of cold temperatures to reduce the harmful impact of western mosquitofish on least chub depends on the degree of separation between the species along the temperature niche axis. Spring ecosystems may provide insufficient separation to promote coexistence even though colder temperatures reduced the aggressive interactions and predatory behavior of western mosquitofish. Reduction of warm shallow marshes could have provided a refuge for least chub if it did not also reduce their recruitment. Alternatively, it may be possible to reduce the availability of warm winter refuges while leaving the marshes intact for spawning and recruitment by least chub.

Transplantation to colder habitats may be the only option in warm springs that lack cold refuges for least chub. Historically least chub occupied a variety of cold habitats including streams and lakes. The niche separation hypothesis suggests that we could transplant least chub to former colder habitats that would eliminate refuges for western mosquitofish. Least chub were likely eliminated from these ecosystems because of habitat alterations attributed to human activities. Thus, translocations would need to be coupled with restoration to re-establish the former conditions conducive to the survival of least chub (e.g. shallow side channels and wetlands in riverine environments).

The concept of habitat modification or translocation to promote coexistence depends on the ability of native species to exploit some niche dimension unavailable to introduced taxa. Habitat alterations, restoration, and translocations may be a valuable tool for promoting coexistence between native and introduced species if there is sufficient niche separation. Temperature is just one of many niche axes that could be used to promote coexistence. We suggest that the niche separation hypothesis has general application to interactions involving native and invasive species along a variety of different niche axes.

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Table 1. Poisson regression of cold and warm temperatures and the presence-absence of western mosquitofish on the number of least chub in experimental mesocosms.

Season	Treatments	χ^2	p-value
September 2006	Temperature	0.00	0.951
	Mosquitofish	13.10	<0.001
	Temperature x Mosquitofish Interaction	6.67	<0.001
May 2007	Temperature	0.57	0.452
	Mosquitofish	2.07	0.150
	Temperature x Mosquitofish Interaction	6.37	0.012
September 2007	Temperature	5.83	0.016

Table 2. Pairwise comparisons of the factor that relates the force of predation at a lower temperature to a higher temperature.

Treatment	Pairwise comparisons	χ^2	p-value
10° versus 15° C	5.09	10.73	0.001
10° versus 20° C	22.45	39.03	<0.001
10° versus 25° C	27.60	35.42	<0.001
15° versus 20° C	4.41	17.72	<0.001
15° versus 25° C	5.42	15.71	<0.001
20° versus 25° C	1.23	0.32	0.572

Table 3. Mixed regression model showing the effects of factors on least chub habitat use (cover versus open).

Location	Factor	χ^2	p-value
Bottom Cover	Temperature	1.33	0.293
	Western mosquitofish Presence/Absence	25.96	<0.001
	Size	1.56	0.213
Bottom Open	Temperature	1.61	0.218
	Western mosquitofish Presence/Absence	22.27	<0.001
	Size	6.87	0.010

Table 4. Mixed regression model showing the effects of factors on least chub feeding frequency (number of bites) in the top versus bottom of the aquarium.

Location	Factor	χ^2	p-value
Top Open	Temperature	13.06	<0.001
	Size	15.50	<0.001
	Size * Temperature	0.85	0.470
Bottom Open	Temperature	5.76	0.002
	Size	1.17	0.284
	Size * Temperature	0.49	0.693
	Western mosquitofish Presence/Absence	55.92	<0.001
	Temperature * Presence/Absence	11.01	<0.001
	Size * Presence/Absence	1.38	0.245

Figure 1. Representation of the ten outdoor and indoor mesocosms in the recruitment experiment showing the flow of water, the relative positions of the mesocosms, and heating/cooling holding tanks. Cross-section shows a side view of an individual mesocosm with the inflow and outflow of water.

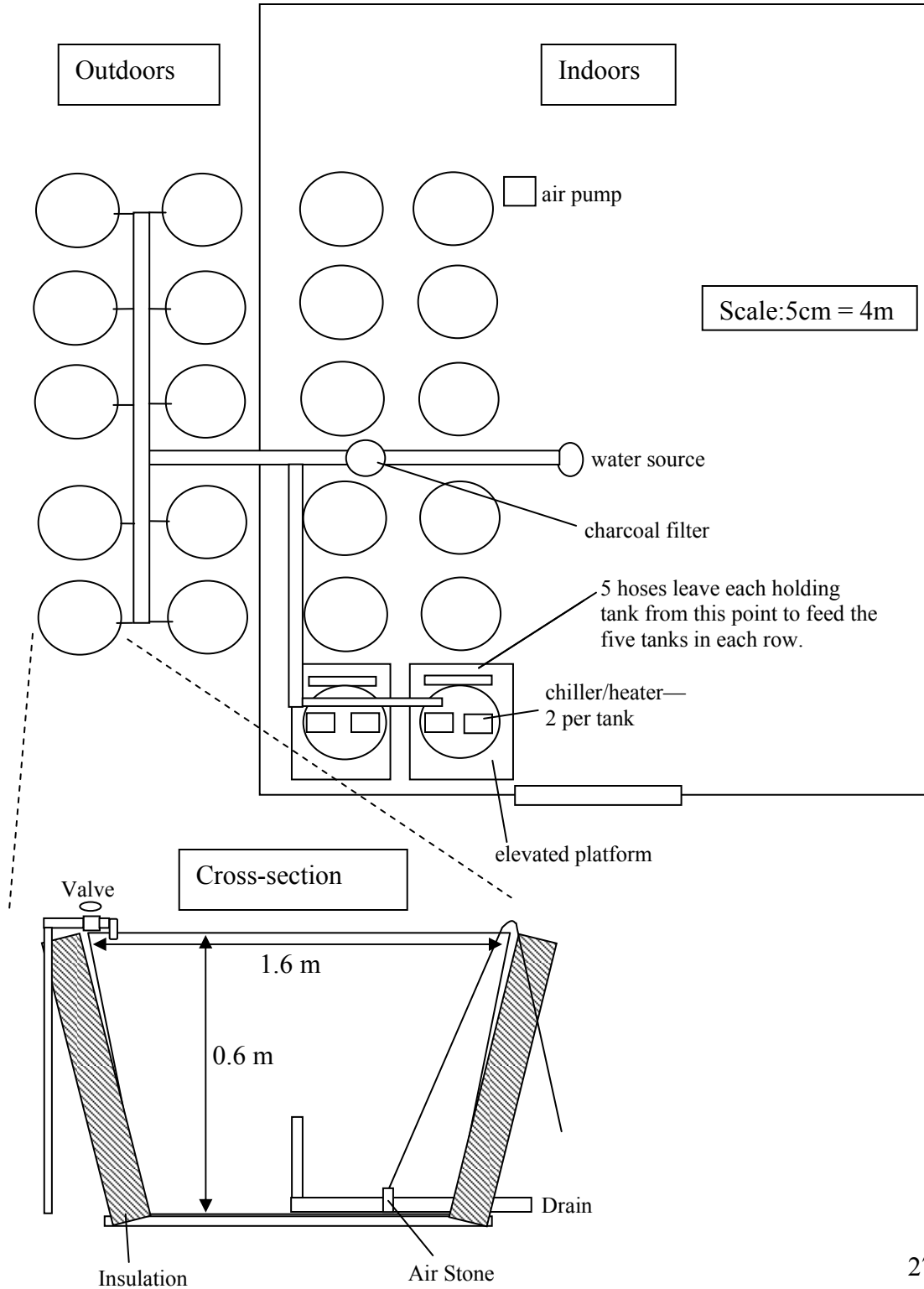


Figure 2. a) Summertime temperatures every two hours from June 14, 2006 until September 1, 2007. During the summer the warm treatment was kept outdoors (\square) and the cold treatment was indoors (\blacktriangle). b) Wintertime temperatures every four hours from October 1, 2006 until May 1, 2007. During the winter the cold treatment was kept outdoors (\square) and the warm treatment was indoors (\blacktriangle).

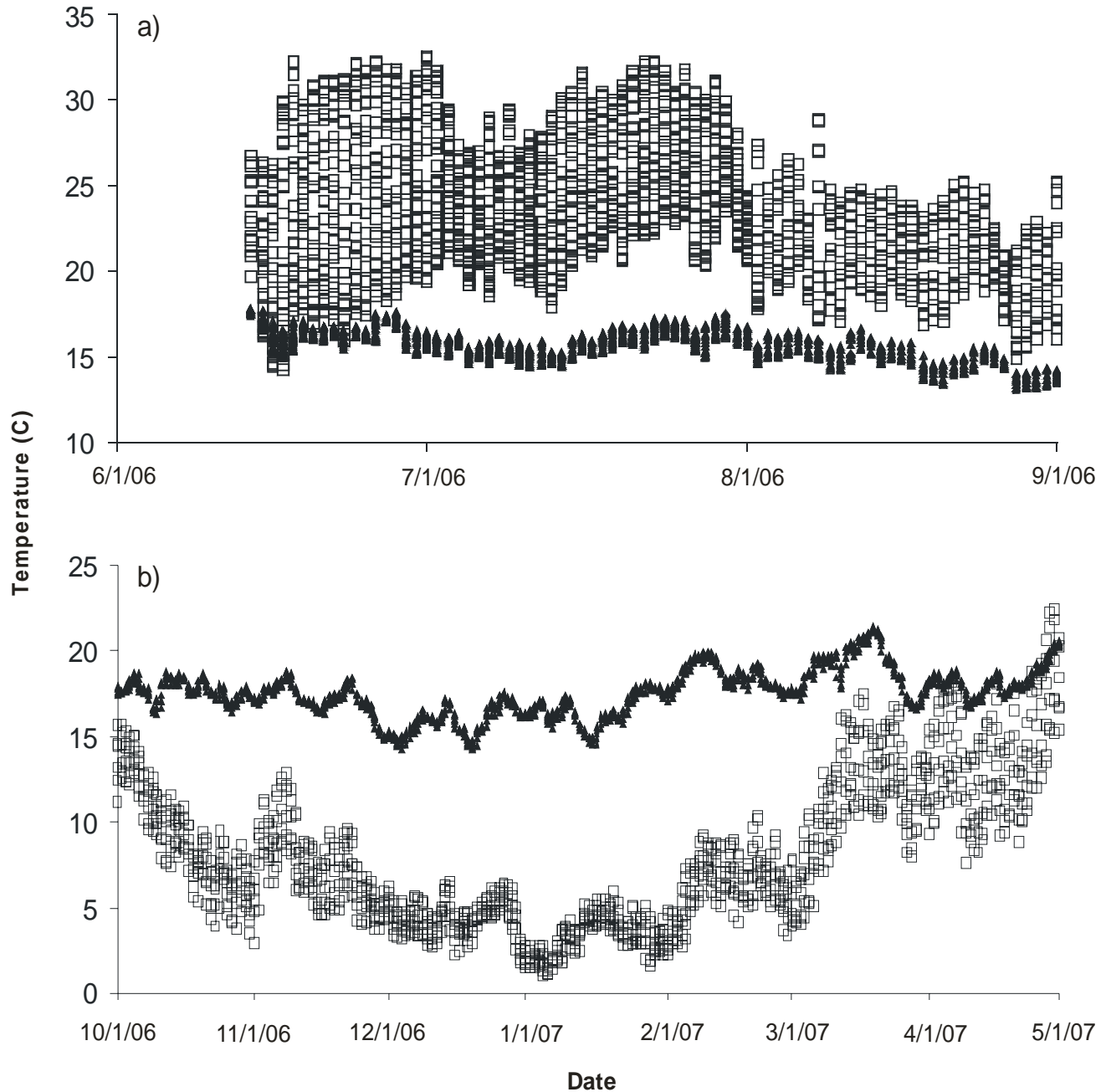


Figure 3. Cumulative percent survival of juvenile least chub in the presence of adult female western mosquitofish at four temperatures over 48 hours.

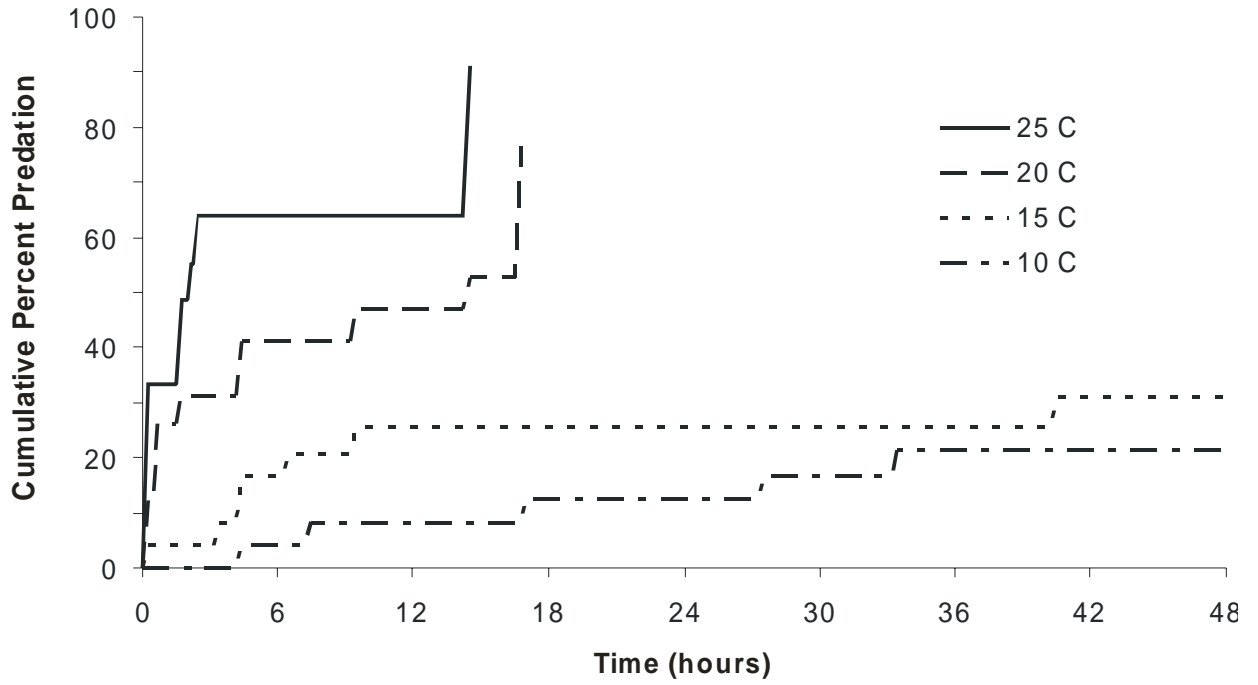


Figure 4. a) Relationship between temperature and the number of aggressive interactions between least chub and western mosquitofish \pm one S.E. b) Use of cover by least chub in the presence (unshaded bars) and absence (shaded bars) of western mosquitofish (error bars represent 95% confidence intervals). c) Activity as the number of line crossings of least chub in the presence and absence of western mosquitofish \pm one S.E. d) Relationship between temperature and feeding rate as the number of bites per trial in the presence and absence of western mosquitofish \pm one S.E.

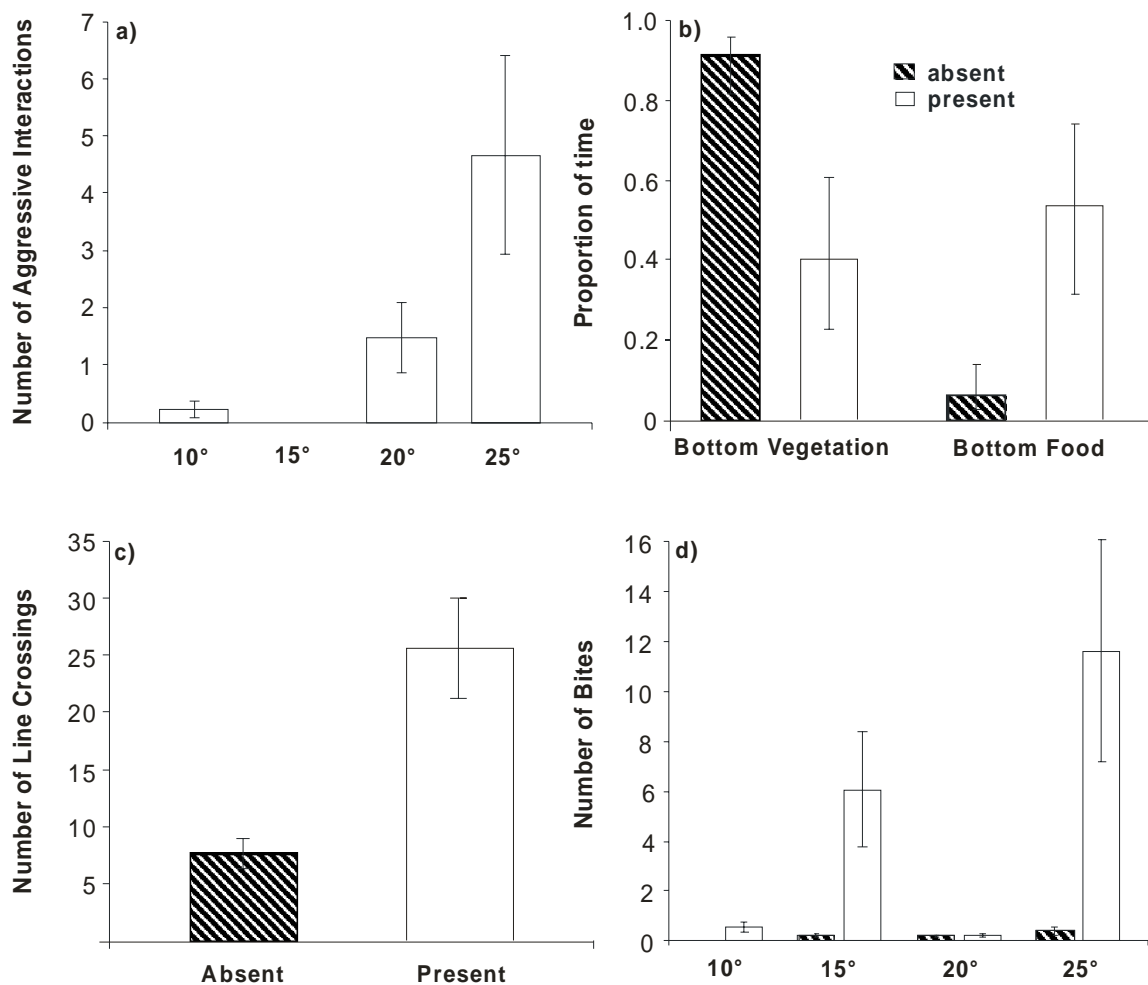


Figure 5. Differences in the mean number of mosquitofish in warm (□) and cold (●) treatments (■) \pm one S.E.

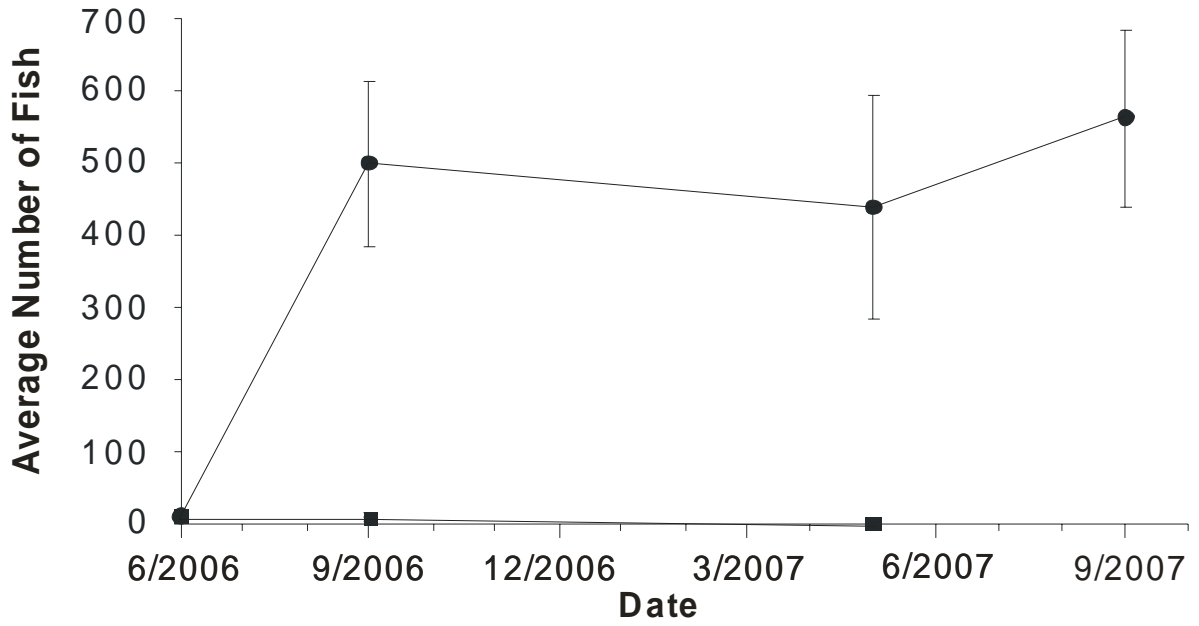


Figure 6. Differences in the mean number of least chub in the cold (a) and warm treatments (b) in the presence (▲) and absence (Δ) of western mosquitofish \pm S.E. Note the change in scale along the Y-axis between temperature treatments.

