Temperature Sensitivity and Predation Risk Cue Detection in Native and
Introduced Populations of the Atlantic Oyster Drill, *Urosalpinx cinerea*

By

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# Introduction

Human-mediated species introductions can result in phenotypic divergence between populations in the introduced and native ranges, which may have an important role in determining introduced species' success and impacts (Reznick and Ghalambor 2001, Richards *et al.* 2006, Strayer *et al.* 2006, Carroll *et al.* 2007). This can occur via several different mechanisms. Since introductions often begin with very small populations, introduced populations are subject to founder effects and genetic drift (Wares *et al.* 2005, Keller and Taylor 2008). Alternately, multiple introductions can bring genotypes together in the introduced range that do not co-occur in the native range, potentially leading to novel phenotypes via intraspecific hybridization (Ellstrand and Schierenbeck 2000, Sloop *et al.* 2009, Grosholz 2010). Faced with new environments in the introduced range, traits can adaptively evolve, often quite rapidly (Thompson 1998, Sakai *et al.* 2001, Maron *et al.* 2004, Keller and Taylor 2008). Although adaptive change has been a more popular topic for study, stochastic mechanisms may ultimately be more important drivers of evolutionary change in introduced populations (Keller and Taylor 2008). Introduced species may also succeed due to trait plasticity, or may evolve increased adaptive plasticity post-introduction (Richards *et al.* 2006, Latta *et al.* 2007). Initial phenotypic plasticity may ultimately lead to adaptive evolution of new trait values via genetic assimilation (Pigliucci and Murren 2003, Pigliucci *et al.* 2006, Lande 2009). While there is no clear consensus about the relative frequency and importance of these different mechanisms for phenotypic divergence in the introduced range, most have been clearly demonstrated.

Direct comparisons between native and introduced populations of a species under common conditions are key to detecting such trait divergence and understanding its consequences (Hierro *et al.* 2005). Examining patterns of trait change in the introduced range and how they relate both to local environment and invasion history can provide insight into the factors that allow all species to expand their ranges and adapt to new conditions — or the factors that limit this ability. Although introduced species are often supposed to owe their success to broad environmental tolerances, closer examination has sometimes shown significant variation in tolerances among introduced populations, with important consequences for the species' impact or spread (Lee 2002, Facon *et al.* 2004). In addition, if species differ in ecologically relevant ways between native and introduced ranges, they may be a moving target for management; predictions of impact or spread based on native range measurements may not apply. Increasingly, such comparisons are being made in terrestrial systems, especially among invasive plants (Callaway and Maron 2006, Richards *et al.* 2006), but most marine introduced species have not been examined to see whether they differ from their native range counterparts (Grosholz and Ruiz 2003).

In this thesis, I present a comparison of populations of the muricid gastropod *Urosalpinx cinerea* from its native Atlantic and introduced Pacific ranges, examining its responses to major abiotic and biotic environmental factors. Specifically, I assessed its ability to right itself across a range of winter temperatures (Chapter 1), and its behavioral responses to cues from potential introduced range predators (Chapter 2). These studies represent the first phenotypic comparisons between introduced and native populations of *U. cinerea*, as well as the first comparisons between *U. cinerea* living in different parts of the introduced range. It was valuable to consider both an abiotic and a biotic environmental variable, since any differing outcomes between the two variables could point the way to larger patterns (Reznick and Ghalambor 2001). In making these comparisons, I investigated whether there is evidence of phenotypic divergence that could reflect underlying post-introduction evolutionary change. Establishing an evolutionary basis for any observed differences would require additional experiments, including raising multiple

generations of snails in captivity. However, testing field-collected adults under common laboratory conditions, as I did here, is an important first step.

*Urosalpinx cinerea* is native to the Atlantic coast of North America and was introduced to the Pacific coast in the late 1800s during efforts to culture the Eastern oyster (Miller 2000). It appeared first in San Francisco Bay, then in other California and Washington estuaries used for oyster culture (Cohen and Carlton 1995). A predator on many sessile and slow-moving intertidal and shallow subtidal species (Carriker 1955, Pratt 1974a, Ordzie and Garofalo 1980b), *U. cinerea* was a significant pest to commercial Eastern oyster (*Crassostrea virginica*) fisheries in its native range (Carriker 1955). In its introduced range, *U. cinerea* is a key player in estuarine food webs (Kimbro *et al.* 2009) and in some cases may hinder restoration efforts targeting the native Pacific oyster *Ostrea lurida* (Buhle and Ruesink 2009). Because *U. cinerea* is likely subject to limited dispersal and high levels of local recruitment (Grosberg and Cunningham 2001), characteristics which increase the potential for local adaptation (Sanford *et al.* 2003), it is a good candidate study species for examining phenotypic divergence between native and introduced range populations. Adult *U. cinerea* move slowly, rely on internal fertilization, and have no swimming larval stage, instead depositing their embryos in benthic capsules from which offspring emerge as crawl-away juveniles (Carriker 1955). In Chapter 1, I examined the righting response of *U. cinerea* at a range of temperatures, focusing on its ability to maintain this response at temperatures representative of winter conditions throughout its native and introduced ranges, which vary markedly. Evidence from the literature suggests that latitudinally separated populations of native range *U. cinerea* have different minimum temperatures for biological functions such as feeding and reproduction (Cole 1942, Stauber 1950, Manzi 1970, Carriker and van Zandt 1973). Studying the snail's sensitivity to cold can also give clues as to how global warming may alter *U. cinerea*'s impacts in the introduced range since the onset of cold winter water temperatures seems to be the major factor regulating *U. cinerea*'s seasonal activity patterns in the native range (Carriker 1955, Ganaros 1958, Carriker and van Zandt 1973).

In Chapter 2, I compared snail behaviors in response to chemical cues from novel and familiar predators, and how ambient water temperature affects any responses. Sensitivity to predator cues has been shown to be a target of selection that can result in locally-adapted populations, such as in the freshwater gastropod *Lymnaea stagnalis* (Dalesman *et al.* 2007b). For *U. cinerea*, Kimbro *et al.* (2009) have suggested that its inability to recognize novel introduced range predators limits the snail's distribution within Tomales Bay, CA, but Grason and Miner (2012) found that *U. cinerea* from Willapa Bay, WA recognize and respond to chemical cues from the novel crab predator *Cancer productus*. This raises the possibility that *U. cinerea* have acquired the ability to recognize novel crab cues in some parts of the introduced range, but not in others (Grason and Miner 2012). Aside from these two, no other studies have focused on *U. cinerea*'s sensory interactions with predators in either the native or introduced range, and no previous studies have made comparisons between the ranges. There is clear evidence that *U. cinerea* has fairly sophisticated chemosensory abilities, at least with regard to feeding. Both adults and newly hatched juveniles use chemical cues to locate prey at a distance and to initiate attacks (Pratt 1974a, Rittschof *et al.* 1983, Williams *et al.* 1983, Rittschof and Gruber 1988), and adult snails can reportedly use chemical cues to distinguish remotely between starved and fed conspecifics (Pratt 1976).

Studying *U. cinerea*'s behavioral response to predator cues is particularly interesting because *U. cinerea* spans predator interaction gradients in both its native and introduced ranges that could result in local differences in sensitivity to various predators. A prominent predator in both the native and introduced ranges is the European green crab, *Carcinus maenas*. Introduced to the mid-Atlantic region of North America in the early 1800s, the green crab currently overlaps the northern two-thirds of *U. cinerea*'s native range, with coexistence times ranging from centuries to decades. Meanwhile, green crabs arrived in California in the 1980s, most likely in bait shipments from the Atlantic coast of North America (Cohen *et al.* 1995), but are abundant only in California bays (Behrens Yamada and Gillespie 2008). Meanwhile, introduced range *U. cinerea*'s patchy distribution

within the bays they inhabit may limit their exposure to native crab predators. For instance, in Tomales Bay, CA, *U. cinerea* are most abundant in the upper portions of the bay where *Cancer antennarius* are least common and *Carcinus maenas* have been most common (Kimbro *et al.* 2009). In Willapa Bay, WA, *Cancer* sp. crabs occur at some sites with abundant *U. cinerea,* but are not known from others (Grason and Miner 2012). Thus, both introduced and native range *U. cinerea* occupy habitats marked by varying lengths of co-occurrence with green crabs, and different suites of native crab predators.

Taken together, these studies emphasize the value of combining biogeographic comparisons with experimental approaches to explore the evolutionary and ecological dynamics of biological invasions. This is a powerful way to take advantage of the circumstances of an invasion to illuminate both fundamental aspects of ecology and the factors that make invasions successful and determine the scale of their effects on an ecosystem.

# Chapter 1.

## Temperature sensitivity of righting response in native and introduced Atlantic oyster drills

### *Abstract*

Anticipating the ecological consequences of anthropogenic climate change and biological invasions for marine ecosystems requires understanding how changing climate regimes affect ecologically relevant behaviors in introduced species. I compared the temperature sensitivity of righting response speed, a behavior related to overall movement and important to surviving dislodgment and evading predators, between native and introduced populations of the predatory muricid gastropod, *Urosalpinx cinerea*. Such comparisons are essential to detecting whether introduced phenotypes have diverged from native range counterparts and have rarely been performed among marine species. Righting speed of snails from two native range bays (in Connecticut and Delaware, USA) and three introduced range bays (in Washington and California, USA) was tested under three temperature treatments spanning winter conditions across much of its range (5°C, 10°C, 15°C) and at 20°C, a temperature previously identified as optimal for feeding and reproduction in the native range. Snails took significantly longer to right themselves as temperatures dropped from 20°C to 5°C, with the greatest temperature sensitivity in the interval from 10°C to 5°C. However, there were no geographic differences, with snails from all regions responding similarly; therefore, local environmental conditions are likely to determine *U. cinerea* activity levels across seasons. Since the interval of greatest temperature sensitivity coincides with winter minimum water temperatures in the introduced range, warmer winters brought on by global climate change could allow *U. cinerea* to be more active throughout the year, with potential concomitant impacts on native oysters and other prey species.

## 1.1. Introduction

Ecosystems worldwide currently face the twin challenges of climate change and nonindigenous species introductions (Sala *et al.* 2000, Grosholz 2002, Walther *et al.* 2002, Root *et al.* 2003). Anthropogenic global warming is predicted to affect existing nonindigenous species populations in many ways, including altering their distributions and their impacts on local ecosystems (Hellmann *et al.* 2008, Rahel and Olden 2008, Walther *et al.* 2009). Understanding these effects hinges on knowing both how introduced species will respond physiologically to warming temperatures throughout their ranges, and the consequences of those responses for ecologically relevant traits.

The temperature sensitivity of an introduced species' metabolism and behaviors is one factor determining success in its new range, and becomes especially important when considering the problem of how introduced species will respond to climate change (Dukes and Mooney 1999, Stachowicz *et al.* 2002, Walther *et al.* 2009, Sorte *et al.* 2010). The introduction of species into novel environments can create conditions conducive to rapid evolution (Prentis *et al.* 2008, Whitney and Gabler 2008, Lee 2011), or new scope for plastic trait expression (Buczkowski 2010). Such changes can be detected using comparisons of ecologically relevant traits between native and introduced populations of a species (Bossdorf *et al.* 2005, Hierro *et al.* 2005), but these comparisons have rarely examined the temperature sensitivity of traits in marine species. In general, phenotypic comparisons between native and introduced populations of marine species are still rare (Grosholz and Ruiz 2003). This study is the first to compare performance between native and introduced range populations of the predatory muricid gastropod, *Urosalpinx cinerea* (Say 1822), and the first to measure temperature sensitivity among Pacific coast *U. cinerea*.

Research into the possible consequences of global warming commonly focuses on thermal limits to survival (Helmuth *et al.* 2002, Stillman 2003, Kuo and Sanford 2009) and critical temperatures for respiration (Portner and Knust 2007) since these factors interact with warming to drive range shifts and threaten the survival of stenothermal species (Fre-

derich and Portner 2000, Peck *et al.* 2004, Portner and Knust 2007). Equally important, however, are sub-lethal temperature limitations on ecological functions such as locomotion, feeding, and reproduction (Peck *et al.* 2004). Within the existing ranges of eurythermal species, the interplay between varying climate and the temperature sensitivity of behavioral traits can cause significant shifts in ecological interactions (Sanford 1999). In this study, I compared the temperature sensitivity of righting response speed between native and introduced populations of *U. cinerea*. Righting response, the time required for a snail to right itself from an inverted position, is a biological function important to survival in marine gastropods and other invertebrates, since swift re-orientation and attachment to the substrate is critical to escaping predation and recovering from wave-driven dislodgment (Kleitman 1941, Lawrence 1975, Peck *et al.* 2004, Ubaldo *et al.* 2007). Righting response integrates physiology and behavior, and has been used in the past as a proxy for ecologically relevant activity levels in *U. cinerea* (Carriker 1955, Carriker and van Zandt 1973).

*Urosalpinx cinerea* is a eurythermal species, capable of surviving at temperatures below 0°C and above 30°C (Carriker 1955), but its ecological functions are temperature sensitive and more narrowly constrained (Cole 1942, Carriker 1955, Hanks 1957, Manzi 1970). As a result, in the native range, *U. cinerea* has a markedly seasonal life cycle (Carriker 1955), ceasing spawning, feeding, and even movement when ambient water temperatures drop in autumn, and remaining inactive and buried in sediment until temperatures rise again in spring (Carriker and van Zandt 1973).

Given that *U. cinerea* has been resident in the introduced range for 50–100 generations (depending on site; (Cohen and Carlton 1995)) and that the introduced range climate differs from the native range climate, *U. cinerea*'s sensitivity to temperature in its introduced range may have diverged from the response seen in the native range. Past workers frequently reported that ecological dormancy is triggered at different temperatures among *U. cinerea* from latitudinally separated regions in the native range, with northern snails having lower minimum temperatures for reproduction, feeding, and activity than

snails from southern sites (Cole 1942, Stauber 1950, Carriker 1955, Hanks 1957, Shick 1972, Carriker and van Zandt 1973). However, no past research ever included common garden experiments establishing whether native range *U. cinerea* evolved cold tolerance as its range expanded northwards from its mid-Atlantic origins (Carriker 1955). Winter temperatures in Pacific coast bays are likely warmer than in the northern native range, the most probable source of the Pacific coast *U. cinerea* (Miller 2000). If indeed northern *U. cinerea* gained costly cold temperature tolerance as their range expanded northwards, this tolerance might have been lost among snails introduced into warmer Pacific coast bays. Losses of costly traits have been widely observed in a variety of taxa over similar time scales under relaxed selection pressure (Lahti *et al.* 2009).

I hypothesized that introduced *U. cinerea* living in bays with warmer winter temperatures than those found in the northern native range might be more sensitive to decreasing water temperatures. By measuring the speed of the righting response at a range of temperatures in adult *U. cinerea* collected from bays on both the Atlantic and Pacific coasts of North America and held under common laboratory conditions, I asked: (a) how snails from each region responded to cooling ambient temperature; (b) over what interval righting speed was most sensitive to decreasing temperature; (c) whether populations from different regions showed different patterns of response; and (d) how the patterns of response related to ambient temperature regimes at the source sites. Since global warming might increase winter temperatures, measuring the temperature sensitivity of a trait important to survival and possibly indicative of underlying metabolism may help predict whether warming would cause temperatures to cross some threshold relevant to ecological function.

## 1.2. Methods

### 1.2.1. Collections

*Collection Sites*

Snails were collected during the summer of 2007 from five embayments, two on the Atlantic coast of North America (Mystic River estuary, CT, a sub-embayment of Long Island Sound; Delaware Bay, DE) and three on the Pacific coast (Willapa Bay, WA; Tomales Bay, CA; San Francisco Bay, CA). Within each of the Pacific coast embayments, collections were made during the summer months (June–September) at two sites at least 5 coastwise kilometers apart. Atlantic coast *Urosalpinx cinerea* used in this study were collected during May and September from one site in each bay (Table 1.1).

*Urosalpinx cinerea* were first recorded from San Francisco Bay in 1890, from Tomales Bay in 1935, and from Willapa Bay in 1948 (Cohen and Carlton 1995). These bays represent almost the entire latitudinal extent of *U. cinerea*'s Pacific coast range (it also occurs in Humboldt Bay, Puget Sound, and Boundary Bay; Carlton 1979, Cohen and Carlton 1995). Although *U. cinerea* has been reported as established in Newport Bay, CA (Cohen and Carlton 1995), the last records are at least 25 years old and a search in 2007 showed no evidence of continued presence (J.C. Blum, unpublished data).

On the Atlantic coast, *U. cinerea* occurs from the Gulf of St. Lawrence to southeastern Florida (Cohen and Carlton 1995), but occurrences north of Massachusetts are highly localized and probably represent human-mediated range extension via oyster transport (Carriker 1955). The most likely source of the *U. cinerea* introduction to the Pacific coast were sites in Long Island Sound and greater New York Bay (Carriker 1955, Miller 2000). However, since there was extensive oyster transport between Chesapeake Bay, Delaware Bay, and New York and New England embayments for ~100 years preceding *U. cinerea*'s introduction to the Pacific coast (Carriker 1955, Miller 2000), the original *U. cinerea* introduction may well have included mixed stock from throughout the region. *U. cinerea* from Long Island Sound and Delaware Bay were included in this study to reflect the puta-

tive source of Pacific introductions; extensive studies of *U. cinerea* from these areas have been conducted over the past century by many workers (Stauber 1950, Carriker 1955, Manzi 1970, Rittschof *et al.* 1983, Rittschof and Gruber 1988).

*Collecting Methods*

A shoreline transect at the tidal height near the approximate center of *U. cinerea*'s intertidal vertical distribution at each site was searched at low tide until ~200 adult snails had been collected. Adult snails were identified as those with shell height ≥ 20 mm (Carriker 1955), except where there were not sufficient snails of this size, in which case the cutoff was decreased to the maximum value that still yielded sufficient numbers; this occurred at the two San Francisco sites and the Connecticut site.

After collection, snails were sexed, individually marked, and measured. Per site mean shell heights for snails used in this study are given in Table 1.1. Snails were maintained in a closed system at 20°C on a diet of juvenile mussels (*Mytilus californianus*) for three to five months before testing, and individuals were randomly drawn from this pool for use in experiments.

## 1.2.2.   Source Temperature Regimes

Information on the ambient temperature regime for each source location was obtained for as many recent years as possible from publicly available data collected by nearby oceanographic data buoys or sensor stations. In general, sensors were located 1m below MLLW and recorded temperatures every 15 minutes. Data sources, time periods and sensor locations are given in Table 1.2. Data for Connecticut and Delaware were recorded by buoys maintained by NOAA's National Ocean Service (National Weather Service 2009).

In Willapa Bay, the Washington Department of Ecology provided temperature data from buoys located in the main channel at Oysterville and Naselle; the latter was used to characterize the National Wildlife Refuge site (Washington State Department of Ecology 2009).

**Table 1.1:** Collection sites.

| Embayment | Site Location | Coordinates | Code | Mean Shell Height ± SD (mm) |
|---|---|---|---|---|
| | *Native Range* | | | |
| Mystic River Estuary / Long Island Sound | Foot of Main Street, Noank, CT | 41° 19' 30"N 71° 59' 4.56"W | CT-N | 22.2 ± 2.4 |
| Delaware Bay | Ferry terminal, Lewes, DE | 38° 46' 56.2794"N 75° 7' 6.96"W | DE-L | 19.8 ± 3.9 |
| | *Introduced Range* | | | |
| Willapa Bay | Willapa National Wildlife Refuge Headquarters boat ramp | 46° 24' 51.4794"N 123° 56' 11.3994"W | WB-N | 26.9 ± 3.6 |
| | Oysterville Sea Farms, Oysterville, WA | 46° 33' 1.08"N 124° 1' 30.3594"W | WB-O | 20.9 ± 2.4 |
| Tomales Bay | Tomasini Point, Tomales Bay State Park | 38° 7' 43.32"N 122° 51' 53.28"W | TB-T | 24.9 ± 2.6 |
| | Shell Beach, Tomales Bay State Park | 38° 6' 58.3194"N 122° 52' 17.76"W | TB-S | 22.9 ± 2.3 |
| San Francisco Bay | Dumbarton fishing pier, Don Edwards San Francisco Bay National Wildlife Refuge | 37° 30' 37.8"N 122° 6' 41.04"W | SF-D | 20.3 ± 1.4 |
| | Seal Slough breakwater (southern side), San Mateo, CA | 37° 34' 19.2"N 122° 17' 34.8"W | SF-S | 21.2 ± 1.5 |

**Table 1.2:** Sources of oceanographic data used to determine ambient temperature regimes at collection sites.

| Embayment | Recording Station | Date Range | Coordinates | Corresponding Site |
|---|---|---|---|---|
| | *Native Range* | | | |
| Mystic River Estuary / Long Island Sound | Thames River Bridge, New London, CT, Station NLNC3-8461490 | 1995–2009 | 41°21'18" N 72°5'12" W | CT-N |
| Delaware Bay | Ferry terminal, Lewes, DE, Station LWSD1-8557380 | 1997–2009 | 38°46'54" N 75°7'12" W | DE-L |
| | *Introduced Range* | | | |
| Willapa Bay | Naselle River, Buoy WPA008 | 1997–2005 | 46° 27' 49.32" N 123° 56' 21.12" W | WB-N |
| | Oysterville, Buoy WPA006 | 1997–2005 | 46° 32' 42.00" N 123° 58' 41.88" W | WB-O |
| Tomales Bay | Tomasini Point station | 1987–1995 | 38° 6' 58.3194"N 122° 52' 17.76"W | TB-T |
| San Francisco Bay | Dumbarton fishing pier, Don Edwards San Francisco Bay National Wildlife Refuge | 1990–2009 | 37° 30' 37.8"N 122° 6' 41.04"W | SF-D |
| | San Mateo Bridge | 1989–2007 | 37° 35' 4.00" N 122° 14' 59.00" W | SF-S |

For San Francisco Bay, temperature data were recorded by USGS San Francisco Bay sensors (U.S. Geological Survey 2010). Data from San Mateo Bridge were used to approximate temperatures at the nearby Seal Slough collection site, while the USGS instrument at Dumbarton Pier was used for the Dumbarton Pier collection site. As there is no current continuous monitoring program in place for Tomales Bay, I used a publicly available long-term temperature dataset collected as part of the Biogeochemical Reactions In Estuaries (BRIE) study from 1987 to 1995 (http://lmer.marsci.uga.edu/tomales/; (Smith and Hollibaugh 1998)). The 16 km station was used to characterize average temperature regimes for both Shell Beach and Tomasini Point. These data were available as 1-day averages binned from readings taken every 30 minutes.

### 1.2.3.  Temperature Treatments

Seven snails per site were randomly assigned to one of three lowered temperature treatments (15°C, 10°C, or 5°C), or to a control treatment that remained at the 20°C holding temperature (overall, n = 224 snails). For each treatment, snails from each site were kept separately in submerged, flow-through containers within a common, static 75 liter tank with constant filtration and air supply. Treatment tanks were situated in a controlled-temperature room that was kept at least 5°C colder than the lowest desired tank temperature at any given time, with temperatures in each tank maintained with aquarium heaters connected to electronic temperature controllers. The Control tank occupied a laboratory whose ambient temperature was set to maintain ~20°C water temperature in the tank. For the lowered temperature treatments, all treatment tanks started at 20°C. Water temperature was then decreased by 1°C per day in all three tanks until a target temperature had been reached. At that point, water temperature was held at the target for 5 days, and at the end of this time all snails were assayed for righting response. If necessary, temperature decreases then resumed at 1°C per day until the next target was reached. Once a treatment tank reached its ultimate treatment temperature, it was held there and re-assayed after 14 and 23 days at that temperature. Therefore, snails in each treatment were assayed after 5,

14, and 23 days at their treatment temperature, as well as after 5 days at any preceding target. Snails in the Control treatment were assayed each time any other assays took place. Sites were assayed in a randomly determined order each time. Only the 23-day assay results, where the snails had the greatest opportunity to acclimate to the lowered temperatures, are presented here.

## 1.2.4.  Righting Response Assays

During an assay, snails from a given population were placed together into a large, flat-bottomed dish filled with seawater at the treatment temperature. These righting arenas floated at the surface of the treatment tanks, so that the water temperature stayed constant throughout the assay. Each snail was initially positioned with its aperture flat against the bottom of the dish, then rotated ~100° around the columellar axis to rest on the side of the body whorl opposite the aperture and allowed to right itself using its foot. The "flipped position" was chosen after several pre-experiment trials to determine an orientation that would be stable for the majority of snails, given variation in shell shape and wear. For snails whose unusual shell shape made the standard flipped position unstable, a small cloth-wrapped hair elastic was used as a prop to stabilize the snail in the flipped position. Each snail was flipped and allowed to right itself three times during an assay, with a minimum of 1 minute between righting and re-flipping. Each assay was videotaped continuously at 30 frames per second using a digital camera on a tripod mounted above the assay arena. Assays were ended after a per-snail maximum of 45 minutes, whether or not the snail had succeeded in righting itself three times.

Righting time data were collected by watching the videos and measuring the length of time (±0.1 seconds) from the start frame (when a snail was secured in the flipped position and the experimenter's fingers had released the shell) until the end frame (when the snail had subsequently completed the righting process). Data were collected only from the 23-day assays in each lowered temperature treatment, to allow time for acclimation. Data

were collected from the last Control assay, since this one would be most conservative if time spent in the experiment had caused an overall decrease in snail responsiveness.

### 1.2.5. Statistical Analysis

Since righting response is used in this study as a measure of physiological performance, and non-righting-related snail behaviors (e.g., startle responses, reaching for substrate in the wrong direction) tended to interfere with the righting process, per-snail minima were selected from the three righting attempts in each assay; all subsequent analyses were performed on these minimum values. The relationship between log-transformed righting time and treatment was modeled as a generalized linear mixed effects model using a gamma distribution and a log link function, with Bay and Treatment as fixed factors and Site and Snail as random factors. Snails were nested within Sites, and Sites within Bays. Snail shell height was used as a covariate. This model was fit using the `PROC GLIMMIX` procedure in Version 9.13 of the SAS System for Windows, and the fixed factors were tested for significance using Wald $F$ tests, while means were separated using Tukey's HSD test ($\alpha = 0.05$). Results were visualized using the `ggplot2` package (Wickham 2009) for R (R Development Core Team 2009).

Separate linear regressions were performed on the log-transformed righting times for each site (Table 1.3). To determine if source environment predicted low temperature performance, the slopes returned by these regressions were then regressed against two indices of environmental conditions in the source location: minimum winter water temperature, and number of days below 10°C. To investigate whether the environmental distance from the putative genetic origin of the introduced *U. cinerea* populations was related to low temperature performance, the slopes of the temperature–righting time relationships for the six introduced range sites were regressed on the difference between each site's environmental index value and a mean index value across all native range sites (since introduced range *U. cinerea* may have genetic roots in both Long Island Sound and mid-

Atlantic estuaries). These analyses were performed in R 2.10.1, using the `lm` function to fit the linear models.

To examine the sensitivity of the righting response to temperature, the $Q_{10}$ temperature coefficient was calculated for each 5°C interval, based on least-squares mean righting times across all bays (output from the generalized linear mixed model described above). $Q_{10}$ is a unitless quantity representing the factor by which a rate changes if temperature is increased by 10 degrees. Here, it was calculated as:

$$Q_{10} = \left( \frac{R_2}{R_1} \right)^{\frac{10}{T_2 - T_1}}$$

where $R_1$ and $R_2$ are righting rates (1 / righting time) at temperatures $T_1$ and $T_2$, respectively, with $T_2 > T_1$.

## 1.3. Results

### 1.3.1. Source Temperature Regimes

Water temperature data from the various collection sites revealed that winter temperatures are lowest at the native range sites (Mystic River and Delaware Bay), warmest at the California introduced range sites (Tomales and San Francisco Bays), and intermediate in Willapa Bay (Figures 1.1, 1.2). Summer temperatures were similar between the native range sites and the California introduced range sites, but somewhat cooler in Willapa Bay.

The distribution of daily temperatures at the native range sites was broadly similar. In both Delaware Bay and Long Island Sound, the lower quartile of observed daily temperatures began below 0° and ended between 5° and 10°C, while the upper quartile began at or above 20°C and extended above 25°C (Figure 1.2). On the Pacific coast, temperature distributions fell into a narrower range at all sites, with most daily temperatures falling between 5° and 25°C. Temperature regimes at the California sites were warmer overall than in Washington; the median observed daily temperature at the California sites fell between 15° and 20°C, while in Willapa Bay it fell between 10° and 15°C. California sites had similar proportions of days above 20°C as the native range sites.
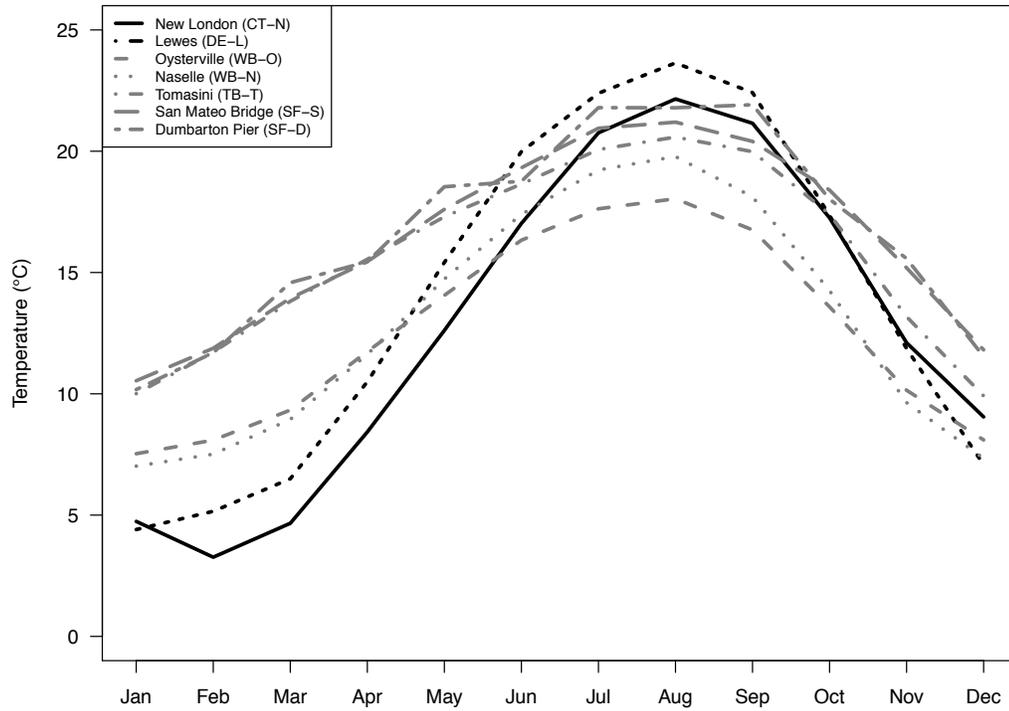
**Figure 1.1:** Monthly mean water temperatures at collection sites. See Table 1.1 for details on site locations.
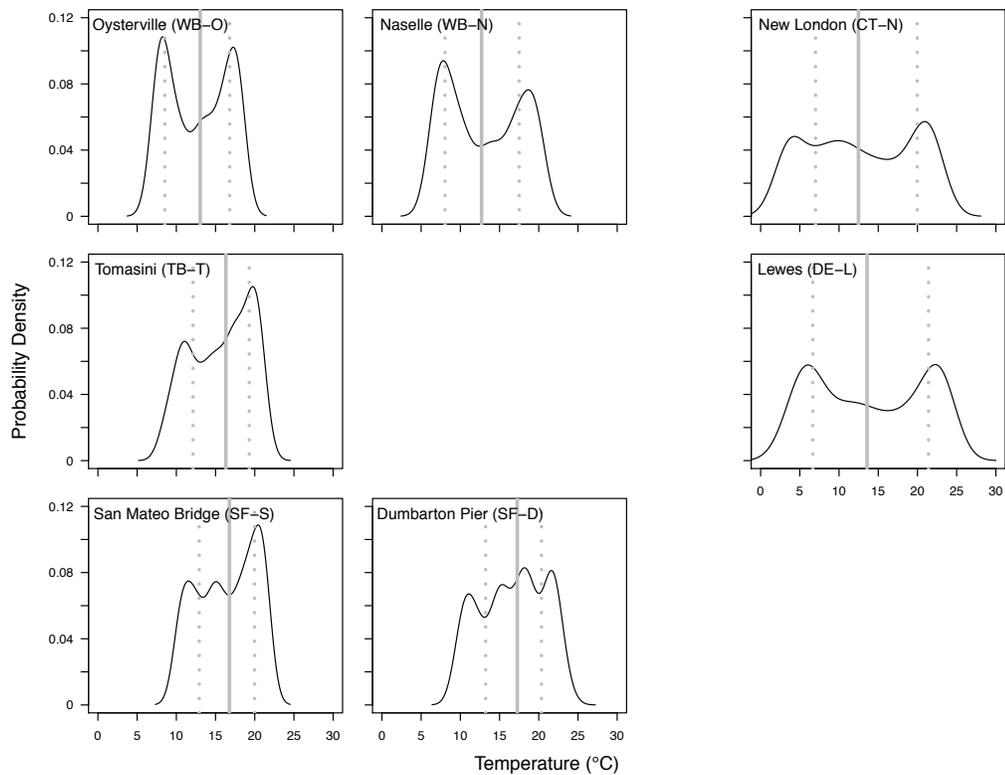


**Figure 1.2:** Probability density functions of daily water temperatures at collection sites, based on all available years of oceanographic data. Solid vertical lines indicate medians, dashed vertical lines indicate upper and lower quartiles.

## 1.3.2.  Righting Response

No *Urosalpinx cinerea* died during the course of the experiment. During the assays re-
ported here, 5 snails (out of 224 total) failed to right themselves at all within 45 minutes,
and 4 snails only righted themselves twice (therefore their recorded minimum righting
times are out of two tries). An additional 5 snails whose righting times were at least 3
standard deviations greater than the treatment means were removed prior to analysis.
These outlier snails came from the following treatment–site combinations: 5°C/WB-N;
10°C/CT-N, SF-S; 15°C/SF-D; 20°C/CT-N. Reviewing the video data confirmed that the
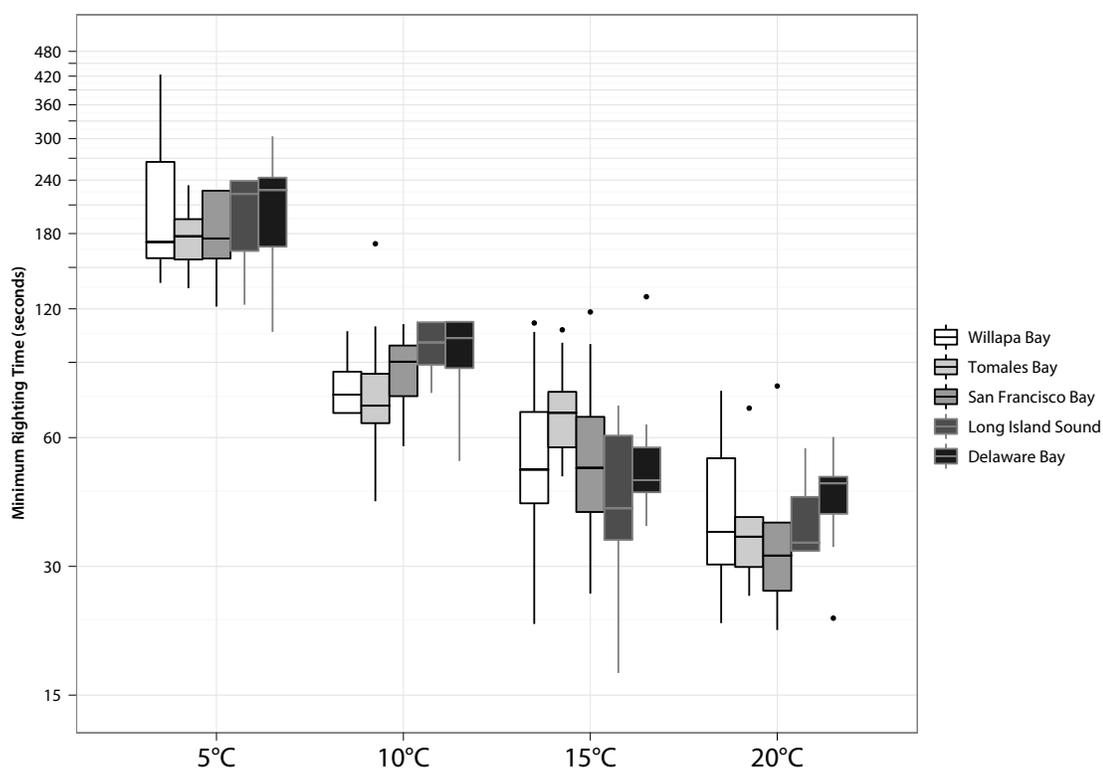


**Figure 1.3:**   Righting time (log scale) of *Urosalpinx cinerea* across
temperature treatments. Boxes indicate inter-quartile range,
while central crossbars indicate the median.

outlier snails' recorded righting times were not inflated due to slow performance of the
flipping maneuver. In all cases, the actual flipping motions occurred at a normal rate for
the treatment, but were delayed either by a startle reaction (with accompanying period of

subsequent inactivity) during the process of flipping, or by simply waiting for a long time before extending the foot and beginning to flip.

Lowered temperature treatment had a strong, significant effect on righting time across all bays, while source embayment did not significantly affect righting time across the different temperatures (Table 1.3; Table 1.4; Figure 1.3). Although mean snail height varied among populations (Table 1.1), inclusion of shell height as a covariate did not alter the results. Each decrease in temperature resulted in significantly slower righting times (Table 1.5; Figure 1.3), and the magnitude of the effect was considerable. At the coldest temperature tested, *U. cinerea* took on average over 3 minutes to successfully right themselves, as compared to less than 45 seconds at the warmest temperature (Figure 1.3). Righting response was most sensitive to temperature in the coldest interval, while righting response across the two warmer intervals showed similar, lower temperature sensitivity ($Q_{10}$ for 5–10°C: 5.18; $Q_{10}$ for 10–15°C: 2.00; $Q_{10}$ for 15–20°C: 2.32). Variation in righting times due to source site nested within source embayment was only a small proportion of the overall variation (Table 1.3).

**Table 1.3:** Results of generalized linear mixed model of righting time.

| *Covariance Parameter Estimates* | | |
|---|---|---|
| **Covariance Parameter** | **Estimate** | **Standard Error** |
| Site (Bay) | 0.020 | 0.019 |
| Snail (Site) | 0.000098 | 0.0057 |
| Residual | 0.094 | 0.011 |

| *Tests of Fixed Effects* | | | | |
|---|---|---|---|---|
| | **df** | | | |
| **Effect** | **Numerator** | **Denominator** | *F* **Value** | *P > F* |
| Bay | 4 | 3 | 0.09 | 0.98 |
| Treatment | 3 | 143 | 232 | **<0.0001** |
| Bay × Treatment | 12 | 143 | 1.24 | 0.26 |

**Table 1.4:** Results of linear regressions of log-transformed righting time on treatment temperature for each source site and minimum winter temperature, days below 10°C, and difference in minimum winter temperatures and days below 10°C in introduced range sites compared to average of native range sites.

| Site | Slope | Intercept | R² | Minimum Temperature (°C) | Days Below 10°C | Δ Minimum Temperature (°C) | Δ Days Below 10°C |
|------|-------|-----------|-----|--------------------------|-----------------|----------------------------|-------------------|
| CT-N | -0.1134 | 5.7522 | 0.84 | 3.26 | 139 | N/A | N/A |
| DE-L | -0.1060 | 5.6899 | 0.78 | 4.40 | 139 | N/A | N/A |
| WB-O | -0.1067 | 5.4643 | 0.83 | 7.53 | 119 | 3.70 | -20 |
| WB-N | -0.1137 | 5.8681 | 0.77 | 7.02 | 141 | 3.19 | 2 |
| TB-S | -0.0912 | 5.4971 | 0.79 | 9.91 | 27 | 6.08 | -112 |
| TB-T | -0.1044 | 5.5880 | 0.77 | 9.91 | 27 | 6.08 | -112 |
| SF-D | -0.1157 | 5.7403 | 0.83 | 10.17 | 5 | 6.34 | -134 |
| SF-S | -0.1207 | 5.7302 | 0.91 | 10.54 | 0 | 6.71 | -139 |

Although minimum winter temperature and number of days below 10°C for each source site varied widely (Table 1.4), variation in the shape of temperature responses among sites was not related to either minimum winter temperature (adjusted $R^2 = -0.16$, $P = 0.87$) or days below 10°C (adjusted $R^2 = -0.16$, $P = 0.99$). Similarly, temperature responses of snails from introduced range sites were not correlated with the difference between native and introduced range minimum winter temperatures (adjusted $R^2 = -0.25$, $P = 0.99$) or days below 10°C (adjusted $R^2 = -0.25$, $P = 0.96$).

**Table 1.5:** Comparison of least-squares mean righting times among temperature treatments; significance of mean separations calculated using Tukey's HSD.

| Temperature (°C) | Mean Righting Time (seconds) | Mean comparisons (P, α = 0.05) | | |
|:---:|:---:|:---:|:---:|:---:|
| 5 | 194.9 | *vs 5* | | |
| 10 | 87.2 | <0.0001 | *vs 10* | |
| 15 | 58.7 | <0.0001 | <0.0001 | *vs 15* |
| 20 | 39.6 | <0.0001 | <0.0001 | <0.0001 |

## 1.4. Discussion

*Urosalpinx cinerea* populations tested in this study have been separated for at least 50 generations and exposed to different ambient temperature regimes, yet the overall pattern of their response to temperature was very similar. This study was not designed to explicitly test for contemporary evolution, but the results could indicate that there has not been enough time or enough selective pressure for local adaptation to occur in the introduced range. Both these data and previous reports on *U. cinerea* temperature responses record plenty of individual variation (Carriker 1955, Hanks 1957, Ganaros 1958, Manzi 1970); although the role of plasticity was not usually explored, this suggests that lack of variation may not explain the absence of divergence in thermal responses. While there are many examples in the literature of adaptive trait change in introduced populations of various

species (Bossdorf *et al.* 2005, Prentis *et al.* 2008, Whitney and Gabler 2008), in many other cases no change has been recorded (Thébaud and Simberloff 2001). Keller and Taylor (2008) further point out that stochastic forces, rather than selective ones, may be most important in producing phenotypic changes in introduced populations. Genetic bottlenecks are unlikely to have featured strongly in *U. cinerea*'s introduction to the Pacific coast, since they arrived among the tens of millions of pounds of oysters that were transported live from the Atlantic coast over the course of 40 years and planted in Pacific coast bays (Miller 2000).

Speedy righting ability is likely important to escaping from predators and avoiding being swept away by waves, so the observed decrease in performance with decreasing temperature may have consequences for *U. cinerea*'s survival and persistence in different parts of its range (Figure 1.3). As righting response was most sensitive to temperature change between 5°C and 10°C, small changes in winter temperature may significantly influence the snail's performance. It may also indicate a potential handicap for the spread of introduced *U. cinerea*, which currently tend to occur in relatively warm and sheltered areas within Pacific bays. Typical water temperatures at the mouths of those bays and on the outer coastline range between 10°C and 15°C (Figures 1.1, 1.2); Pacific coast *U. cinerea* in these experiments took on average between 1 and 1.5 minutes to right themselves at these temperatures, and therefore might be at greater risk of dislodgment-driven mortality in such conditions. Native range sites get as cold and even colder in winter, but *U. cinerea* there reportedly overwinter buried in sediment or in other subtidal shelter, concentrating their feeding and reproductive activities during the warm summer months (Carriker and van Zandt 1973). Snails clearly could not use this overwintering strategy year-round in the consistently cool environments found at the mouths of Pacific bays, and it is not known whether introduced *U. cinerea* in the inner portions of Pacific bays bury themselves or retreat to subtidal shelters during colder months. However, in this study, *U. cinerea* were tested in still water and in the absence of predation threat, so it is possible that cold temperature righting behaviors might change under different risk scenarios. Further studies

more directly examining the ecological consequences of temperature-dependent righting performance in *U. cinerea* would be informative.

The pattern of temperature sensitivity observed in this study generally matches the results of previous work on *U. cinerea* from the northern portion of its native range. In the only study of its type conducted on *U. cinerea*, Shick (1972) found that oxygen consumption was most sensitive to temperature in the coldest intervals tested (2.5–7.5°C, 7.5–12.5°C) and relatively insensitive to temperature over warmer intervals (12.5–17.5°C, 17.5–22.5°C) for snails from Massachusetts, Virginia, and North Carolina. Almost all $Q_{10}$ values in the coldest intervals were greater than 2.5 and ranged as high as 10, while $Q_{10}$ in the warmer intervals was less than 2 (Shick 1972). This roughly matches the results presented here, where righting time was most sensitive between 5°C and 10°C, while sensitivity over the two warmer intervals was consistently lower. In ectotherms, temperature sensitivity that increases steeply as temperatures fall may reflect an evolved strategy for overwintering, where by not preventing biological processes from slowing, they reap the benefits of decreased energetic costs during a season when resources are sparse (Hochachka 1991).

Comparison with previous studies also offers some possible insight into the connection between righting time and other temperature-sensitive traits. In Carriker's (1955) review of the numerous published and unpublished accounts of *U. cinerea* biology then available, the lower temperature limit for feeding among *U. cinerea* in northeastern bays falls between 8°C and 12°C, and Hanks (1957) reports 7.5°C for Long Island Sound *U. cinerea*. The correspondence between these reports and the consistent pattern of temperature sensitivity I observed for righting response in native and introduced populations suggests that *U. cinerea* across the introduced range could have similar temperature thresholds for important ecological functions as *U. cinerea* in the northern native range. Although *U. cinerea* poses a threat to native oyster (*Ostrea lurida*) restoration on the Pacific coast (Grosholz *et al.* 2007, Buhle and Ruesink 2009), no studies have been done to determine the temperature sensitivity of feeding or reproduction in introduced populations. Such

studies would be useful to pursue, and the work presented here might help target key ranges of temperatures to investigate. If the pattern observed here — consistent temperature sensitivity across widely separated regions — holds true for ecologically relevant traits other than flipping, then fundamental aspects of *U. cinerea* ecology could vary across different local environments. For example, in the more southerly portions of the introduced range, where 85–98% of days in each year are likely to have an average temperature above 10°C (Figure 1.2, TB-T, SF-S and SF-D), *U. cinerea* might spend a greater proportion of each year actively moving and feeding, and consequently the impact of *U. cinerea* predation might be increased. Since *U. cinerea* is a generalist predator (Carriker 1955), such an outcome could have wide-ranging food web impacts and would be of concern to native oyster restoration efforts. Therefore, future work might examine how foraging behavior depends on temperature in different parts of the introduced range. Similarly, if the temperature sensitivity of *U. cinerea* reproduction is consistent across the native and introduced range, then California egg capsules might be able to survive the winter and adults might enjoy an extended reproductive season, while Pacific northwest *U. cinerea* might have more seasonal phenology. In the native range, *U. cinerea* embryos held at 10°C for almost 3 months develop very slowly, but can complete development with considerable survivorship if water temperatures subsequently increase (Ganaros 1958). Global warming could exacerbate these effects by increasing winter minimum temperatures (Stachowicz *et al.* 2002). This possibility could be investigated via comparative demographic studies in embayments that experience different temperature regimes, such as Willapa Bay and San Francisco Bay, as well as studies determining the temperature requirements for gametogenesis and larval development in Pacific coast *U. cinerea*.

Finally, the fact that *U. cinerea* activity was most sensitive to temperature increases in the lowest interval tested implies that small increases in winter average temperatures, such as are predicted to occur due to anthropogenic global warming, could have significant effects on *U. cinerea*'s activity levels. These results highlight the need for more investigations of how behavioral performance is affected by warmer winter water temperatures in ma-

rine systems. If the temperature sensitivity results in this study do correlate with sensitivity of other traits as hypothesized above, then warmer winters might result in an extension of *U. cinerea*'s annual period of ecological activity in the northern native range. In the introduced range, where winters are already milder, further winter warming could open the door to year-round activity, increased predation, and faster population growth.

In conclusion, in one of the few studies comparing an ecologically relevant phenotype between native and introduced populations of a marine species, I showed that despite divergent climate regimes and considerable residence times for even the youngest populations, sensitivity to temperature was consistent among populations. This implies that variation in local environmental conditions is the most important predictor of performance in a trait relevant to survival — and, possibly, overall success and ecological impact — across *U. cinerea*'s introduced range.

# Chapter 2.

# Detection of predation risk cues in *Urosalpinx cinerea* from the native and introduced ranges

*Abstract*

Determining the factors governing the success of introduced predators is key to predicting and managing their impacts. By exploring how an introduced predator uses cues to detect predation risk from top predators in the introduced range, and by comparing individuals from the native and introduced range, we can gain insight into the roles of predator recognition and naïveté in introductions. This study measured cue recognition in the predatory gastropod *Urosalpinx cinerea*, and examined how snails collected from several populations in the native and introduced ranges responded to chemical cues from two crab predators and injured conspecifics. Both native and introduced range *U. cinerea* responded to *Cancer antennarius* and *Carcinus maenas* kairomones, and to conspecific alarm cues. This is the first report of native range individuals of an introduced species demonstrating a pre-existing ability to recognize chemical cues from an introduced range predator with which they had no prior experience. *U. cinerea* may have benefitted from similarity between their native community and the resident community in their introduced range, as they were capable of recognizing ostensibly unfamiliar crab predators, possibly by relying on common cues or on generalization from predators *U. cinerea* evolved with in their native range. The ability to avoid disadvantages of novelty may aid the successful establishment of many introduced species.

## 2.1. Introduction

Introduced predators can substantially affect native prey populations, causing extensive changes in native communities (Catling *et al.* 1999, Croll *et al.* 2005, Salo *et al.* 2007, Kurle

*et al.* 2008). However, observed impacts are not consistently high and can be negligible (Elton 1958, Grosholz *et al.* 2000, Ross *et al.* 2003). Predicting and managing the impacts of introduced predators, a major challenge for invasion biology (Parker *et al.* 1999, Sih *et al.* 2010), depends on determining the factors governing their success. While it may seem most natural to think of an introduced predator's success in terms of interactions with species it preys on, introduced predators themselves can be the prey of top predators encountered in the introduced range. Therefore, one important factor influencing an introduced predator's success is its ability to detect threats from introduced range top predators (Sih *et al.* 2010), since naïveté to predator threat cues generally has severe consequences for populations of the species being preyed upon (e.g., Gamradt and Kats 1996, Li *et al.* 2011, Wanger *et al.* 2011).

Introduced predators may acquire the ability to recognize introduced range top predators through learning or adaptation (Ferrari *et al.* 2007, Ferrari *et al.* 2010, Sih *et al.* 2010). Alternatively, introduced predators may arrive already using cues in ways that allow them to detect threats from ostensibly novel top predators (Ferrari *et al.* 2010, Sih *et al.* 2010). Relying on general threat cues is one way for introduced predators to overcome top predator novelty. However, an introduced predator that relies on specific cues still might escape a novelty disadvantage if top predators in its introduced range produce cues similar to those produced by its native range enemies (Sih *et al.* 2010).

It is not yet clear which of these alternatives is most common, since there are relatively few studies examining introduced predators' ability to detect cues produced by introduced range top predators. The post-introduction acquisition of an ability to recognize novel top predator cues has been reported in three introduced crayfish (Hazlett *et al.* 2002, Gherardi *et al.* 2011), but there are not any confirmed cases of an introduced predator arriving with a pre-existing ability to recognize cues from top predators encountered in the introduced range. However, in some cases there has not been enough information available to establish whether or not an introduced predator's capacity to recognize introduced range top predators was present prior to introduction (Pearl *et al.* 2003, Grason and Miner

2012). An effective approach for differentiating between these scenarios is to compare how individuals from both the introduced and native range respond to introduced range top predator cues under common conditions. Comparisons between native and introduced populations provide essential context for evaluating introduced species performance (Hierro *et al.* 2005), yet are infrequently made, especially in marine systems (Vermeij *et al.* 2009).

Studies that employ native–introduced range comparisons to explore introduced predators' cue use and their degree of naïveté to introduced range top predators can provide insight into the potential for biotic resistance by the local community (deRivera *et al.* 2005, Carlsson *et al.* 2009, Li *et al.* 2011). They can also be useful in predicting the expected balance of consumptive and non-consumptive effects experienced by introduced predators (Preisser *et al.* 2005, Sih *et al.* 2010). This information can help shape management strategies for existing introductions (Sih *et al.* 2010), as well as suggest tactics for responding to new introductions of the same predator in other regions.

The Atlantic oyster drill *Urosalpinx cinerea* (Say 1822) is a major predator of shellfish and other sessile invertebrates in its native range (Carriker 1955, Pratt 1974a, Peterson 1979) as well as in its Pacific coast introduced range. In the introduced range, heavy *U. cinerea* predation has been cited as a factor impeding the restoration of the threatened Olympia oyster *Ostrea lurida* (Kimbro *et al.* 2009, Koeppel 2011). In the habitats where *U. cinerea* occurs on the Pacific coast, the principal local predators include two species of native rock crabs, *Cancer antennarius* and *Cancer productus*, and the recently introduced European green crab, *Carcinus maenas*. The rock crabs are reported from all the Pacific coast embayments where *U. cinerea* is found (Garth and Abbott 1980, Carroll and Winn 1989), but the green crab only occurs in significant numbers in central California bays (Behrens Yamada and Kosro 2010, deRivera *et al.* 2011; E.D. Grosholz, *pers. comm.*). *U. cinerea* occur patchily within Pacific coast bays (J.C. Blum *pers. obs.*; Grosholz *et al.* 2007, Buhle and Ruesink 2009, Koeppel 2011), and it has been suggested that *U. cinerea*'s naïveté

to native crab cues controls the snail's distribution in some parts of its introduced range (Kimbro *et al.* 2009).

Waterborne chemical cues are commonly used by a range of gastropod species to trigger both behavioral and plastic morphological defenses (Appleton and Palmer 1988, Trussell and Nicklin 2002, Trussell *et al.* 2003, Ferrari *et al.* 2010). Gastropods may rely on specific chemical cues emitted by predators themselves (kairomones), or on alarm cues emitted by attacked or damaged conspecifics (Dalesman *et al.* 2007a, Ferrari *et al.* 2010, Grason and Miner 2012). It is well established that *U. cinerea* depends on chemical cues when foraging for its own prey (Carriker 1955, Wood 1968, Pratt 1974a, Rittschof and Gruber 1988), but no studies have investigated how *U. cinerea* might use olfactory cues to detect predator threats in its native range. Although Rittschof *et al.* (1983) tested whether cues from some native range predator species were attractive to newly hatched juvenile *U. cinerea*, their study was not designed to detect defensive or evasive responses; unsurprisingly, the hatchlings were not attracted to the predators.

In the introduced range, Kimbro *et al.* (2009) found that *Cancer antennarius* were effective predators of *U. cinerea* from Tomales Bay, CA, yet the snails did not appear to recognize the rock crabs as a threat. The Tomales Bay *U. cinerea* also seemed not to respond to *Carcinus maenas*, although green crabs were ineffective predators of the large adult snails used in the study. In contrast, Grason and Miner (2012) found that chemical cues from *Cancer productus* and from injured conspecifics each consistently elicited hiding behavior among *U. cinerea* from Willapa Bay, WA. This could indicate that *U. cinerea* have acquired novel crab cue detection abilities in some parts of the introduced range, but not in others (Grason and Miner 2012). However, crabs are common intertidal and shallow subtidal predators in *U. cinerea*'s native range (Gosner 1971, Peterson 1979), so it is also possible that introduced *U. cinerea* arrived able to recognize a cue shared among related crab species or able to generalize between native range and introduced range crab cues (Ferrari *et al.* 2007, Ferrari *et al.* 2010). The contrasting reports from Willapa and Tomales Bays could then reflect a secondary loss of this ability in some parts of the intro-

duced range (Blumstein *et al.* 2004, Dalesman *et al.* 2007b). To distinguish among these scenarios, it is crucial to compare cue detection ability between snails across the introduced and native range.

Variation in the abiotic environment can substantially alter aquatic prey's recognition of and response to cues signaling predation risk (Ferrari *et al.* 2010). This can potentially shift the balance of consumptive and non-consumptive effects on prey, reducing anti-predator behaviors and increasing mortality from predation (Ferrari *et al.* 2011). For an introduced predator, such extrinsic environmental effects on its interaction with local top predators might create constraints on the introduced predator's overall success or impact, but to my knowledge this has not been previously studied in marine systems. The effect of abiotic environmental variation on predator–prey interactions may be substantial in estuaries, where water conditions such as salinity, pH, and temperature can vary considerably both temporally and spatially (Conomos 1979, Largier *et al.* 1997, Thom *et al.* 2003). There is some evidence that molluscan anti-predator behaviors may be sensitive to low temperatures (Ordzie and Garofalo 1980a, Jacobsen and Stabell 1999), and cooler water temperatures significantly decrease the speed at which *U. cinerea* is able to carry out certain critical behaviors (see Chapter 1).

In this context, I compared cue detection among *U. cinerea* from regions across their introduced and native ranges to examine the role predator recognition and naïveté have played in *U. cinerea*'s invasion history. I quantified how *U. cinerea* movement is affected over short timescales by the presence of alarm cues from crushed conspecifics and predator cues from two introduced range crab species, and how *U. cinerea* responded when presented with a choice between cue-laden and cue-free environments. I also investigated whether water temperature affects *U. cinerea*'s response to predation risk cues. This is the first study comparing cue responses between *U. cinerea* from the native and introduced range, and between *U. cinerea* from different regions of each range. It is also the only study I am aware of to examine the effect of abiotic environmental conditions on anti-predator behavior in an introduced marine predator.

## 2.2.  Methods

### 2.2.1.  Study System

All experiments used a common set of threat cue sources, including two species of crab predators and conspecific alarm cues that might signal predation by any crushing predator. The two crab species used were *Cancer antennarius* and *Carcinus maenas*. *Cancer antennarius* is a rock crab native to the Pacific coast of North America, and is common in low intertidal and shallow subtidal habitats. *Carcinus maenas*, the European green crab, is native to northern Europe. It was first introduced to the Atlantic coast of North America in the early 1800s and to California in the 1980s (Carlton and Cohen 2003), and is common from mid-intertidal to shallow subtidal habitats.

*Urosalpinx cinerea* has co-occurred with the two crab species for different lengths of time in different portions of its range (summarized in Figure 2.1). *Carcinus maenas* was introduced to *U. cinerea*'s native range along the Atlantic coast of North America almost 100 years before *U. cinerea* was first introduced to the Pacific coast of North America (Carriker 1955, Miller 2000, Carlton and Cohen 2003), but *Carcinus maenas* populations took nearly 200 years (and separate introduction events) to spread to its current extent along the Atlantic coast of North America, overlapping approximately two-thirds of *U. cinerea*'s native range (Roman 2006, Blakeslee *et al.* 2010). However, the earliest *Carcinus maenas* introductions were reported from New York Harbor and Long Island Sound (Carlton and Cohen 2003), the same regions that are the likely source of Pacific coast *U. cinerea* introductions (Miller 2000).

Once introduced to the Pacific coast of North America, *U. cinerea* were separated from *Carcinus maenas* for 50–100 years, depending on region. Green crabs were introduced to California in the 1980s, overlapping with *U. cinerea* in San Francisco and Tomales Bays (Cohen *et al.* 1995). Green crabs expanded to Washington during an El Niño event in 1998, but remain rare in Willapa Bay and are not as yet established in Puget Sound (Behrens Yamada and Gillespie 2008).
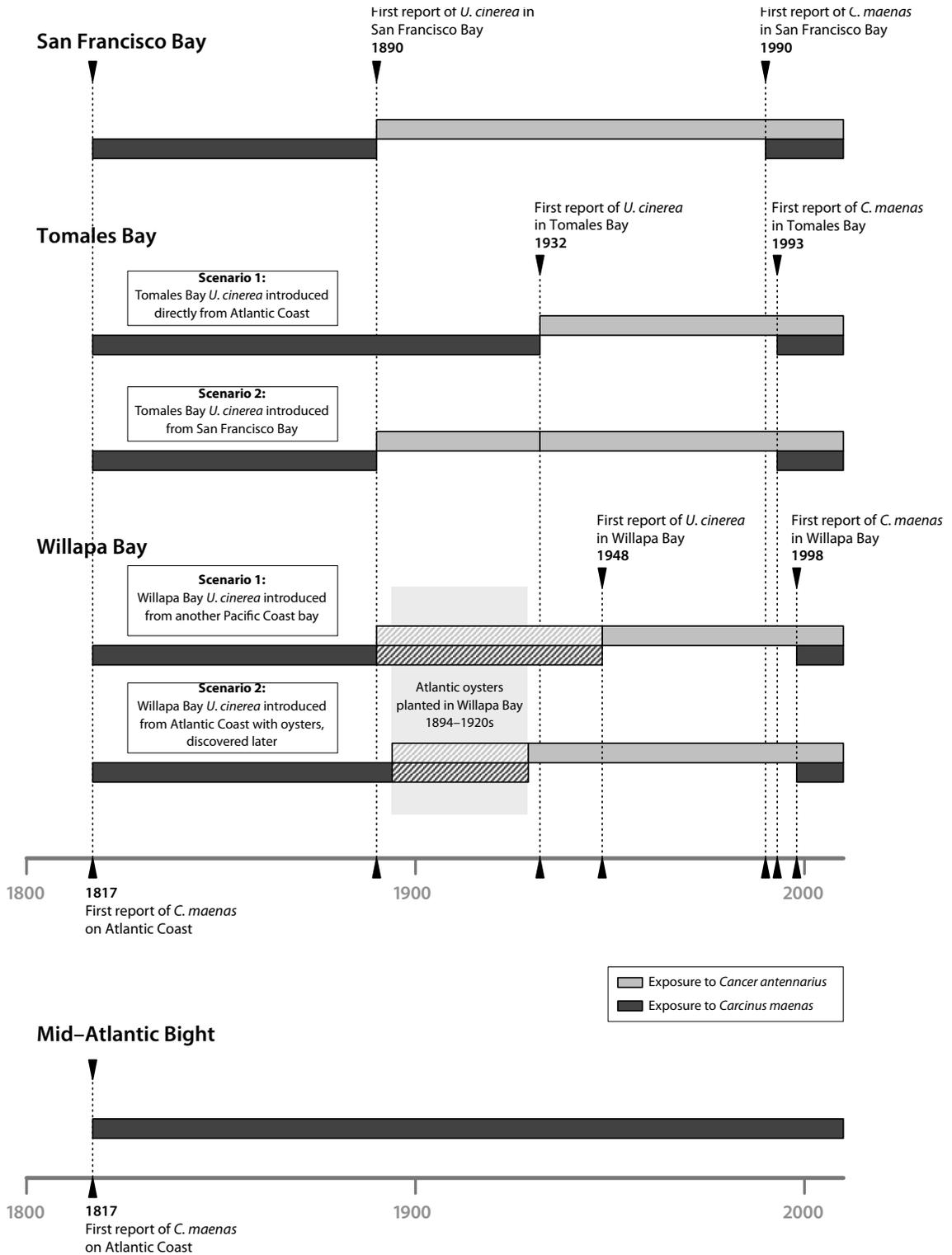
**Figure 2.1:** History of *Urosalpinx cinerea*'s coexistence with *Carcinus maenas* and *Cancer antennarius* in regions of its native and introduced range.

**Table 2.1:** Collection sites

| Embayment | Site Location | Coordinates | Code |
|---|---|---|---|
| | *Native Range* | | |
| Narragansett Bay | Narragansett Bay | 41° 36' 00" N 71° 21' 00" W | RI |
| Mystic River Estuary / Long Island Sound | Foot of Main Street, Noank, CT | 41° 19' 30"N 71° 59' 4.56"W | CT-N |
| | Shore Avenue, Groton Long Point, CT | 41° 18' 43"N 72° 0' 13"W | CT-G |
| Delaware Bay | Ferry terminal, Lewes, DE | 38° 46' 56.2794"N 75° 7' 6.96"W | DE-L |
| | *Introduced Range* | | |
| Willapa Bay | Willapa National Wildlife Refuge Headquarters | 46° 24' 51.4794"N 123° 56' 11.3994"W | WB-N |
| | Oysterville Sea Farms, Oysterville, WA | 46° 33' 1.08"N 124° 1' 30.3594"W | WB-O |
| Tomales Bay | Tomasini Point, Tomales Bay State Park | 38° 7' 43.32"N 122° 51' 53.28"W | TB-T |
| | Shell Beach, Tomales Bay State Park | 38° 6' 58.3194"N 122° 52' 17.76"W | TB-S |
| San Francisco Bay | Dumbarton fishing pier, Don Edwards San Francisco Bay National Wildlife Refuge | 37° 30' 37.8"N 122° 6' 41.04"W | SF-D |
| | Seal Slough breakwater (southern side), San Mateo, CA | 37° 34' 19.2"N 122° 17' 34.8"W | SF-S |

### 2.2.2. *Urosalpinx* Collections

I examined *U. cinerea* from three sites in the native range: Narragansett Bay, RI; Long Island Sound (CT); and Delaware Bay, DE, and three sites in the introduced range: Willapa Bay, WA; Tomales Bay, CA; and San Francisco Bay, CA (Table 2.1).

*Recirculating/No Choice Experiment*

Approximately 160 *U. cinerea* per site were collected from Narragansett Bay and from Tomales Bay (site TB-S, Table 2.1) during the summer of 2006. Adult snails (≥ ~20mm) were picked up by hand at low tide along low intertidal transects at each site, and maintained in flowing seawater (TB-S snails) or a static, outdoor tank (RI snails) on a diet of *Mytilus californianus*. Individuals were randomly drawn from these pools for use in the Recirculating/No Choice (R/NC) experiment.

*Flow-through/Choice Experiment*

During the summer of 2007, Atlantic coast collections of *U. cinerea* were made in Mystic River estuary, CT (a sub-embayment of Long Island Sound) and in Delaware Bay. On the Pacific coast, snails were collected from Willapa Bay, Tomales Bay, and San Francisco Bay. Collections occurred at two sites at least 5 coastwise km apart within each bay, except for Delaware Bay, where snails were collected from only one site (Table 2.1).

Snails were collected as described in Section 1.2.1, and were sexed, individually marked, and measured. They were maintained at 20° C on a diet of juvenile mussels (*Mytilus californianus*), and individuals were randomly drawn from this pool for use in the Flow-through/Choice (FT/C) experiment.

### 2.2.3. Crab Collections

For the R/NC experiment, *Cancer antennarius* were collected from Bodega Harbor, a small inlet of Bodega Bay, CA, and *Carcinus maenas* were collected from Tomales Bay, CA and Bodega Harbor. For the FT/C experiment, *Cancer antennarius* were collected from Bodega

Harbor, while *Carcinus maenas* were collected from the Seadrift Lagoon in Stinson Beach, CA, an artificial lagoon connected to Bolinas Lagoon via a managed intake and outflow.

## 2.2.4. Recirculating/No Choice Experiment

*Apparatus Design*

Trials were conducted in small recirculating systems at 14°C, the approximate temperature of ambient seawater in the sea tables and tanks where *U. cinerea* were being held. For each treatment, filtered seawater was pumped from a sump bucket containing the cue source into the experimental arena, and then drained back into the sump bucket (Figure 2.2a). The experimental arenas were 42 cm diameter plastic circular pans with 6 cm tall outer walls. Two holes were tapped 3 cm up the outer wall at opposite sides of each pan and fitted with plastic nozzles connected via plastic tubing to each sump bucket. Small aquarium pumps (Marineland Penguin 1140 powerheads), were used to pump water from the sump bucket through the inflow tubing, while the outflow tubing drained via gravity.

*Cue Treatments*

The cue treatments used in this experiment were: (a) *Cancer antennarius* (1 crab); (b) *Carcinus maenas* (1 crab); (c) crushed conspecifics (5 *U. cinerea* whose shells were broken and bodies injured using tin snips); or (d) seawater only ("No Cue").

*Snail Sources*

The *U. cinerea* used in this experiment came from two collection sites, Narragansett Bay, RI, and the TB-S site within Tomales Bay, CA.

*Trial Procedure*

For each trial, three replicate snails from each site were randomly assigned to each treatment. The order in which the snails participated in the trial was randomized. A single complete round of trials (12 snails per site) was considered a block, and there were 10 blocks (240 total snails). New crabs and crushed conspecifics were used for each block and

the experimental equipment was thoroughly cleaned between blocks. The *Cancer antennarius* used in this experiment had a mean carapace width of 8.3cm (1.6cm SD), while the *Carcinus maenas* used had a mean carapace width of 7.6cm (0.37cm SD).

At the start of a trial, a snail was placed at the center of an arena, facing into the inflow current. The snail's position was then recorded every 5 minutes for the next 45 minutes using a centimeter-scale polar grid printed on the floor of the arena. All four treatments were run at the same time for any given trial. After each trial, the arena was wiped with a paper towel to remove snail mucus trails. If snails reached the arena's outer wall during a trial, they typically climbed it and then continued to move, traveling around the circumference of the arena. In these cases, I continued to record the snail's position on the wall relative to the radial grid lines. Thus measurements of the total distance a snail traveled during a trial were not constrained by the size of the arena, although these measurements were conservative for snails that reached the outer wall since I did not track their vertical movement. However, the arena walls were short enough that snails primarily moved along the walls in one dimension.

## 2.2.5.   Flow-through/Choice Experiment

*Apparatus Design*

This experiment used a modified Y-maze apparatus modeled after the one used by Campbell *et al.* (2001). During an experimental run, aged seawater flowed by gravity (controlled with a stopcock) from a head tank into two smaller stimulus chambers, one of which contained an effluent source. From there, small aquarium pumps fed water into the assay chamber ($405 \times 80 \times 50$ mm) in opposing directions, draining through a perforated plate in the center of the chamber (Figure 2.2b). Dye tests showed that the two water streams (cue-bearing and cue-free) did not mix until directly over the drain holes.
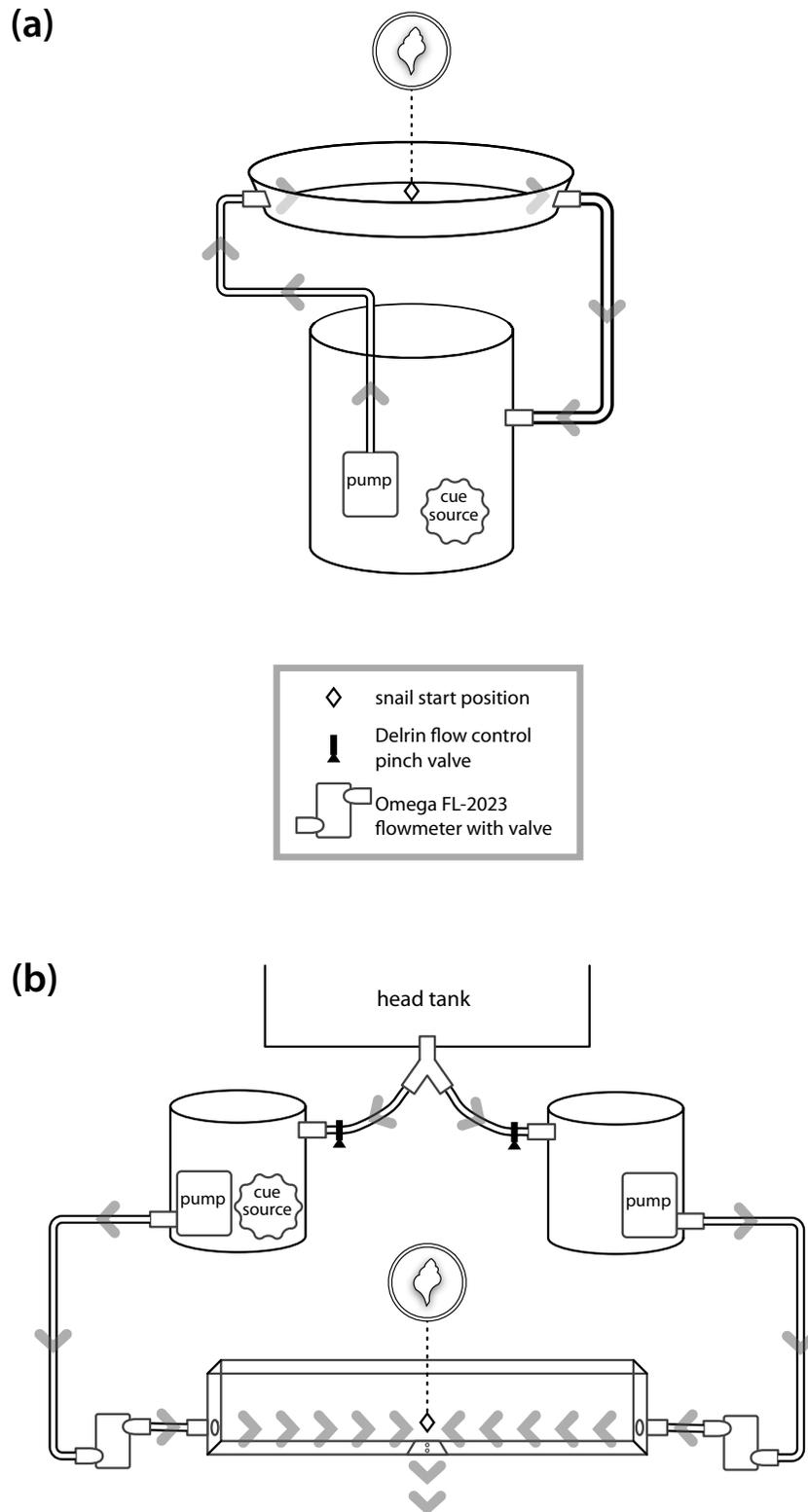
**Figure 2.2:** Apparatus designs used in (a) Recirculating/No Choice, and (b) Flow-through/Choice experiments.

The various chambers were connected using silicone tubing, and flow rate into the assay chamber was controlled using Omega FL–2023 flow meters set at 5 gallons per hour (~5.25 mL/s). *U. cinerea* exhibit positive rheotaxis and tend to follow currents upstream even in the absence of any attractants (Rittschof *et al.* 1983). Since increasing current velocity stimulates *U. cinerea* movement at lower velocities but inhibits it at higher velocities (Rittschof *et al.* 1983), I used data from cue-free pilot trials to choose the above flow rate, which best balanced snail responsiveness with water throughput.

Three apparatuses were constructed and run simultaneously for each trial, one for each cue treatment.

*Cue Treatments*

Cue treatments used in this experiment were similar to those used in the R/NC experiment: (a) *Cancer antennarius* (1 crab), (b) *Carcinus maenas* (1 crab), and (c) crushed conspecifics (20 *U. cinerea* whose shells were broken and bodies injured using tin snips).

*Snail Sources*

*U. cinerea* from Long Island Sound, Delaware Bay, Willapa Bay, Tomales Bay, and San Francisco Bay were used in this experiment. Due to limited snail availability, snails from different collection sites were pooled within bays. For the same reason, Delaware Bay *U. cinerea* were not included in one experimental run (10°C run — see below).

*Trial Procedure*

At the beginning of a trial, one snail from a given bay was placed on each drain plate perpendicular to the water flow. To control for turning bias (Marko and Palmer 1991), snail headings were alternated based on a randomly determined initial heading such that 50% of all snails tested faced each direction. Snail position was recorded every 5 minutes for 20 minutes using a printed half-centimeter grid on the bottom of the assay chambers. No snails ever reached the end of a chamber during any trial, so measurements of distance

traveled were not constrained by chamber size. After each trial, the interior surfaces of the arena were wiped with an algae scrubber to remove snail mucus trails.

### CONTROL RUN

Initially, 10 blocks of trials were run at 20°C with no cue source in any of the stimulus chambers, to test for any inherent bias in the apparatus (10 blocks; 5 bays; 150 snails tested). Snails from each bay were randomly assigned to each apparatus such that there was one replicate snail per combination of bay, apparatus, and block. The order in which snails participated in the Control run was randomized. During a single block of trials, snails from each bay were tested simultaneously and the order of bays was randomized. The Control run was conducted in a laboratory whose air temperature was set to maintain 20°C water temperature in the equipment.

### EXPERIMENTAL RUNS

The experiment was repeated with cue sources, both at 20°C (10 blocks; 5 bays; 150 snails tested) and at 10°C (9 blocks; 4 bays; 108 snails tested). These temperatures reflect average summer and winter water temperatures *U. cinerea* experiences in the introduced range (see Figures 1.1, 1.2).

Before the start of an experimental run, snails from each bay were randomly assigned to each treatment such that there was one replicate snail per combination of bay, treatment, and block. The order in which these snails participated in the experimental run was randomized. During a single block of trials, snails from each bay were tested simultaneously and the order of bays was randomized. New crabs and crushed conspecifics were introduced for each block and the experimental equipment was cleaned between blocks. The *Cancer antennarius* used had a mean carapace width of 7.8cm (1.1cm SD) for the 20°C run and 8.8cm (1.3cm SD) for the 10°C run. The *Carcinus maenas* had a mean carapace width of 6.9cm (0.31cm SD) for the 20°C run and 6.8cm (0.35cm SD) for the 10°C run.

The 10°C run was conducted in a cold room, while the 20°C run was conducted in a laboratory whose air temperature was set to maintain 20°C water temperature in the

equipment. *U. cinerea* used in the 10°C run were acclimated to the lower temperature by stepping down the temperature of their holding tanks by 2°C per day from a starting temperature of 20°C. Upon reaching 10°C, they were then held at that temperature for 14 days prior to the beginning of the run.

## 2.2.6. Statistical Analysis

Analyses were carried out in R 2.10.1 (R Development Core Team 2009), using the `glm` function to fit models and the packages `vcd` (version 1.2–7, Meyer *et al.* 2006, Zeileis *et al.* 2007, Meyer *et al.* 2009) and `ggplot2` (version 0.8.8, Wickham 2009) to visualize results.

*Binary responses*

I used logistic regression to determine how the factors of source range and cue treatment (or apparatus, for the FT/C Control run) affected certain binary response variables: whether snails moved at all and, given that they did move, whether they reached the outer wall of the arena (R/NC), or moved toward or away from the cue source (FT/C). Since R/NC snails would be most likely to reach the arena wall if they moved in a given direction steadily and relatively quickly during a trial, achieving this goal was used to differentiate wandering movement from more directed movement that might be involved in fleeing. The source range factor had two groups, Native and Introduced. For the R/NC experiment, these groups simply corresponded to the two source bays (Narragansett Bay, RI and Tomales Bay, CA), while in the FT/C experiment, source bays in each range were grouped together. Thus the FT/C Native Range group included snails from Long Island Sound and Delaware Bay, while the Introduced Range group included snails from Willapa Bay, WA, Tomales Bay, CA, and San Francisco Bay, CA.

For each response, a set of logistic models was considered: a model where the probability of observing the response was constant across all groups, models including the effect of each predictor alone, a model including the additive effects of both predictors on

the probability of observing the response, and a model including interacting effects of both predictors. Models were fit to grouped data and goodness-of-fit was assessed by comparing a model's deviance statistic to a χ2 distribution with $n - p$ degrees of freedom, where $n$ is the number of groups and $p$ is the number of parameters, intercept included. Likelihood-ratio tests were used to test the significance of particular model terms.

As a general guideline, group sizes are considered large enough for fitting two-factor logistic models when 80% of expected counts are greater than 5 (Agresti 2002). Where my data did not meet this guideline, I only fitted the relevant one-way models, allowing investigation of individual gross effects but not additive or interactive combinations. This was only necessary in the analysis of the direction snails moved during the FT/C experiment. For the Control run, there were only sufficient numbers of moving snails to fit one-way models of the effect of Range and Apparatus on direction moved. For both the 20°C and 10°C experimental runs, I fitted only one-way models for the effect of Range and Treatment on direction moved. The 10°C data, where the smallest numbers of snails moved, were also borderline insufficient for fitting the one-way Treatment model (2 of the 6 expected counts were just under 5, at 4.8 and 4.4).

*Continuous responses*

To examine the effects of source range and cue treatment (or apparatus, for the FT/C Control run) on the total distance snails traveled in both experiments, I modeled the distance moved in any direction among those snails that moved at all as a generalized linear model with a Gamma response distribution and identity link function. In the FT/C experiment, I treated source bay as a subsample of Range, averaging across the distances moved in each Block × Treatment × Bay combination (for the Control run, each Block × Apparatus × Bay combination). Likelihood-ratio tests were employed to evaluate the support for the various possible individual and combined effects of the two predictor factors.

# 2.3.  Results

## 2.3.1.  Recirculating/No Choice Experiment

*Probability of moving*

67.5% of *Urosalpinx cinerea* (162 snails) moved at some point during the trials; snails in the two crab cue treatments moved in over 70% of trials, while in the Crushed Conspecific treatment only 43–50% of snails moved (Figure 2.3a). Treatment was the primary factor influencing the probability that *U. cinerea* moved during trials. Both the overall effect of Treatment and the effect of Treatment within Range were significant (Table 2.2a).



**Figure 2.3:**  *Recirculating/No Choice: Probability of moving.* Mosaic plots depicting predicted (in parentheses) and observed counts of *Urosalpinx cinerea* from the native or introduced range that moved during a 45 minute trial when exposed to various cue treatments in test arenas with recirculating water flow.

(a)  Observed data with predictions based on constant probability model.

(b)  Expected values based on best model (Moved ~ Treatment).

Cue treatments are *Carcinus maenas* (CM), *Cancer antennarius* (CA), Crushed Conspecifics (CC), and No Cue (NC). Dashed lines indicate a value less than expected based on the model predictions. Shading represents the Pearson residual for that observation relative to the model prediction.

**Table 2.2:** *Recirculating/No Choice: Probability of moving.*
**a. Top:** Goodness-of-fit for models of whether *Urosalpinx cinerea* from the native and introduced range moved during a 45 minute trial when exposed to various cue treatments in test arenas with recirculating water flow. *Bottom:* Results of likelihood ratio tests comparing nested models relating whether *Urosalpinx cinerea* moved to source range (R) and cue treatment (T).

| Code | Model | | Deviance | df | $P > \chi^2$ |
|------|-------|---|----------|----|----|
| *m0* | Moved ~ 1 | | 23.48 | 7 | **0.0014** |
| *mR* | Moved ~ Range | | 21.58 | 6 | **0.0014** |
| *mT* | Moved ~ Treatment | | 2.46 | 4 | 0.65 |
| *mR+T* | Moved ~ Range + Treatment | | 0.37 | 3 | 0.95 |
| *mR×T* | Moved ~ Range × Treatment | *(saturated model)* | 0 | 0 | |

| Likelihood Ratio Test | | Δ Deviance | Δ df | $P > \chi^2$ |
|-----|-----|------|----|----|
| mR *vs* m0 | *(gross Range effect)* | 1.90 | 1 | 0.17 |
| mR+T *vs* mT | *(net Range effect)* | 2.09 | 1 | 0.15 |
| mT *vs* m0 | *(gross Treatment effect)* | 21.02 | 3 | **<0.001** |
| mR+T *vs* mR | *(net Treatment effect)* | 21.21 | 3 | **<0.0001** |

**b.** Predicted probabilities and relative effects (expressed as odds ratios) for the one-factor model relating cue treatment to whether *Urosalpinx cinerea* moved during a 45 minute trial in test arenas with recirculating water flow.

| Group | | Probability of moving | Odds Ratio (95% CI) | |
|-------|---|-----------------------|---------------------|---|
| Treatment | *Cancer antennarius* | 0.78 | 2.1 | (0.94, 4.8) |
| | *Carcinus maenas* | 0.82 | **2.6** | (1.1, 6.1) |
| | Crushed Conspecifics | 0.47 | 0.51 | (0.24, 1.1) |
| | No Cue | 0.63 | — | — |

The presence of crab cues resulted in a 2 to 2.5–fold increase in a snail's odds of moving (Table 2.2b, Figure 2.3b), and the effects of the two crab treatments were very similar. In contrast, Crushed Conspecific cues halved the odds of a snail moving during a trial relative to the No Cue treatment (Table 2.2b). Although the confidence intervals on the effects of the *Cancer antennarius* and Crushed Conspecific treatments included 1 (representing no effect relative to the cue-free treatment), the weight of evidence suggests that these effects are meaningful.

*Probability of reaching an arena wall*

40% of *U. cinerea* that moved also reached the outer wall of the arena during a trial. Range clearly influenced whether or not moving *U. cinerea* reached the arena wall during a trial: both the overall effect of Range and the net effect of Range after adjusting for Treatment were significant (Table 2.3a). Introduced Range snails reached the wall more frequently than Native Range snails (54% of the time for all Introduced Range snails and 28% of the time for all Native Range snails; Figure 2.4a).
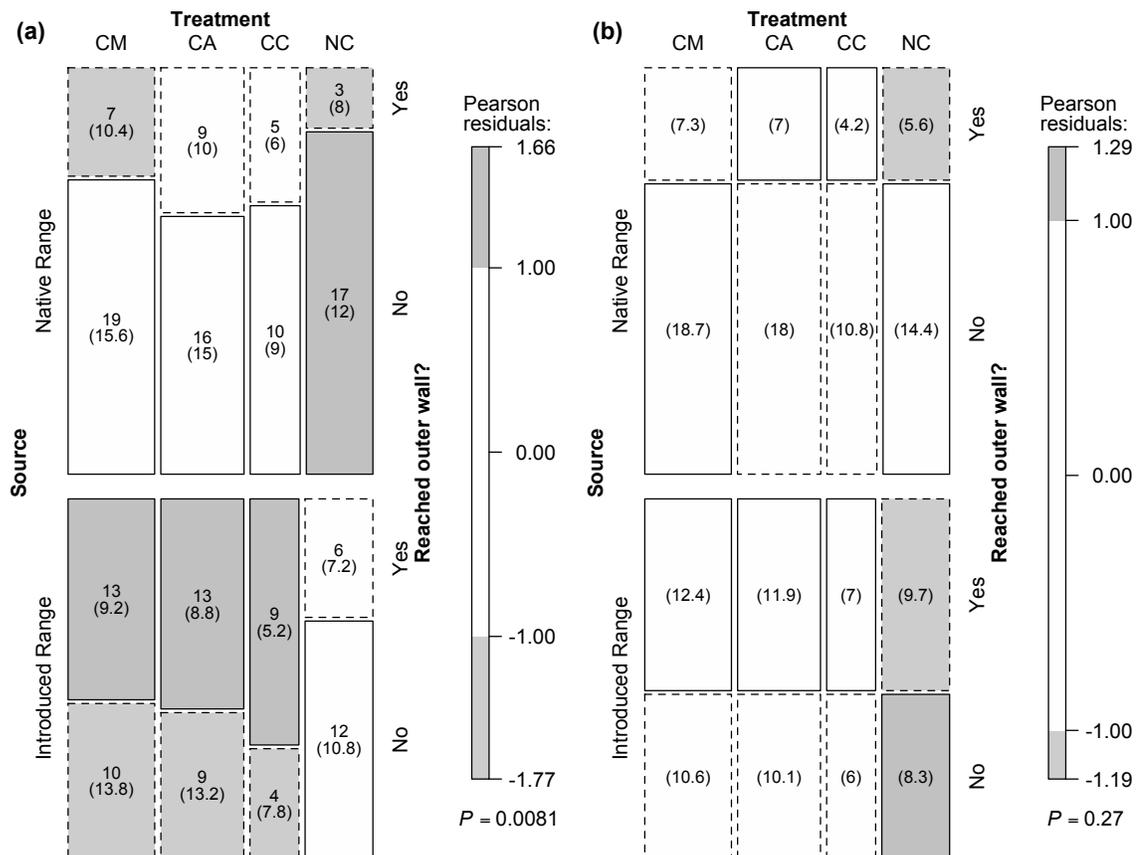


**Figure 2.4:** *Recirculating/No Choice: Probability of reaching an arena wall.* Mosaic plots depicting predicted (in parentheses) and observed counts of *Urosalpinx cinerea* from the native or introduced range that reached the arena wall during a 45 minute trial when exposed to various cue treatments in test arenas with recirculating water flow.

    (a)   Observed data with predictions based on constant probability model.

    (b)   Expected values based on best model (Reached Wall ~ Range).

Cue treatments are *Carcinus maenas* (CM), *Cancer antennarius* (CA), Crushed Conspecifics (CC), and No Cue (NC). Dashed lines indicate a value less than expected based on the model predictions. Shading represents the Pearson residual for that observation relative to the model prediction.

**Table 2.3:** *Recirculating/No Choice: Probability of reaching arena wall.*
**a. Top:** Goodness-of-fit for models of moving native and introduced range *Urosalpinx cinerea*'s chance of reaching the test arena wall during a 45 minute trial when exposed to various cue treatments in recirculating water flow. **Bottom:** Results of likelihood ratio tests comparing nested models relating reaching the arena wall to source range (R) and cue treatment (T).

| Code | Model | Deviance | df | $P > \chi^2$ |
|---|---|---|---|---|
| *m0* | Reached Wall ~ 1 | 19.03 | 7 | **0.0081** |
| *mR* | Reached Wall ~ Range | 7.53 | 6 | 0.27 |
| *mT* | Reached Wall ~ Treatment | 12.46 | 4 | **0.014** |
| *mR+T* | Reached Wall ~ Range + Treatment | 0.36 | 3 | 0.95 |
| *mR×T* | Reached Wall ~ Range × Treatment *(saturated model)* | 0 | 0 | |

| *Likelihood Ratio Test* | | $\Delta$ *Deviance* | $\Delta$ *df* | $P > \chi^2$ |
|---|---|---|---|---|
| mR *vs* m0 | *(gross Range effect)* | 11.50 | 1 | **<0.001** |
| mR+T *vs* mT | *(net Range effect)* | 12.10 | 1 | **<0.001** |
| mT *vs* m0 | *(gross Treatment effect)* | 6.57 | 3 | 0.087 |
| mR+T *vs* mR | *(net Treatment effect)* | 7.17 | 3 | 0.067 |

**b. Top:** Goodness-of-fit for models pooling across cue presence. **Bottom:** Results of likelihood ratio tests comparing nested models relating reaching the arena wall to source range (R) and cue presence (C).

| Code | Model | Deviance | df | $P > \chi^2$ |
|---|---|---|---|---|
| *m0* | Reached Wall ~ 1 | 17.92 | 3 | **<0.001** |
| *mR* | Reached Wall ~ Range | 6.43 | 2 | **0.040** |
| *mC* | Reached Wall ~ Cue Presence | 12.05 | 2 | **0.0024** |
| *mR+C* | Reached Wall ~ Range + Cue Presence | 0.03 | 1 | 0.87 |
| *mR×C* | Reached Wall ~ Range × Cue Presence *(saturated model)* | 0 | 0 | |

| *Likelihood Ratio Test* | | $\Delta$ *Deviance* | $\Delta$ *df* | $P > \chi^2$ |
|---|---|---|---|---|
| mR *vs* m0 | *(gross Range effect)* | 11.50 | 1 | **<0.001** |
| mR+C *vs* mC | *(net Range effect)* | 12.02 | 1 | **<0.001** |
| mC *vs* m0 | *(gross Cue Presence effect)* | 5.88 | 1 | **0.015** |
| mR+C *vs* mR | *(net Cue Presence effect)* | 6.40 | 1 | **0.011** |

How Treatment influenced whether moving snails reached the outer wall was less clear. For snails from a given range, those in the No Cue treatment reached the wall infrequently (15% of the time for Native Range snails and 33% of the time for Introduced Range snails), while those in the three cue treatments reached the wall at frequencies that were noticeably higher (Figure 2.4a). A Treatment-only model was clearly rejected (Table 2.3a), and while including a Treatment term along with Range substantially decreased model deviances, it did so at the cost of 3 degrees of freedom, so the effect of Treatment was not quite significant at $\alpha = 0.05$ (Table 2.3a, $P = 0.067$). Therefore, with a 4-level Treatment factor, the model including only Range (Figure 2.4b) best balanced fit and parsimony.

However, when the treatments where any cue was present were grouped together (Figure 2.5a), there was support for both Range and Cue Presence (no cue vs any cue) as significant factors influencing the likelihood that *U. cinerea* reached the outer wall of the arena during a trial. For the re-grouped data, the additive Range + Cue Presence model (Figure 2.5b) fit best, both single factor models were rejected, and the effects of Range and Cue Presence were both significant (Table 2.3b).

For both ways of grouping the data, the best model estimated a 3-fold effect of Range on the probability of a snail reaching the wall. The one-factor Range model favored when considering each treatment separately estimated that snails from the Introduced Range were 3.0 times (95% CI: 1.6–5.9 times) more likely to reach the arena wall than snails from the Native Range, while the two-factor Range + Cue Presence model estimated that Introduced Range snails were 3.2 times (95% CI: 1.7–6.3 times) more likely to reach the wall. The Range + Cue Presence model also estimated that the presence of cues had a similar magnitude effect, increasing a snail's probability of reaching the arena wall by almost 3-fold (Cue Present odds ratio: 2.9; 95% CI: 1.3–7.1).
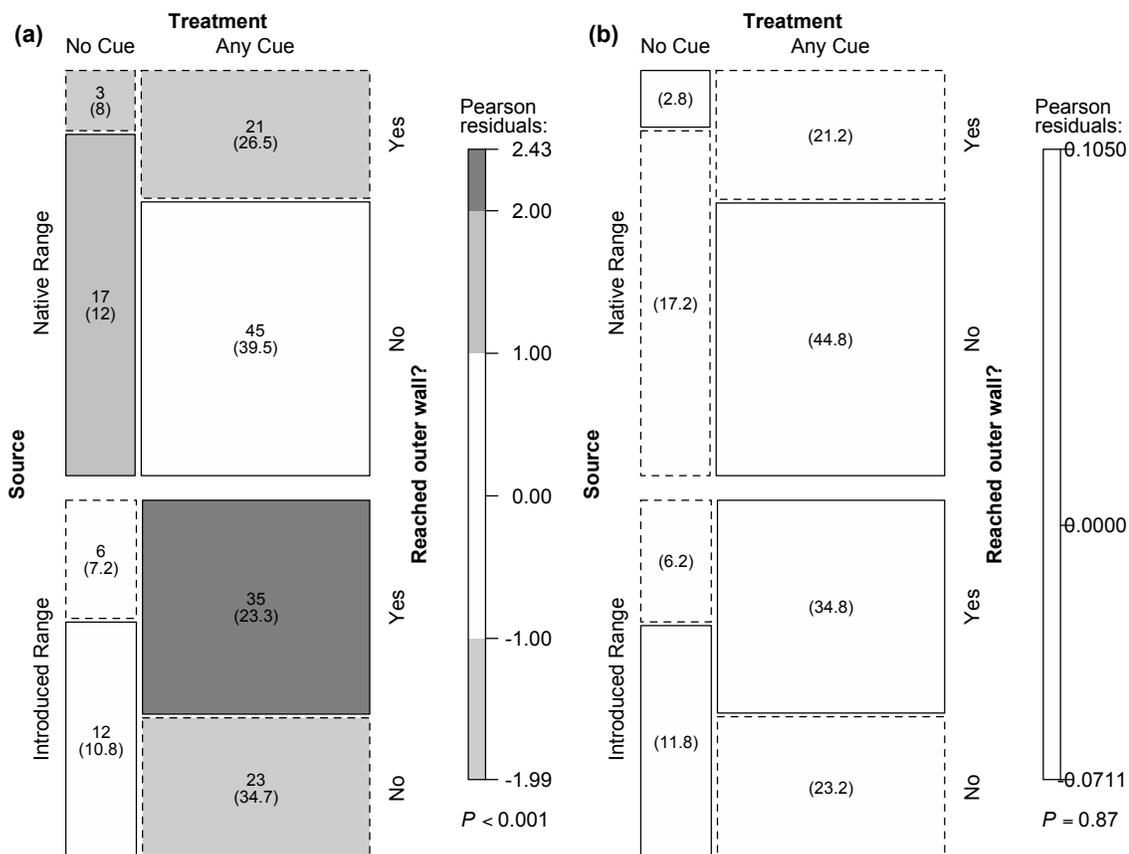
**Figure 2.5:** *Recirculating/No Choice: Probability of reaching an arena wall.* Mosaic plots depicting predicted (in parentheses) and observed counts of *Urosalpinx cinerea* from the native or introduced range that reached the arena wall during a 45 minute trial when exposed to various cue treatments in test arenas with recirculating water flow.

(a) Observed data with predictions based on constant probability model.

(b) Expected values based on best model (Reached Wall ~ Range + Cue Presence).

Dashed lines indicate a value less than expected based on the model predictions. Shading represents the Pearson residual for that observation relative to the model prediction.

*Distance traveled*

Among *U. cinerea* that moved at all, average distances traveled were consistently greater for Introduced Range snails, regardless of cue treatment (Figure 2.6). A one-factor model including only Range best explained the distance *U. cinerea* moved during a trial (Table 2.4), with Introduced Range *U. cinerea* moving an estimated 10.2 cm (95% CI: 5.66–15.4 cm) farther than Native Range snails, which traveled a mean of 12.4 cm (95% CI: 10.4–14.8 cm). Since this Range-based difference in distance traveled appeared both when cues were present and absent, it seems most likely that the Tomales Bay snails were simply able to sustain greater speeds than the Narragansett Bay snails, possibly due

to site-specific differences in snail condition (e.g., age or parasite load). Within Range, snails traveled similar distances in the three cue treatments and slightly less far under No Cue conditions, although there was a great deal of overlap.

**Table 2.4:** *Recirculating/No Choice: Distance traveled.* Results of likelihood ratio tests comparing nested models relating the distance moved by *Urosalpinx cinerea* from the native and introduced ranges to source range and cue treatment.

| *Likelihood Ratio Test* | *Δ Deviance* | *Δ df* | *P > χ2* |
|---|---|---|---|
| Distance ~ Range x Treatment *vs* <br> Distance ~ Range + Treatment | 0.16 | 3 | 0.97 |
| Distance ~ Range + Treatment *vs* <br> Distance ~ Treatment | 16.41 | 1 | **<0.0001** |
| Distance ~ Range *vs* <br> Distance ~ 1 | 14.50 | 1 | **<0.0001** |
| Distance ~ Range + Treatment vs <br> Distance ~ Range | 4.35 | 3 | 0.11 |
| Distance ~ Treatment *vs* <br> Distance ~ 1 | 2.44 | 3 | 0.33 |
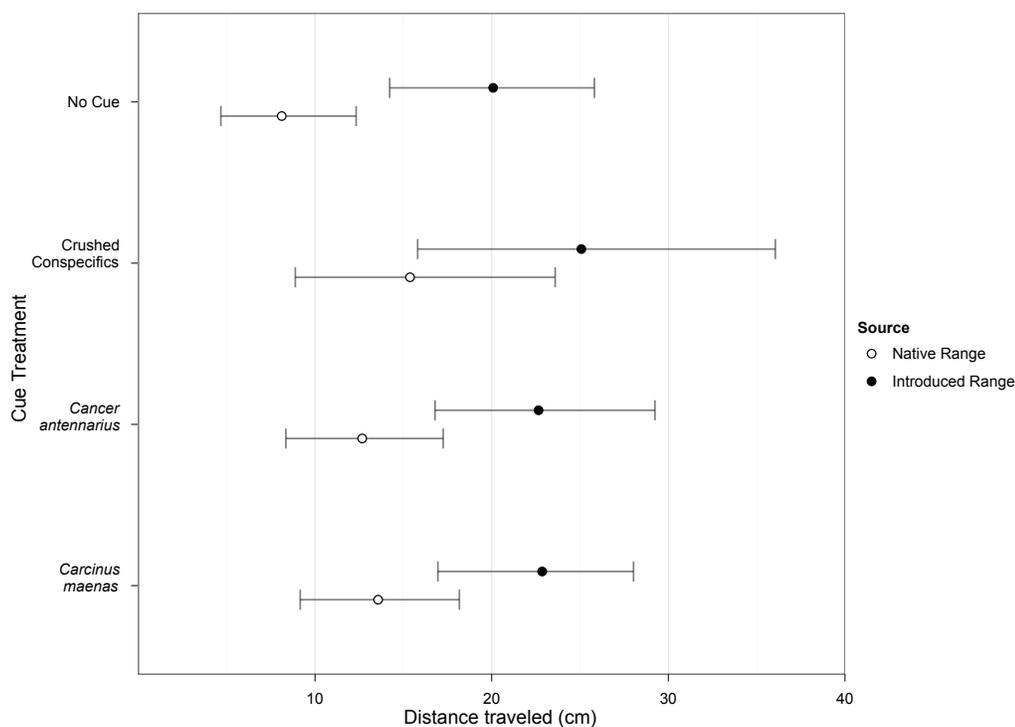


**Figure 2.6:** *Recirculating/No Choice: Distance traveled.* Mean distance moved by *Urosalpinx cinerea* from a native range site (Narragansett Bay, RI) and an introduced range site (Tomales Bay, CA) during a 45 minute trial when exposed to various cue treatments in test arenas with recirculating water flow. Error bars indicate bootstrapped 95% confidence intervals.

## 2.3.2.   Flow-through/Choice Experiment

*Control Run (20°C)*

57% of all *U. cinerea* (84 snails) moved at some point during the Control run. There was no Apparatus- or Range-based influence on probability of moving or distance traveled. Across all groups, snails moved an estimated constant mean distance of 5.3 cm (95% CI: 4.3–6.6 cm; Figure 2.7a). Apparatus did not affect the direction snails moved while running the experiment without any cue sources present, but the effect of Range was significant ($\Delta$ deviance = 4.52, $\Delta$ *df* = 1, *P* = 0.03). Among snails that moved at all, those from the Introduced Range were biased in favor of moving in the "Toward" direction (direction labels here refer to the location of cue sources in the experimental runs), while snails from the Native Range showed no directional bias (estimated probability of moving in the "Away" direction: 32.7% [95% CI: 21.0%–46.1%] for Introduced Range snails and 56.3% [95% CI: 39.1%–72.5%] for Native Range snails).

*Experimental Runs (20°C and 10°C)*

### PROBABILITY OF MOVING

At 20°C, 41% of all *U. cinerea* (62 snails) moved at some point during the run, and a single-factor model including only Treatment best explained the snails' probability of moving (Table 2.5a). Snails exposed to *Carcinus maenas* cues moved 58% of the time (Table 2.5b), while exposure to Crushed Conspecific cues decreased a snail's odds of moving by almost 4-fold, and exposure to *Cancer antennarius* cues decreased the odds of moving by over 2-fold (Table 2.5b). Since *U. cinerea* in the *Carcinus maenas* treatment moved with similar probability as snails in the cue-free Control run, while snails exposed to *Cancer antennarius* and crushed conspecific cues were more likely than not to stay still (Table 2.5b), it seems reasonable to take these results as indicating diminished movement in response to cues from crushed conspecifics and *Cancer antennarius*, but not *Carcinus maenas*. These patterns were consistent between Ranges (Figure 2.7a).

**Table 2.5:** *20° Flow-through/Choice: Probability of moving.*
**a. Top:** Goodness-of-fit for models of whether *Urosalpinx cinerea* from the native and introduced range moved during a 20 minute trial when exposed to various cue treatments in test chambers with one-way water flow and temperature held at 20° C. **Bottom:** Results of likelihood ratio tests comparing nested models relating whether *Urosalpinx cinerea* moved to source range (R) and cue treatment (T).

| Code | Model | | Deviance | df | $P > \chi^2$ |
|------|-------|--|----------|-----|-------------|
| *m0* | Moved ~ 1 | | 11.02 | 5 | 0.051 |
| *mR* | Moved ~ Range | | 10.12 | 4 | **0.038** |
| *mT* | Moved ~ Treatment | | 1.34 | 3 | 0.72 |
| *mR+T* | Moved ~ Range + Treatment | | 0.37 | 2 | 0.83 |
| *mR×T* | Moved ~ Range × Treatment | *(saturated model)* | 0 | 0 | |

| Likelihood Ratio Test | | Δ Deviance | Δ df | $P > \chi^2$ |
|-----------------------|--|-----------|------|-------------|
| mR *vs* m0 | *(gross Range effect)* | 0.90 | 1 | 0.34 |
| mR+T *vs* mT | *(net Range effect)* | 0.96 | 1 | 0.33 |
| mT *vs* m0 | *(gross Treatment effect)* | 9.68 | 2 | **0.0079** |
| mR+T *vs* mR | *(net Treatment effect)* | 9.75 | 2 | **0.0077** |

**b.** Predicted probabilities and relative effects (expressed as odds ratios) for the one-factor model relating cue treatment to whether *Urosalpinx cinerea* moved during a 20 minute trial in test chambers with one-way water flow and temperature held at 20°C.

| Group | | Probability of moving (95% CI) | | Odds Ratio (95% CI) | |
|-------|--|-------------------------------|--|---------------------|--|
| Treatment | Crushed Conspecifics | 0.28 | *(0.17, 0.41)* | **0.28** | *(0.12, 0.64)* |
| | *Cancer antennarius* | 0.38 | *(0.25, 0.52)* | **0.44** | *(0.20, 0.98)* |
| | *Carcinus maenas* | 0.58 | *(0.44, 0.71)* | — | |

At 10°C, 43% of all *U. cinerea* (46 snails) moved during the trials. In contrast to the 20°C run, here the most movement was in the *Cancer antennarius* treatment, where 52–78% of snails moved at some point, compared to 35–40% of snails in the Crushed Conspecific and *Carcinus maenas* treatments (Figure 2.7c). However, support for the significance of this trend was weak, likely because there were fewer moving snails at 10°C, despite the proportion being similar to the 20°C run.

**20°C**

**10°C**
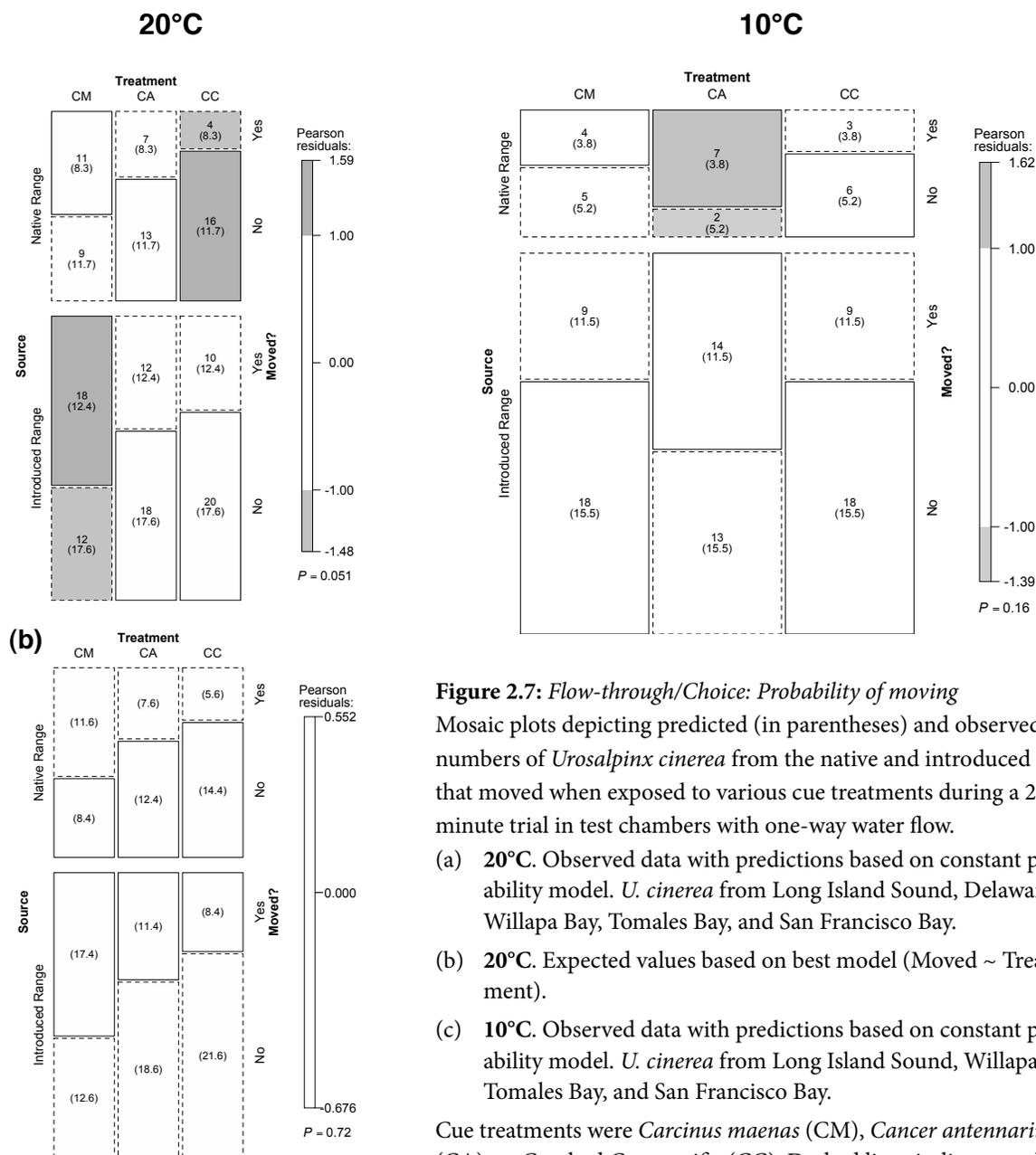
**Figure 2.7:** *Flow-through/Choice: Probability of moving*

Mosaic plots depicting predicted (in parentheses) and observed numbers of *Urosalpinx cinerea* from the native and introduced ranges that moved when exposed to various cue treatments during a 20 minute trial in test chambers with one-way water flow.

(a) **20°C**. Observed data with predictions based on constant probability model. *U. cinerea* from Long Island Sound, Delaware Bay, Willapa Bay, Tomales Bay, and San Francisco Bay.

(b) **20°C**. Expected values based on best model (Moved ~ Treatment).

(c) **10°C**. Observed data with predictions based on constant probability model. *U. cinerea* from Long Island Sound, Willapa Bay, Tomales Bay, and San Francisco Bay.

Cue treatments were *Carcinus maenas* (CM), *Cancer antennarius* (CA), or Crushed Conspecific (CC). Dashed lines indicate a value less than expected based on the model predictions. Shading represents the Pearson residual for that observation relative to the model prediction.

The model including only Treatment had the lowest deviance with the greatest number of degrees of freedom (deviance = 2.33, *df* = 3, *P* = 0.51), but the constant probability model was not rejected (deviance = 7.85, *df* = 5, *P* = 0.16), and the effect of the Treatment term was not quite significant at α = 0.05 (gross Treatment effect: Δ deviance = 5.52, Δ *df* = 2, *P* = 0.063; net Treatment effect: Δ deviance = 5.59, Δ *df* = 2, *P* = 0.061).

### DIRECTION MOVED

At both 20°C and 10°C, neither Range nor Treatment significantly affected whether snails moved away from the cue source, but overall directional bias differed between the temperatures. Snails moved away with an estimated probability of 56.5% (95% CI: 44.0%–68.3%) at 20°C, and 37.0% (95%CI: 24.0%–51.3%) at 10°C. Thus there was a bias toward the cue source during the 10°C run, but no apparent bias in either direction during the 20°C run. However, since Introduced Range snails showed a bias in the "Toward" direction during the Control run when no cue sources were present, it seems unlikely the bias at 10°C demonstrates meaningful attraction to cues.

### DISTANCE TRAVELED

As in the Control run, the distribution of distances moved was positively skewed at both experimental temperatures: most *U. cinerea* that moved did not go very far, while a few snails traveled greater distances. At 20°C, Range, but not Treatment, significantly influenced distance moved (Figure 2.8b; Table 2.6). Introduced Range *U. cinerea* were estimated to move on average 2.6 cm less far (95%CI: 1.0–4.6 cm) than Native Range snails, which traveled a mean of 5.8 cm (95%CI: 4.4–7.6 cm).

At 10°C, models fit with two outlying points removed (see Figure 2.8c) showed no significant effect of Range or Treatment on distance moved. However, snails traveled less far at 10°C than in the warmer-temperature runs, with an estimated constant mean distance moved of 1.9 cm (95%CI: 1.5–2.4 cm).

**Figure 2.8:** *Flow-through/Choice: Distance traveled.*

Mean distances moved by *Urosalpinx cinerea* during a 20 minute trial in test chambers with one-way water flow and constant temperature.

   (a) **Control**.
      *U. cinerea* from Long Island Sound, Delaware Bay, Willapa Bay, Tomales Bay, and San Francisco Bay. Ambient temperature was 20°C. No cue source was present in any experimental apparatus.

   (b) **20°C**.
      *U. cinerea* from Long Island Sound, Delaware Bay, Willapa Bay, Tomales Bay, and San Francisco Bay.

   (c) **10°C**.
      *U. cinerea* from Long Island Sound, Willapa Bay, Tomales Bay, and San Francisco Bay.

Open dots (○) represent Native Range snails; solid dots (●) represent Introduced Range snails. Error bars indicate bootstrapped 95% confidence intervals. Open triangles (△) represent outliers removed from 10°C plot (Native Range, *Cancer antennarius* treatment)
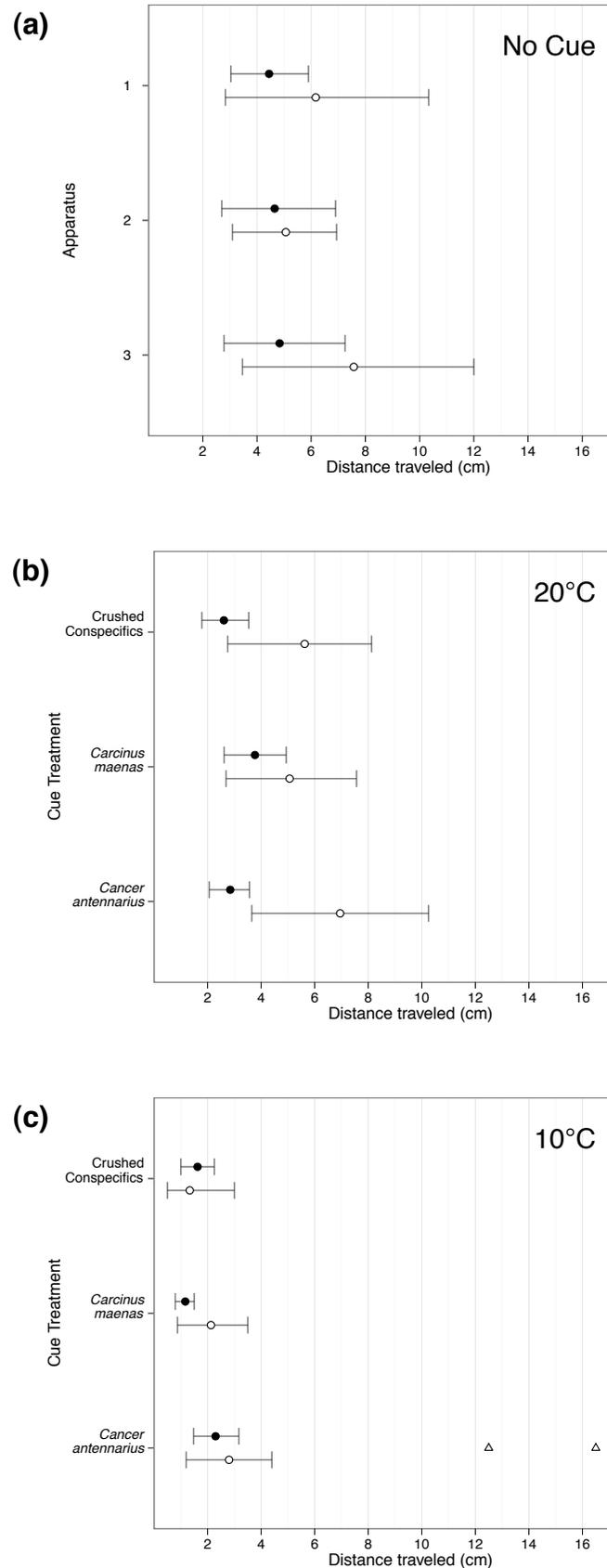
**Table 2.6:** *Flow-through/Choice, 20°C: Distance traveled.* Results of likelihood ratio tests comparing nested models relating how far *Urosalpinx cinerea* from the native and introduced ranges moved to source range and cue treatment.

| Likelihood Ratio Test | Δ Deviance | Δ df | P > χ2 |
|---|---|---|---|
| Distance ~ Range x Treatment *vs* <br> Distance ~ Range + Treatment | 0.60 | 2 | 0.41 |
| Distance ~ Range + Treatment *vs* <br> Distance ~ Treatment | 3.91 | 1 | **<0.001** |
| Distance ~ Range *vs* <br> Distance ~ 1 | 3.77 | 1 | **<0.001** |
| Distance ~ Range + Treatment vs <br> Distance ~ Range | 0.37 | 2 | 0.58 |
| Distance ~ Treatment *vs* <br> Distance ~ 1 | 0.22 | 2 | 0.72 |

## 2.4. Discussion

### 2.4.1. How did *Urosalpinx* respond to risk cues?

*Urosalpinx cinerea* from the native range are able to recognize cues from an introduced range crab predator with which they have no prior experience. In two different flow environments, *U. cinerea* from three native range regions — Narragansett Bay (R/NC experiment), Long Island Sound (FT/C experiment), and Delaware Bay (FT/C experiment) — altered their behavior when exposed to chemical cues from *Cancer antennarius*. The *Cancer antennarius* used in these experiments were collected from areas where *U. cinerea* does not occur and were not fed *U. cinerea* prior to or during the experiments, so the results are best explained by native range *U. cinerea* detecting *Cancer antennarius* kairomones rather than any sort of conspecific alarm cue or digestive cue (Ferrari *et al.* 2010). This suggests that introduced *U. cinerea* may have arrived on the Pacific coast of North America "pre-adapted" to the local predator regime, able to detect threats from ostensibly novel predators. Sih *et al.* (2010) hypothesized that the ability to circumvent novelty disadvantages may be a necessary precondition for successful establishment of introduced predators, but

this is the first study that I am aware of experimentally demonstrating an apparently pre-existing ability to recognize introduced range predator cues among native range individuals of an introduced species.

It seems likely that native range *U. cinerea*'s recognition of the novel introduced range predator *Cancer antennarius* may result from generalizing an innate or learned ability to recognize cues from native range crab predators. The blue crab *Callinectes sapidus* and larger xanthid mud crabs are dominant predators on the Atlantic coast oyster reefs and sheltered nearshore areas that make up the bulk of *U. cinerea*'s historical habitat (Carriker 1955, Gosner 1971, Peterson 1979, Rodney and Paynter 2006). Additionally, juveniles of the rock crab *Cancer irroratus* can be abundant in shallow estuarine habitats in Southern New England (Reilly and Saila 1978), and adults migrate into the lower Chesapeake Bay in fall and winter (Haefner and Engel 1975). Therefore, native range *U. cinerea* are likely to be at risk of predation from a variety of crabs, possibly including at least one species closely related to *Cancer antennarius*. Minnows and larval frogs that have been conditioned to recognize the kairomones of one predator can generalize this response to novel species closely related to that predator, and, in the case of the frogs, also to distantly related species if perceived risk during conditioning is high (Ferrari *et al.* 2007, Ferrari *et al.* 2009). Similarly, for some freshwater snails, phylogenetic relatedness and history of sympatry both affect which alarm cues the snails innately recognize, with snails responding to alarm cues from both closely related snail species and some distant species with which they co-occur (Dalesman *et al.* 2007a). These sorts of generalized responses could come about due to related taxa producing chemically identical cues, or due to flexibility in prey species' reception of relatively similar signals (Ferrari *et al.* 2007), but the chemistry involved has yet to be worked out (Ferrari *et al.* 2010). That *U. cinerea* seem to either rely on cues shared across related crab taxa or be prone to generalizing between similar crab cues fits with the theory that prey which cannot easily escape their predators should favor general over specific cues, since the cost of failing to respond will be higher than that of responding unnecessarily (Sih *et al.* 2010). Slow moving *U. cinerea* would seem to have few

defenses against fast, dexterous crabs other than avoidance. The results of this study also align with the previous report that introduced range *U. cinerea* from Willapa Bay, WA recognize and respond defensively to chemical cues from the introduced range crab predator *Cancer productus* (Grason and Miner 2012). In demonstrating that *U. cinerea* from Tomales Bay (R/NC, FT/C experiments), San Francisco Bay (FT/C experiment), and Willapa Bay (FT/C experiment) responded to chemical cues from *Cancer antennarius*, this study extends what is known about *U. cinerea* predator recognition in the introduced range both geographically and taxonomically. While these results can't rule out the possibility that *U. cinerea* in Willapa Bay have evolved a unique ability to recognize *Cancer productus* since their introduction, that hypothesis now seems less likely.

However, my results are at odds with the work by Kimbro *et al.* (2009) that showed no response by Tomales Bay *U. cinerea* to *Cancer antennarius* or *Carcinus maenas*. Here, Tomales Bay *U. cinerea* responded to *Cancer antennarius* cues under both recirculating and flow-through conditions, and responded to *Carcinus maenas* cues in at least recirculating conditions. One cause of this disparity could be that cues were more concentrated in the small volume, long residence time R/NC experiment than in the Kimbro *et al.* mesocosms. In this case, the Kimbro *et al.* study may have been more realistic, since cues in laboratory test arenas can be artificially high (Dickey and McCarthy 2007), a phenomenon that has been implicated in mismatches between the strength of trait-mediated interactions measured in the lab and in the field (Winkler and Van Buskirk 2012). On the other hand, my study's frequent observations of isolated, focal snails made over a short timespan might also have been more sensitive to subtle responses than the methods used by Kimbro *et al.*, where the positions of fifteen or twenty undifferentiated snails were recorded intermittently over several days. Their results could also have been affected by behavioral trade-offs between risk and hunger (Ferrari *et al.* 2010), or by *U. cinerea* responding to increased conspecific density with greater risk tolerance (Roberts 1996). Grason and Miner (2012) did not find evidence for density dependence in *U. cinerea*'s response to predation risk, but they did not allow snails to interact directly with each other as did

Kimbro *et al.* Future studies of anti-predator responses in *U. cinerea* might consider combining the short term, detailed behavioral observations used here with a longer term focal snail approach as used by Grason and Miner, with attention paid to intraspecific interactions and the naturalism of predator cue concentrations.

*Urosalpinx cinerea* seem to employ more than one defensive strategy, and might switch between them depending on the perceived degree of risk. Two modes of behavior were observed here in response to threat cues: (1) an escape or refuge-seeking response, where snails moved more than when no cues were present, tending to crawl toward and up the walls of their container; and (2) a shelter-in-place response, where snails moved less often than when no cues were present. These patterns of behavior fall within the range of known gastropod anti-predator responses, which frequently include flight, moving out of the water, sheltering under structure, or decreasing overall movement (Paine 1969, Pratt 1974b, Schmitt 1981, McKillup 1982, Rochette *et al.* 1996). In the R/NC experiment, crab cues seemed to elicit refuge-seeking behavior, while conspecific alarm cues elicited shelter-in-place behavior—although the minority of snails exposed to alarm cues that did move seemed to exhibit refuge-seeking behavior, traveling just as far as snails exposed to crab cues and reaching the outer wall at similar frequencies. Meanwhile, in the FT/C experiment, only shelter-in-place type behavior was observed, but here it occurred in response to both a crab cue and to alarm cues. It should be adaptive for prey to tailor their mode of response to different types of risk (Ferrari *et al.* 2010, Sih *et al.* 2010), and species across a variety of systems vary their behaviors in response to different combinations of predator cues and alarm cues (Phillips 1977, Turner 1996, Dalesman *et al.* 2007b). In this case, crushed conspecifics signal actual predation events, and therefore might imply a more imminent danger than crab odors alone. Indeed, alarm cues elicited the strongest long term hiding behavior Grason and Miner (2012) observed in *U. cinerea*.

### 2.4.2. Does environmental context affect cue detection?

*Flow environment*

In contrast to the *Cancer antennarius* results, *U. cinerea*'s response to *Carcinus maenas* varied between the R/NC and FT/C experiments, pointing to a possible role for threat sensitivity in *U. cinerea*'s anti-predator behavior. Fish, frog larvae, and mosquito larvae have all been shown to tailor the intensity of their anti-predator behavior to cue concentration (Jachner and Rydz 2002, Mirza *et al.* 2006, Zhao *et al.* 2006, Ferrari *et al.* 2008), and such threat sensitivity should generally be adaptive when the costs of unnecessary responses are sufficiently high (Ferrari *et al.* 2010). *U. cinerea* from both ranges recognized *Carcinus maenas* cues in the R/NC experiment, but snails exposed to *Carcinus maenas* cues in the FT/C experiment seemed to behave largely as they did when no cues were present, perhaps because of the reduced cue concentration under flow-through conditions. That *U. cinerea* seemed to respond to *Cancer antennarius* and conspecific alarm cues under both flow regimes might indicate that the overall risk associated with these cues is higher or more consistent, with *U. cinerea* therefore responding to them at lower concentration thresholds than for green crab cues. On the other hand, *Cancer antennarius* may have simply produced greater concentrations of cue per crab since they tend to be larger than *Carcinus maenas.* Since this study did not explicitly control cue concentration or evaluate the degree of threat posed by different predators, it can only hint in this direction. However, prey species that confront multiple predators may be most sensitive to the predators that pose the greatest risk (Dalesman *et al.* 2007b), and there is some evidence that green crabs may not be important predators of adult *U. cinerea* (Kimbro *et al.* 2009).

When *U. cinerea* had a choice between cue-laden and cue-free flows, snails showed no sign of avoiding threat cues. This contrasts with results from the Campbell *et al.* (2001) study whose apparatus design inspired the one used here; in that study, echinoderms clearly moved into a cue-free flow when the cue-laden one contained conspecific alarm cues. Due to the design of the FT/C apparatus, *U. cinerea* which did move away from the cue-laden flow would almost immediately find themselves in a cue-free flow environment,

effectively turning off the threat signal. This could have muted avoidance responses, or it might have activated a trade-off between the need for prey to acquire information about predators and to avoid predation (Ferrari *et al.* 2010), causing *U. cinerea* to prefer to remain in range of the cue signal. For example, some fish prefer shelters that provide access to predator cue signals, choosing refuges nearby a cue source in slow moving water and more distant refuges in faster currents (Wisenden *et al.* 2010); in field settings, fish may also preferentially move from upstream to downstream of a predator (Wisenden *et al.* 2010). On the other hand, alarmed *U. cinerea* might simply move in any direction in the hopes of finding refuge. Given that crab predators move much faster than *U. cinerea*, it is not clear that there would be much advantage to snails in trying to identify the location of a crab and move away from it.

*Temperature*

There was no evidence that cooler water temperatures inhibited *U. cinerea*'s ability to detect threat cues, but they might interfere with the snails' ability to carry out an effective response. Snails in the 10°C FT/C run moved just as often on average as snails in the 20°C run — in both cases, substantially less often than when cues were absent — but snails that moved at 10°C did not manage to crawl very far. This is consistent with the results from Chapter 1, where cooler temperatures resulted in much slower righting times. Thus at 10°C, a typical winter temperature in *U. cinerea*'s introduced range, the snails' ability to deploy an avoidance response might be limited, restricting them to relying on a shelter-in-place strategy. The effect of seasonal temperature shifts on the effectiveness of *U. cinerea* anti-predator behaviors merits further investigation. Old reports from the native range suggest that *U. cinerea* suffered elevated predation when oyster beds were dredged in the winter due to compromised ability to escape predators (Carriker 1955), and there is evidence from other Atlantic coast molluscs that seasonal cold temperatures reduce the effectiveness of their anti-predator behaviors (Ordzie and Garofalo 1980a).

### 2.4.3. Future Work

The results of this study point to a few avenues for future research. To fully understand how predator interactions affect the impact of introduced range *U. cinerea*, it will be important to measure the effectiveness of the observed snail responses against predators (Sih *et al.* 2010), and to make tests in natural environments (Ferrari *et al.* 2010), where the details of an escape response (for instance, whether snails seek refuge out of water or under rocks) are more apparent and relevant. An introduced species might still be vulnerable to novel predators if its defensive behaviors are a poor match for the predators' foraging behaviors (MacDonald and Harrington 2003).

The implications of cue generalization in aquatic predator–prey interactions are just beginning to be worked out, especially in invertebrates, and little is known about the degree of phylogenetic conservation of many predation threat cues (Ferrari *et al.* 2010). *U. cinerea* seems to present an interesting case in which to consider the mechanisms of generalization and its role in species introductions. Future studies along these lines should include *U. cinerea* from both the Mid– and South Atlantic Bights, since local predator regimes vary latitudinally in the native range. It would also be interesting to examine *U. cinerea* responses to additional native and introduced range predators. Sea stars, in particular, deserve attention; in the northern part of *U. cinerea*'s native range, they may be more important intertidal and shallow subtidal predators than crabs (Carriker 1955), while their abundances are very low inside some Pacific coast estuaries (J.C. Blum *pers. obs.*).

### 2.4.4. Conclusion

*Urosalpinx cinerea* appear to have been in a position to benefit from the similarity between their native community and the resident community in their Pacific coast introduced range, having arrived in the introduced range already capable of recognizing ostensibly novel crab predators, likely because of their history with crab predators encountered in their native range. The case of *U. cinerea* therefore seems to at least partially follow the prediction that introduced predators will have the greatest impact when the introduced

range community is similar to their native community, but lacks a species similar to the introduced predator (Sih *et al.* 2010). It remains to be explored to what extent *U. cinerea* lacks analogs in the introduced range community, and what novelty advantages it may enjoy, especially with regards to its predation on Olympia oysters. This work highlights the importance of comparing between the introduced and native range when considering the role of introduced species traits in the success and impacts of introductions, and illustrates how the study of introduced predators can provide more general insight into the roles that information and novelty play in predator–prey interactions.

# Literature Cited

Agresti, A. 2002. *Categorical Data Analysis, Second Edition.* John Wiley & Sons, Hoboken, New Jersey.

Appleton, R. D., and A. R. Palmer. 1988. Water-borne stimuli released by predatory crabs and damaged prey induce more predator-resistant shells in a marine gastropod. *Proceedings of the National Academy of Sciences of the United States of America* **85**:4387–4391.

Behrens Yamada, S., and P. Kosro. 2010. Linking ocean conditions to year class strength of the invasive European green crab, *Carcinus maenas. Biological Invasions* **12**:1791–1804.

Behrens Yamada, S., and G. E. Gillespie. 2008. Will the European green crab (*Carcinus maenas*) persist in the Pacific Northwest? *ICES Journal of Marine Science* **65**:725–729.

Blakeslee, A. M. H., C. H. McKenzie, J. A. Darling, J. E. Byers, J. M. Pringle, and J. Roman. 2010. A hitchhiker's guide to the Maritimes: anthropogenic transport facilitates long-distance dispersal of an invasive marine crab to Newfoundland. *Diversity and Distributions* **16**:879–891.

Blumstein, D. T., J. C. Daniel, and B. P. Springett. 2004. A test of the multi-predator hypothesis: rapid loss of antipredator behavior after 130 years of isolation. *Ethology* **110**:919–934.

Bossdorf, O., H. Auge, L. Lafuma, W. E. Rogers, E. Siemann, and D. Prati. 2005. Phenotypic and genetic differentiation between native and introduced plant populations. *Oecologia* **144**:1–11.

Buczkowski, G. 2010. Extreme life history plasticity and the evolution of invasive characteristics in a native ant. *Biological Invasions* **12**:3343–3349.

Buhle, E. R., and J. L. Ruesink. 2009. Impacts of invasive oyster drill on Olympia oyster (*Ostrea lurida* Carpenter 1864) recovery in Willapa Bay, Washington, USA. *Journal of Shellfish Research* **28**:87–96.

Callaway, R. M., and J. L. Maron. 2006. What have exotic plant invasions taught us over the past 20 years? *Trends in Ecology & Evolution* **21**:369–374.

Campbell, A. C., S. Coppard, C. D'Abreo, and R. Tudor-Thomas. 2001. Escape and aggregation responses of three echinoderms to conspecific stimuli. *Biological Bulletin* **201**:175–185.

Carlsson, N. O. L., O. Sarnelle, and D. L. Strayer. 2009. Native predators and exotic prey — an acquired taste? *Frontiers in Ecology and the Environment* **7**:525–532.

Carlton, J. T. 1979. History, biogeography, and ecology of the introduced marine and estuarine invertebrates of the Pacific coast of North America [PhD Dissertation]. University of California, Davis, CA. 904 pp.

Carlton, J. T., and A. N. Cohen. 2003. Episodic global dispersal in shallow water marine organisms: The case history of the European shore crabs *Carcinus maenas* and *C. aestuarii. Journal of Biogeography* **30**:1809–1820.

Carriker, M. R. 1955. Critical review of biology and control of oyster drills *Urosalpinx* and *Eupleura*. Special Scientific Report: Fisheries no. 148. U S Fish and Wildlife Service, Washington, DC. 150 pp.

Carriker, M. R., and D. van Zandt. 1973. Activity of the Marine Gastropod *Urosalpinx cinerea* in the Absence of Hibernation. *Chesapeake Science* **14**:285–288.

Carroll, J. C., and R. N. Winn. 1989. Species profiles: life histories and environmental requirements of coastal invertebrates (Pacific Southwest)—brown rock crab, red rock crab, and yellow crab. U.S. Fish and Wildlife Service Biological Report no. 82(11.117). U.S. Army Corps of Engineers, TR EL–82–4. 16 pp.

Carroll, S. P., A. P. Hendry, D. N. Reznick, and C. W. Fox. 2007. Evolution on ecological time-scales. *Functional Ecology* **21**:387–393.

Catling, P. C., A. Hertog, R. J. Burt, R. I. Forrester, and J. C. Wombey. 1999. The short-term effect of cane toads (*Bufo marinus*) on native fauna in the Gulf Country of the Northern Territory. *Wildlife Research* **26**:161–185.

Cohen, A. N., and J. T. Carlton. 1995. Nonindigenous aquatic species in a United States estuary: A case study of the biological invasions of the San Francisco Bay and Delta. Report PB96–166525. U S Fish and Wildlife Service, Washington, D.C.

Cohen, A. N., J. T. Carlton, and M. C. Fountain. 1995. Introduction, dispersal and potential impacts of the green crab *Carcinus maenas* in San Francisco Bay, California. *Marine Biology* **122**:225–237.

Cole, H. A. 1942. The American whelk tingle, *Urosalpinx cinerea* Say, on British oyster beds. *Journal of the Marine Biological Association of the United Kingdom* **25**:477–508.

Conomos, T. J. 1979. Properties and Circulation of San Francisco Bay Waters. Pages 47–84 *in* Conomos, T. J., editor. *San Francisco Bay: the Urbanized Estuary*. Pacific Division of the American Association for the Advancement of Science, San Francisco, California.

Croll, D. A., J. L. Maron, J. A. Estes, E. M. Danner, and G. V. Byrd. 2005. Introduced predators transform subarctic islands from grassland to tundra. *Science* **307**:1959–1961.

Dalesman, S., S. D. Rundle, D. T. Bilton, and P. A. Cotton. 2007a. Phylogenetic relatedness and ecological interactions determine antipredator behavior. *Ecology* **88**:2462–2467.

Dalesman, S., S. D. Rundle, and P. A. Cotton. 2007b. Predator regime influences innate anti-predator behaviour in the freshwater gastropod *Lymnaea stagnalis*. *Freshwater Biology* **52**:2134–2140.

deRivera, C. E., E. D. Grosholz, and G. M. Ruiz. 2011. Multiple and long-term effects of an introduced predatory crab. *Marine Ecology Progress Series* **429**:145–155.

deRivera, C. E., G. M. Ruiz, A. H. Hines, and P. Jivoff. 2005. Biotic resistance to invasion: Native predator limits abundance and distribution of an introduced crab. *Ecology* **86**:3364–3376.

Dickey, B. F., and T. M. McCarthy. 2007. Predator—prey interactions between crayfish (*Orconectes juvenilis*) and snails (*Physa gyrina*) are affected by spatial scale and chemical cues. *Invertebrate Biology* **126**:57–66.

Dukes, J. S., and H. A. Mooney. 1999. Does global change increase the success of biological invaders? *Trends in Ecology & Evolution* **14**:135–139.

Ellstrand, N. C., and K. A. Schierenbeck. 2000. Hybridization as a stimulus for the evolution of invasiveness in plants? *Proceedings of the National Academy of Sciences of the United States of America* **97**:7043–7050.

Elton, C. S. 1958. *The Ecology of Invasions By Animals and Plants*. University of Chicago Press, Chicago and London.

Facon, B., E. Machline, J. P. Pointier, and P. David. 2004. Variation in desiccation tolerance in freshwater snails and its consequences for invasion ability. *Biological Invasions* **6**:283–293.

Ferrari, M., F. Messier, and D. Chivers. 2008. Threat-sensitive learning of predators by larval mosquitoes *Culex restuans*. *Behavioral Ecology and Sociobiology* **62**:1079–1083.

Ferrari, M. C. O., G. E. Brown, F. Messier, and D. P. Chivers. 2009. Threat-sensitive generalization of predator recognition by larval amphibians. *Behavioral Ecology and Sociobiology* **63**:1369–1375.

Ferrari, M. C. O., D. L. Dixson, P. L. Munday, M. I. McCormick, M. G. Meekan, A. Sih, and D. P. Chivers. 2011. Intrageneric variation in antipredator responses of coral reef fishes affected by ocean acidification: implications for climate change projections on marine communities. *Global Change Biology* **17**:2980–2986.

Ferrari, M. C. O., B. D. Wisenden, and D. P. Chivers. 2010. Chemical ecology of predator–prey interactions in aquatic ecosystems: a review and prospectus. *Canadian Journal of Zoology* **88**:698–724.

Ferrari, M. C., A. Gonzalo, F. Messier, and D. P. Chivers. 2007. Generalization of learned predator recognition: an experimental test and framework for future studies. *Proceedings of the Royal Society B: Biological Sciences* **274**:1853–1859.

Frederich, M., and H. O. Portner. 2000. Oxygen limitation of thermal tolerance defined by cardiac and ventilatory performance in spider crab, *Maja squinado*. *American Journal of Physiology – Regulatory, Integrative and Comparative Physiology* **279**:R1531–1538.

Gamradt, S. C., and L. B. Kats. 1996. Effect of introduced crayfish and mosquitofish on California newts. *Conservation Biology* **10**:1155–1162.

Ganaros, A. E. 1958. On development of early stages of *Urosalpinx cinerea* (Say) at constant temperatures and their tolerance to low temperatures. *Biological Bulletin* **114**:188–195.

Garth, J. S., and D. P. Abbott. 1980. Brachyura: The true crabs. Pages 592–630 *in* Morris, R. H., D. P. Abbott, and E. C. Haderlie, editors. *Intertidal Invertebrates of California*. Stanford University Press, Stanford, California.

Gherardi, F., K. M. Mavuti, N. Pacini, E. Tricarico, and D. M. Harper. 2011. The smell of danger: chemical recognition of fish predators by the invasive crayfish *Procambarus clarkii*. *Freshwater Biology* **56**:1567–1578.

Gosner, K. L. 1971. *Guide to Identification of Marine and Estuarine Invertebrates: Cape Hatteras to the Bay of Fundy*. John Wiley and Sons, New York, New York.

Grason, E., and B. Miner. 2012. Behavioral plasticity in an invaded system: non-native whelks recognize risk from native crabs. *Oecologia* **169**:105–115.

Grosberg, R. K., and C. W. Cunningham. 2001. Genetic structure in the sea: from populations to communities. Pages 61–84 *in* Bertness, M. D., M. E. Hay, and S. D. Gaines, editors. *Marine Community Ecology*. Sinauer Associates, Sunderland, Massachusetts.

Grosholz, E. 2002. Ecological and evolutionary consequences of coastal invasions. *Trends in Ecology & Evolution* **17**:22–27.

Grosholz, E. 2010. Avoidance by grazers facilitates spread of an invasive hybrid plant. *Ecology Letters* **13**:145–153.

Grosholz, E. D., J. Moore, C. J. Zabin, S. Attoe, and R. Obernolte. 2007. Planning for Native Oyster Restoration in San Francisco Bay. Final Report to California Coastal Conservancy Agreement# 05–134. 40 pp.

Grosholz, E. D., and G. M. Ruiz. 2003. Biological invasions drive size increases in marine and estuarine invertebrates. *Ecology Letters* **6**:700–705.

Grosholz, E. D., G. M. Ruiz, C. A. Dean, K. A. Shirley, J. L. Maron, and P. G. Connors. 2000. The impacts of a nonindigenous marine predator in a California bay. *Ecology* **81**:1206–1224.

Haefner, P. A., Jr., and W. A. v. Engel. 1975. Aspects of molting, growth and survival of male rock crabs, *Cancer irroratus*, in Chesapeake Bay. *Chesapeake Science* **16**:253–265.

Hanks, J. E. 1957. The rate of feeding of the common oyster drill, *Urosalpinx cinerea* (Say), at controlled water temperatures. *Biological Bulletin* **112**:330–335.

Hazlett, B. A., P. Acquistapace, and F. Gherardi. 2002. Differences in memory capabilities in invasive and native crayfish. *Journal of Crustacean Biology* **22**:439–448.

Hellmann, J. J., J. E. Byers, B. G. Bierwagen, and J. S. Dukes. 2008. Five potential consequences of climate change for invasive species. *Conservation Biology* **22**:534–543.

Helmuth, B., C. D. Harley, P. M. Halpin, M. O'Donnell, G. E. Hofmann, and C. A. Blanchette. 2002. Climate change and latitudinal patterns of intertidal thermal stress. *Science* **298**:1015–1017.

Hierro, J. L., J. L. Maron, and R. M. Callaway. 2005. A biogeographical approach to plant invasions: the importance of studying exotics in their introduced and native range. *Journal of Ecology* **93**:5–15.

Hochachka, P. W. 1991. Temperature — the ectothermy option. *Biochemistry and Molecular Biology of Fishes* **1**:313–322.

Jachner, A., and M. A. Rydz. 2002. Behavioural response of roach (*Cyprinidae*) to different doses of chemical alarm cues (Schreckstoff). *Archiv für Hydrobiologie* **155**:369–381.

Jacobsen, H. P., and O. B. Stabell. 1999. Predator-induced alarm responses in the common periwinkle, *Littorina littorea*: dependence on season, light conditions, and chemical labelling of predators. *Marine Biology* **134**:551–557.

Keller, S. R., and D. R. Taylor. 2008. History, chance and adaptation during biological invasion: separating stochastic phenotypic evolution from response to selection. *Ecology Letters* **11**:852–866.

Kimbro, D., E. Grosholz, A. Baukus, N. Nesbitt, N. Travis, S. Attoe, and C. Coleman-Hulbert. 2009. Invasive species cause large-scale loss of native California oyster habitat by disrupting trophic cascades. *Oecologia* **160**:563–575.

Kleitman, N. 1941. The effect of temperature on the righting of echinoderms. *Biological Bulletin* **80**:292–298.

Koeppel, J. A. 2011. High predation may hinder native oyster (*Ostrea lurida* Carpenter, 1864) restoration in north Humboldt Bay, California [MS Thesis]. Humboldt State University, Arcata, CA. 44 pp.

Kuo, E. S. L., and E. Sanford. 2009. Geographic variation in the upper thermal limits of an intertidal snail: implications for climate envelope models. *Marine Ecology Progress Series* **388**:137–146.

Kurle, C. M., D. A. Croll, and B. R. Tershy. 2008. Introduced rats indirectly change marine rocky intertidal communities from algae- to invertebrate-dominated. *Proceedings of the National Academy of Sciences* **105**:3800–3804.

Lahti, D. C., N. A. Johnson, B. C. Ajie, S. P. Otto, A. P. Hendry, D. T. Blumstein, R. G. Coss, K. Donohue, and S. A. Foster. 2009. Relaxed selection in the wild. *Trends in Ecology & Evolution* **24**:487–496.

Lande, R. 2009. Adaptation to an extraordinary environment by evolution of phenotypic plasticity and genetic assimilation. *Journal of Evolutionary Biology* **22**:1435–1446.

Largier, J., J. Hollibaugh, and S. Smith. 1997. Seasonally hypersaline estuaries in Mediterranean-climate regions. *Estuarine, Coastal and Shelf Science* **45**:789–797.

Latta, L. C., J. W. Bakelar, R. A. Knapp, and M. E. Pfrender. 2007. Rapid evolution in response to introduced predators II: the contribution of adaptive plasticity. *BMC Evolutionary Biology* **7**:21.

Lawrence, J. M. 1975. The effect of temperature–salinity combinations on the functional well-being of adult *Lytechinus variegatus* (Lamarck) (Echinodermata, Echinoidea). *Journal of Experimental Marine Biology and Ecology* **18**:271–275.

Lee, C. E. 2002. Evolutionary genetics of invasive species. *Trends in Ecology & Evolution* **17**:386–391.

Lee, C. E. 2011. Evolution of invasive populations. *in* Simberloff, D., and M. Rejmánek, editors. *The Encyclopedia of Biological Invasions*. University of California Press, Berkeley.

Li, Y., Z. Ke, S. Wang, G. R. Smith, and X. Liu. 2011. An exotic species is the favorite prey of a native enemy. *PLoS ONE* **6**:e24299.

MacDonald, D. W., and L. A. Harrington. 2003. The American mink: The triumph and tragedy of adaptation out of context. *New Zealand Journal of Zoology* **30**:421–441.

Manzi, J. J. 1970. Combined effects of salinity and temperature on the feeding, reproductive, and survival rates of *Eupleura caudata* (Say) and *Urosalpinx cinerea* (Say) (Prosobranchia: Muricidae). *Biological Bulletin* **138**:35–46.

Marko, P. B., and A. R. Palmer. 1991. Responses of a rocky shore gastropod to the effluents of predatory and nonpredatory crabs — avoidance and attraction. *Biological Bulletin* **181**:363–370.

Maron, J. L., M. Vila, and J. Arnason. 2004. Loss of enemy resistance among introduced populations of St. John's Wort (*Hypericum perforatum*). *Ecology* **85**:3243–3253.

McKillup, S. C. 1982. The selective advantage of avoidance of the predatory whelk *Lepsiella vinosa* (Lamarck) by *Littorina unifasciata* (Philippi). *Journal of Experimental Marine Biology and Ecology* **63**:59–66.

Meyer, D., A. Zeileis, and K. Hornik. 2006. The strucplot framework: Visualizing multi-way contingency tables with vcd. *Journal of Statistical Software* **17**:1–48.

Meyer, D., A. Zeileis, and K. Hornik. 2009. vcd: Visualizing Categorical Data v.1.2–7. http://cran.r-project.org/package=vcd

Miller, A. W. 2000. Assessing the importance of biological attributes for invasion success: Eastern oyster (*Crassostrea virginica*) introductions and associated molluscan invasions of Pacific and Atlantic coastal systems [D.Env. Dissertation]. University of California, Los Angeles. 192 pp.

Mirza, R. S., M. C. O. Ferrari, J. M. Kiesecker, and D. P. Chivers. 2006. Responses of American toad tadpoles to predation cues: Behavioural response thresholds, threat-sensitivity and acquired predation recognition. *Behaviour* **143**:877–889.

National Weather Service. 2009. National Data Buoy Center. Accessed: 24 May 2009. http://www.ndbc.noaa.gov/

Ordzie, C. J., and G. C. Garofalo. 1980a. Behavioral recognition of molluscan and echinoderm predators by the bay scallop *Argopecten irradians* (Lamarck) at two temperatures. *Journal of Experimental Marine Biology and Ecology* **43**:29–38.

Ordzie, C. J., and G. C. Garofalo. 1980b. Predation attack success and attraction to the bay scallop *Argopecten irradians* by the oyster drill *Urosalpinx cinerea*. *Journal of Experimental Marine Biology and Ecology* **47**:95–100.

Paine, R. T. 1969. The *Pisaster–Tegula* interaction: prey patches, predator food preference, and intertidal community structure. *Ecology* **50**:950–961.

Parker, I. M., D. Simberloff, W. M. Lonsdale, K. Goodell, M. Wonham, P. M. Kareiva, M. H. Williamson, B. Von Holle, P. B. Moyle, J. E. Byers, and L. Goldwasser. 1999. Impact: toward a framework for understanding the ecological effects of invaders. *Biological Invasions* **1**:3–19.

Pearl, C. A., M. J. Adams, G. S. Schuytema, and A. V. Nebeker. 2003. Behavioral responses of anuran larvae to chemical cues of native and introduced predators in the Pacific Northwestern United States. *Journal of Herpetology* **37**:572–576.

Peck, L. S., K. E. Webb, and D. M. Bailey. 2004. Extreme sensitivity of biological function to temperature in Antarctic marine species. *Functional Ecology* **18**:625–630.

Peterson, C. H. 1979. The importance of predation and competition in organizing the intertidal epifaunal communities of Barnegat Inlet, New Jersey. *Oecologia* **39**:1–24.

Phillips, D. W. 1977. Avoidance and escape responses of the gastropod mollusc *Olivella biplicata* (Sowerby) to predatory asteroids. *Journal of Experimental Marine Biology and Ecology* **28**:77–86.

Pigliucci, M., and C. J. Murren. 2003. Perspective: genetic assimilation and a possible evolutionary paradox: can macroevolution sometimes be so fast as to pass us by? *Evolution* **57**:1455–1464.

Pigliucci, M., C. J. Murren, and C. D. Schlichting. 2006. Phenotypic plasticity and evolution by genetic assimilation. *Journal of Experimental Biology* **209**:2362–2367.

Portner, H. O., and R. Knust. 2007. Climate change affects marine fishes through the oxygen limitation of thermal tolerance. *Science* **315**:95–97.

Pratt, D. M. 1974a. Attraction to prey and stimulus to attack in the predatory gastropod *Urosalpinx cinerea*. *Marine Biology* **27**:37–45.

Pratt, D. M. 1974b. Behavioral defenses of *Crepidula fornicata* against attack by *Urosalpinx cinerea*. *Marine Biology* **27**:47–49.

Pratt, D. M. 1976. Intraspecific signalling of hunting success or failure in *Urosalpinx cinerea*. *Journal of Experimental Marine Biology and Ecology* **21**:7–9.

Preisser, E. L., D. I. Bolnick, and M. F. Benard. 2005. Scared to death? The effects of intimidation and consumption in predator–prey interactions. *Ecology* **86**:501–509.

Prentis, P. J., J. R. Wilson, E. E. Dormontt, D. M. Richardson, and A. J. Lowe. 2008. Adaptive evolution in invasive species. *Trends in Plant Science* **13**:288–294.

R Development Core Team. 2009. R: A Language and Environment for Statistical Computing v.2.10.1. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org/

Rahel, F. J., and J. D. Olden. 2008. Assessing the effects of climate change on aquatic invasive species. *Conservation Biology* **22**:521–533.

Reilly, P. N., and S. B. Saila. 1978. Biology and ecology of the rock crab, *Cancer irroratus* Say, 1817, in southern New England waters (Decapoda, Brachyura). *Crustaceana* **34**:121–140.

Reznick, D. N., and C. K. Ghalambor. 2001. The population ecology of contemporary adaptations: what empirical studies reveal about the conditions that promote adaptive evolution. *Genetica* **112**:183–198.

Richards, C. L., O. Bossdorf, N. Z. Muth, J. Gurevitch, and M. Pigliucci. 2006. Jack of all trades, master of some? On the role of phenotypic plasticity in plant invasions. *Ecology Letters* **9**:981–993.

Rittschof, D., and G. Gruber. 1988. Response to prey odors by oyster drills, *Urosalpinx cinerea cinerea*, *Urosalpinx cinerea follyensis* and *Eupleura caudata etterae*. *Marine Behaviour and Physiology* **13**:185–199.

Rittschof, D., L. G. Williams, B. Brown, and E. R. Carriker. 1983. Chemical attraction of newly hatched oyster drills. *Biological Bulletin* **164**:493–505.

Roberts, G. 1996. Why individual vigilance declines as group size increases. *Animal Behaviour* **51**:1077–1086.

Rochette, R., J. N. McNeil, and J. H. Himmelman. 1996. Inter- and intra-population variations in the response of the whelk *Buccinum undatum* to the predatory asteroid *Leptasterias polaris*. *Marine Ecology Progress Series* **142**:193–201.

Rodney, W. S., and K. T. Paynter. 2006. Comparisons of macrofaunal assemblages on restored and non-restored oyster reefs in mesohaline regions of Chesapeake Bay in Maryland. *Journal of Experimental Marine Biology and Ecology* **335**:39–51.

Roman, J. 2006. Diluting the founder effect: cryptic invasions expand a marine invader's range. *Proceedings of the Royal Society B: Biological Sciences* **273**:2453–2459.

Root, T. L., J. T. Price, K. R. Hall, S. H. Schneider, C. Rosenzweig, and J. A. Pounds. 2003. Fingerprints of global warming on wild animals and plants. *Nature* **421**:57–60.

Ross, D. J., C. R. Johnson, and C. L. Hewitt. 2003. Variability in the impact of an introduced predator (*Asterias amurensis*: Asteroidea) on soft-sediment assemblages. *Journal of Experimental Marine Biology and Ecology* **288**:257–278.

Sakai, A. K., F. W. Allendorf, J. S. Holt, D. M. Lodge, J. Molofsky, K. A. With, S. Baughman, R. J. Cabin, J. E. Cohen, N. C. Ellstrand, D. E. McCauley, P. O'Neil, I. M. Parker, J. N. Thompson, and S. G. Weller. 2001. The population biology of invasive species. *Annual Review of Ecology and Systematics* **32**:305–332.

Sala, O. E., F. S. Chapin, III, J. J. Armesto, E. Berlow, J. Bloomfield, R. Dirzo, E. Huber-Sanwald, L. F. Huenneke, R. B. Jackson, A. Kinzig, R. Leemans, D. M. Lodge, H. A. Mooney, M. Oesterheld,n, N. L. Poff, M. T. Sykes, B. H. Walker, M. Walker, and D. H. Wall. 2000. Global biodiversity scenarios for the year 2100. *Science* **287**:1770–1774.

Salo, P., E. Korpimäki, P. B. Banks, M. Nordström, and C. R. Dickman. 2007. Alien predators are more dangerous than native predators to prey populations. *Proceedings of the Royal Society B: Biological Sciences* **274**:1237–1243.

Sanford, E. 1999. Regulation of keystone predation by small changes in ocean temperature. *Science* **283**:2095–2097.

Sanford, E., M. S. Roth, G. C. Johns, J. P. Wares, and G. N. Somero. 2003. Local selection and latitudinal variation in a marine predator–prey interaction. *Science* **300**:1135–1137.

Say, T. 1822. An account of some of the marine shells of the United States. *Journal of the Academy of Natural Sciences of Philadelphia* **2**:221–248.

Schmitt, R. J. 1981. Contrasting anti-predator defenses of sympatric marine gastropods (family Trochidae). *Journal of Experimental Marine Biology and Ecology* **54**:251–263.

Shick, J. M. 1972. Temperature sensitivity of oxygen consumption of latitudinally separated *Urosalpinx cinerea* (Prosobranchia: Muricidae) populations. *Marine Biology* **13**:276–283.

Sih, A., D. I. Bolnick, B. Luttbeg, J. L. Orrock, S. D. Peacor, L. M. Pintor, E. Preisser, J. S. Rehage, and J. R. Vonesh. 2010. Predator–prey naïveté, antipredator behavior, and the ecology of predator invasions. *Oikos* **119**:610–621.

Sloop, C., D. Ayres, and D. Strong. 2009. The rapid evolution of self-fertility in *Spartina* hybrids (*Spartina alterniflora* x *foliosa*) invading San Francisco Bay, CA. *Biological Invasions* **11**:1131–1144.

Smith, S. V., and J. T. Hollibaugh. 1998. Tomales Bay LMER/BRIE water temperature data. Accessed: 24 May 2009. http://lmer.marsci.uga.edu/tomales/tb_watertemp_metadata.html

Sorte, C. J. B., A. Fuller, and M. E. S. Bracken. 2010. Impacts of a simulated heat wave on composition of a marine community. *Oikos Oikos* **119**:1909–1918.

Stachowicz, J. J., J. R. Terwin, R. B. Whitlatch, and R. W. Osman. 2002. Linking climate change and biological invasions: Ocean warming facilitates nonindigenous species invasions. *Proceedings of the National Academy of Sciences of the United States of America* **99**:15497–15500.

Stauber, L. A. 1950. The problem of physiological species with special reference to oysters and oyster drills. *Ecology* **31**:109–118.

Stillman, J. H. 2003. Acclimation capacity underlies susceptibility to climate change. *Science* **301**:65.

Strayer, D. L., V. T. Eviner, J. M. Jeschke, and M. L. Pace. 2006. Understanding the long-term effects of species invasions. *Trends in Ecology & Evolution* **21**:645–651.

Thébaud, C., and D. Simberloff. 2001. Are plants really larger in their introduced ranges? *The American Naturalist* **157**:231–236.

Thom, R. M., A. B. Borde, S. Rumrill, D. L. Woodruff, G. D. Williams, J. A. Southard, and S. L. Sargeant. 2003. Factors influencing spatial and annual variability in eelgrass (*Zostera marina* L.) meadows in Willapa Bay, Washington, and Coos Bay, Oregon, estuaries. *Estuaries* **26**:1117–1129.

Thompson, J. N. 1998. Rapid evolution as an ecological process. *Trends in Ecology & Evolution* **13**:329–332.

Trussell, G. C., and M. O. Nicklin. 2002. Cue sensitivity, inducible defense, and trade-offs in a marine snail. *Ecology* **83**:1635–1647.

Trussell, G. C., P. J. Ewanchuk, and M. D. Bertness. 2003. Trait-mediated effects in rocky intertidal food chains: Predator risk cues alter prey feeding rates. *Ecology* **84**:629–640.

Turner, A. M. 1996. Freshwater snails alter habitat use in response to predation. *Animal Behaviour* **51**:747–756.

U.S. Geological Survey. 2010. Water Quality of San Francisco Bay. Accessed: 24 May 2010. http://sfbay.wr.usgs.gov/access/wqdata

Ubaldo, J. P., F. A. Uy, and D. T. Dy. 2007. Temperature tolerance of some species of Philippine intertidal echinoderms. *The Philippine Scientist* **44**:105–119.

Vermeij, M., T. Smith, M. Dailer, and C. Smith. 2009. Release from native herbivores facilitates the persistence of invasive marine algae: A biogeographical comparison of the relative contribution of nutrients and herbivory to invasion success. *Biological Invasions* **11**:1463–1474.

Walther, G. R., E. Post, P. Convey, A. Menzel, C. Parmesan, T. J. Beebee, J. M. Fromentin, O. Hoegh-Guldberg, and F. Bairlein. 2002. Ecological responses to recent climate change. *Nature* **416**:389–395.

Walther, G. R., A. Roques, P. E. Hulme, M. T. Sykes, P. Pysek, I. Kuhn, M. Zobel, S. Bacher, Z. Botta-Dukat, H. Bugmann, B. Czucz, J. Dauber, T. Hickler, V. Jarosik, M. Kenis, S. Klotz, D. Minchin, M. Moora, W. Nentwig, J. Ott, V. E. Panov, B. Reineking, C. Robinet, V. Semenchenko, W. Solarz, W. Thuiller, M. Vila, K. Vohland, and J. Settele. 2009. Alien species in a warmer world: risks and opportunities. *Trends in Ecology & Evolution* **24**:686–693.

Wanger, T. C., A. C. Wielgoss, I. Motzke, Y. Clough, B. W. Brook, N. S. Sodhi, and T. Tscharntke. 2011. Endemic predators, invasive prey and native diversity. *Proceedings of the Royal Society B: Biological Sciences* **278**:690–694.

Wares, J. P., A. R. Hughes, and R. K. Grosberg. 2005. Mechanisms that drive evolutionary change: insights from species introductions and invasions. Pages 229–257 *in* Sax, D. F., J. J. Stachowicz, and S. D. Gaines, editors. *Species Invasions: Insights into Ecology, Evolution, and Biogeography*. Sinauer Associates, Sunderland, Massachusetts.

Washington State Department of Ecology. 2009. Willapa Bay Water Quality Data.

Whitney, K. D., and C. A. Gabler. 2008. Rapid evolution in introduced species, 'invasive traits' and recipient communities: challenges for predicting invasive potential. *Diversity and Distributions* **14**:569–580.

Wickham, H. 2009. *ggplot2: Elegant Graphics for Data Analysis*. Springer, New York, NY.

Williams, L. G., D. Rittschof, B. Brown, and M. R. Carriker. 1983. Chemotaxis of oyster drills *Urosalpinx cinerea* to competing prey odors. *Biological Bulletin* **164**:536–548.

Winkler, J. D., and J. Van Buskirk. 2012. Influence of experimental venue on phenotype: multiple traits reveal multiple answers. *Functional Ecology* **26**:513–521.

Wisenden, B. D., C. L. Binstock, K. E. Knoll, A. J. Linke, and B. S. Demuth. 2010. Risk-sensitive information gathering by cyprinids following release of chemical alarm cues. *Animal Behaviour* **79**:1101–1107.

Wood, L. 1968. Physiological and ecological aspects of prey selection by the marine gastropod *Urosalpinx cinerea* (Prosobranchia: Muricidae). *Malacologia* **6**:267–320.

Zeileis, A., D. Meyer, and K. Hornik. 2007. Residual-based shadings for visualizing (conditional) independence. *Journal of Computational and Graphical Statistics* **16**:507–525.

Zhao, X. X., M. C. O. Ferrari, and D. P. Chivers. 2006. Threat-sensitive learning of predator odours by a prey fish. *Behaviour* **143**:1103–1121.