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ORIGINAL PAPER

Physiological tolerances across latitudes: thermal sensitivity of larval marine snails (*Nucella* spp.)

Mackenzie L. Zippay · Gretchen E. Hofmann

Abstract A critical step in understanding how temperature will affect biodiversity in coastal ecosystems is to gain insight into how the tolerances, and ultimately survival, of early life history stages will influence the distribution and abundance of adults. We assessed the thermal tolerance of encapsulated veliger-stage larvae of a common dogwhelk, *Nucella ostrina*, that occur in the rocky intertidal zone on the west coast of North America. Results showed that veligers collected from northern latitudes in Washington State were less tolerant of heat stress than those from central sites in California. For all sites, we found there to be a subtle difference between the temperatures at which veligers first began to die compared to when veligers reached 100% mortality. On a biogeographic scale, the LT_{50} temperatures, a measure of larval sensitivity, for *N. ostrina* veligers displayed a strong latitudinal trend. These findings provide a conservative measurement of the upper thermal limits of encapsulated veligers while illustrating how these early life history stages could be physiologically compromised under future climate warming scenarios.

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Introduction

Although larval forms have been traditionally recognized as a vulnerable stage in the life history of marine organisms (Wilson 1973; Jackson and Strathmann 1981, but see Hamdoun and Epel 2007), few studies have explored the tolerances of embryos or larvae in broad ecological terms (Fernández et al. 2007). Existing research has focused on thermal tolerance differences among developmental stages (e.g., Pedersen and Tande 1992; Sewell and Young 1999; Lu et al. 2004) and temperature effects on the pelagic larval duration (PLD) and their ecological consequences (O'Connor et al. 2007). The importance of understanding the vulnerabilities of larval life history stages in marine invertebrates lends recognition to the emerging field of ecological development (see Sultan 2007). In this study, we tested the thermal tolerance of veligers of the marine dogwhelk, *Nucella ostrina*, a common, broadly distributed inhabitant of the rocky intertidal of the Northeastern Pacific. Additionally, we tested whether there were any differences in physiological tolerance that could be linked to biogeographic distribution.

The dogwhelks of the Northeastern Pacific coast are an ideal system with which to address the role of physiological capacities, such as thermal tolerance, in setting species range boundaries in the rocky intertidal zone. These intertidal snails lack a planktonic larval stage and develop in egg capsules to juveniles that hatch out and 'crawl away' (Morris et al. 1980). Females lay yellow, stalk-like egg capsules that contain numerous developing embryos (Spight and Emlen 1976), fixed on benthic substrates (Thorson 1950). Thus, these egg capsules are routinely exposed to elevated air temperatures during emersion and cooler seawater temperatures during immersion, making them an ideal biological indicator for environmental thermal stress. *Nucella*

ostrina are commonly found in the mid-high intertidal zone within and among mussel beds and barnacles. In coastal sites along the US Pacific Northwest, female *N. ostrina* can produce egg capsules year-round, although they are more abundant during the winter and spring when food supply is more favorable (Seavy 1977; Moran and Emlet 2001). During development to trochophore and later to veliger stages, embryos feed on nurse eggs (unfertilized eggs or non-developing embryos) within the egg capsule (LeBoeuf 1971). After 2.5–4 months of encapsulated development, individuals hatch as metamorphosed juvenile snails (Costello and Henley 1971; Morris et al. 1980). Unlike juvenile and adult stages of *Nucella*, the sessile egg capsules are not able to actively avoid abiotic stressors (e.g., desiccation, temperature) by moving to less stressful microhabitats. As a result, developing larvae may represent a significant stage of vulnerability for this marine gastropod. Thus, understanding the physiological responses underlying the development of encapsulated embryos is a key step in defining environmental parameters that can contribute to setting a species range boundaries.

Previous studies have shown that survivorship of early life history stages can be significantly impacted by environmental factors and ultimately influence adult populations (barnacles, Connell 1985; polychaetes, Qian and Chia 1994; oysters, Roegner and Mann 1995; snails, Gosselin and Qian 1997; Moran and Emlet 2001). Additionally, a few studies have looked at the effects of temperature on encapsulated development (Boon-Niermeijer and Van de Scheur 1984; Przeslawski 2005; Fernández et al. 2007); however, to our knowledge, none have addressed survivorship during encapsulated development in *Nucella*. For later stages, mortality data on *N. lamellosa* juveniles estimate that 90–99% die within the first year (Spight 1976) and only 1–2% of *N. lapillus* survive the first few months of life (Feare 1970). Other investigators have addressed potential biotic and abiotic sources of mortality (e.g., salinity—Pechenik 1983; desiccation—Gosselin and Chia 1995a; Rawlings 1999; sun exposure—Moran and Emlet 2001; predation—Spight 1976; Gosselin and Rehak 2007; wave exposure—Etter 1996; Gosselin and Rehak 2007; ultraviolet radiation—Rawlings 1996) in juvenile and encapsulated individuals. However, temperature, in particular, has not been well studied with respect to earlier stages of development. In regard to temperature tolerances of *N. ostrina*, very little is known about how thermal stress affects embryonic survivorship. Gosselin and Chia (1995b) found that *N. ostrina* (formerly *N. emarginata*, Marko 1998) hatchlings around Barkley Sound (Vancouver Island, Canada) were tolerant of temperatures as high as 26°C; all hatchlings survived 8 h of exposure at 22 and 26°C. Mortality among hatchlings did occur at 30°C, whereas adults

survived all temperature treatments. This study exemplifies the dichotomy that can exist between the impacts of temperature on juvenile and adult marine invertebrates.

To further explore the relationship of thermal tolerance and early life history stages, we characterized the temperature tolerance of encapsulated veligers of *N. ostrina*. This is the first study to measure the temperature tolerance of encapsulated *Nucella* veligers. In addition, given that *N. ostrina* has an expansive range distribution, from Yakutat, Alaska to Pt. Conception, CA (Vermeij et al. 1990; Collins et al. 1996), we tested the thermal tolerance of veligers collected from multiple sites within the species' biogeographic range in order to assess the relationship between latitudinal distribution and thermal tolerance. By identifying the upper thermal limits for these embryos, we hoped to contribute to our understanding of how the physiological tolerances of larval stages maps onto the distribution of the adult population.

Materials and methods

Nucella collections

During the breeding season, *N. ostrina* egg capsules were collected from seven mid- to high-intertidal sites between the months of May and July 2006 along the west coast of the United States across ~13° of latitude from Washington State to Central California. The collection locations are as follows: Cattle Point, San Juan Island, WA (CP); Boiler Bay, OR (BB); Strawberry Hill, OR (SH); Coos Bay, OR (CB); Humboldt, CA (HUM); Bodega Cove, CA (BML); Cambria, CA (RM) (see Table 1). At one collection site (Rancho Marino Reserve in Cambria, CA), *N. ostrina* overlaps in distribution with *N. emarginata* near Point Conception (Marko 1998). However, for this study, since genotyping was not conducted on the veligers, egg capsules collected from this site were called *N. ostrina* resembling the 'northern form' described by Palmer (1990) and later classified as *N. ostrina* by Marko (1998). At all sites, 15–30 egg capsules were haphazardly collected from 10–25 clutches by scraping egg capsules off the substrate and placing them in a mesh holding container. After collection, all egg capsules were immediately transported back to a marine facility near the site. Upon arrival, the egg capsules were placed in a flow-through seawater tank containing seawater adjusted to the temperature of the location where the capsules were collected (10–19°C). On average, experiments were run about 1–3 h after collection, and no collection of egg capsules was held for more than 12 h before experimentation began.

Table 1 Collecting sites for *Nucella ostrina*

Site of collection	Species collected	Coordinates
Cattle Point, WA (CP)	*Nucella ostrina*	N 48°27.001′ W 122°57.803′
Boiler Bay, OR (BB)	*Nucella ostrina*	N 44°50.001′ W 124°03.846′
Strawberry Hill, OR (SH)	*Nucella ostrina*	N 44°14.995 W 124°06.808
Coos Bay, OR (CB)	*Nucella ostrina*	N 43°20.968′ W 124°19.808′
Humboldt, CA (HUM)	*Nucella ostrina*	N 41°03.432′ W 124°08.957′
Bodega Marine Reserve Bodega Cove, CA (BML)	*Nucella ostrina*	N 38°18.250′ W 123°03.540′
Rancho Marino Reserve Cambria, CA (RM)	*Nucella ostrina*[a]	N 35°33.290′ W 121°10.580′

[a] Records may include *N. emarginata* in the southern part of the range of *Nucella* spp.

Thermal tolerance trials

Using a protocol modified after Sewell and Young (1999), the egg capsules were exposed to a range of temperatures (from 13 to 34.5°C, see Table 2), including some of the higher temperatures that could be experienced in the intertidal zone during emersion (Zippay 2009). While some of the temperatures were outside the range of ecological relevancy, it was important for this study to identify the physiological limits imposed by temperature on survival for developing veligers. The number of temperature treatments varied slightly from site to site due to the number of egg capsules available for collection. For the actual assay, five to eight egg capsules were placed in an unsealed 20 mL glass scintillation vial containing filtered seawater (0.35 μm), in triplicate at each of the different temperatures (Table 2). To eliminate the confounding effect of desiccation stress as a variable, egg capsules were exposed to the temperature treatments while immersed in seawater. After the 1-h incubation, egg capsules (*n* = 5–8) were cut open, and larvae were examined under a dissecting microscope and were scored for survivorship. Larvae that appeared to

have ciliary movement around their velum were considered alive and those with no movement were scored as dead. Each capsule contained approximately 5–22 larvae.

Methodologically, temperature exposures of 1–2 h in duration are commonly used to analyze the physiological performance of larvae (Boon-Niermeijer and Van de Scheur 1984; Sewell and Young 1999; Brown et al. 2004). Although it is likely that *Nucella* egg capsules might experience more prolonged exposures to thermal stress in the field, we took a conservative approach in this study and chose a 1 h period for the assessment of survivorship. It is important to note that only advanced veliger-stage larvae were used for this experiment (as described by Gallardo 1979). Namely, if the larvae did not have distinct velar lobes, appearance of shell, eyespots, formation of foot, and operculum, then the whole egg capsule was eliminated from the experiment. These thermal tolerance trials were designed to measure veliger mortality across different temperatures, and these data were used to calculate the LT_{50} for that particular site. LT_{50} refers to the temperature at which 50% of the total experimental population was killed by the heat treatment (Stillman and Somero 2000; Hamdoun et al. 2003).

Recovery experiment

To assess if the observed LT_{50} was a true indication of larval mortality as opposed to a temporary state of torpor (i.e., a temporary state of decreased physiological activity) induced by the acute heat stress, a second experiment was conducted on *N. ostrina* larvae from Strawberry Hill, OR. Thirty-five egg capsules were collected from the field and subjected to a lethal (34.5°C) and an acute (31.7°C) heat shock for 1 h and allowed to recover for up to 1 h at the ambient seawater temperature for this population (11°C). *N. ostrina* veligers were exposed to 31.7 and 34.5°C because these temperatures represent the LT_{50} and lethal temperature, respectively, for the Strawberry Hill, OR site.

Using the same thermal tolerance protocol as above, egg capsules (*n* = 35) were exposed to a 1 h heat shock, in triplicate, at the two temperatures (LT_{50} = 31.7°C and lethal = 34.5°C). Immediately following the exposure, seven egg capsules were dissected and larvae survival rates

Table 2 Temperature incubation regimes for *Nucella ostrina* egg capsules for a particular site

Latitude	Sites	1-h incubation temperatures (°C)	LT_{50} (°C)
North	CP	13, 15, 17.5, 19.5, 21.5, 23.5, 25.5, 27.5, 29.5, 31.5, 33.5	30.1
	BB	13, 19.5, 25.5, 29.5, 31.5, 34.5	32.3
	SH	13, 19.5, 21.5, 25.5, 29.5, 31.5, 34.5	31.7
	CB	13, 17.5, 19.5, 21.5, 25.5, 29.5, 31.5, 33.5, 34.5	31.8
	HUM	13, 19.5, 21.5, 23.5, 25.5, 29.5, 31.5, 33.5	32.1
	BML	13, 19.5, 21.5, 25.5, 29.5, 31.5, 34.5	33.6
South	RM	13, 16.5, 19.5, 21.5, 25.5, 29.5, 31, 34	33.9

were determined. The remaining 28 egg capsules for each temperature were placed in the seawater table to recover. Every 15 min up to 1 h, seven egg capsules were removed from the recovery seawater table and survival rates were determined. To obtain a baseline measurement of larval condition in the egg capsules with no heat stress ("control"), survival rates of larvae from 21 *N. ostrina* egg capsules were quantified prior to any high temperature exposures.

Statistical analyses

For the thermal tolerance assays, analyses were performed using JMP 7.0 statistical software (SAS Institute Inc.). The LT_{50} of *Nucella* for each site was calculated using a 95% confidence interval where upper and lower limits of the 50% mortality were given. Analyses for the recovery experiment were performed using SigmaStat 3.0 statistical software. The average mortality was calculated for each recovery time point for veligers that were heat shocked at the LT_{50} temperature of 31.7°C and those that were heat shocked at 34.5°C. All values were Box-Cox transformed to meet the assumptions of normality. The mean mortality values for each heat shock temperature were compared using one-way analyses of variance.

Results

Survivorship of *Nucella ostrina* veligers

Veliger larvae from all sites survived temperatures from 13 to 27.5°C (Fig. 1). As temperatures further increased, survivorship rapidly decreased within a narrow window of temperatures. Overall, regardless of the biogeographic collection site of the *Nucella ostrina* veligers tested in the thermal tolerance trials, the temperature at which death was first observed was separated by only ~3–5°C from the temperature that caused nearly 100% mortality. For example, veligers from Cattle Point first experienced mortality at 29.5°C with 47.5% dead; this population experienced 100% mortality at 33.5°C, a range of only 4°C (Fig. 1). A similar pattern was seen for other sites, such as Strawberry Hill and Humboldt, where only a few degrees (5 and 3°C, respectively) separate the initial onset of mortality and 100% mortality (Fig. 1).

These mortality data were used to calculate the LT_{50} values for each collection site. In order to confirm that our calculated LT_{50} was a true lethal point for the veligers, we performed recovery experiments where veligers were assessed for mortality at two different temperatures and allowed to recover for 1 h. Results showed no veligers survived the heat stress at the highest temperature of 34.5°C (Fig. 2), whereas veligers exposed to the lower tempera-
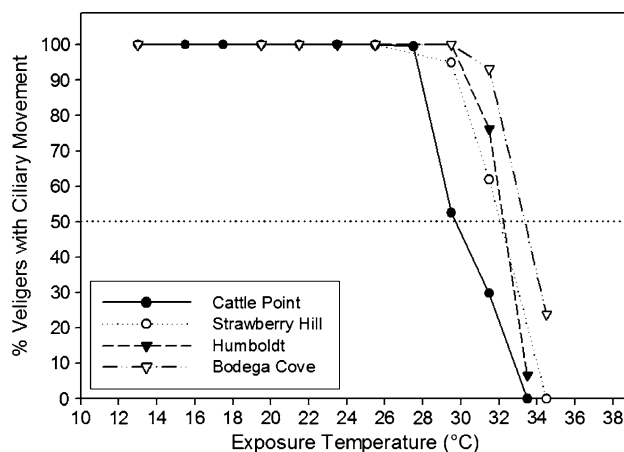
Fig. 1 The thermal tolerance profile for *Nucella ostrina* veligers from four out of the seven sites during May–July 2006. The *x-axis* corresponds to the exposure temperatures of egg capsules after 1-h incubation. The *y-axis* is an index of survivorship based upon veligers with ciliary movement around the velum after exposure. Each *line* represents the number alive compared to the overall total number of larvae used ($n = 5$–8 egg capsules, $n = 5$–22 embryos per egg capsule)

ture, 31.7°C (the LT_{50} for Strawberry Hill), regained some ciliary movement over time. Using a one-way analysis of variance, the differences in the mean values among the recovery time points for the LT_{50} temperature (31.7°C) were not significantly different ($F = 1.998$, df = 4, $n = 100$, $P = 0.1008$), indicating that our protocol during the thermal trials was accurate and decisions to score larvae as dead were not biased by reversible inactivity of the larvae.

Relationship of thermal tolerance to site of collection

In the thermal tolerance trials, there was a relationship between larval thermal tolerance and the latitude at which the *Nucella ostrina* egg capsules were collected. Specifically, the northern populations of veligers were more sensitive to higher temperatures when compared to the veligers collected in the southern part of the range (Fig. 3). *N. ostrina* veligers collected from the most northerly site of Cattle Point had an LT_{50} of 30.1, 3.8°C lower than the LT_{50} for *N. ostrina* veligers from the most southern site of Rancho Marino ($LT_{50} = 33.9$°C, Fig. 3 and Table 2). When considered as a group, the veliger LT_{50}'s showed a pattern of least to most tolerance of high temperatures in the following order: CP < BB > SH ≈ CB < HUM < BML ≈ RM (Table 2). This latitudinal trend was confirmed in a linear regression model (Fig. 3, $P = 0.0011$, $R^2 = 0.8995$).

Discussion and conclusions

In this study, we assessed the thermal tolerance of veliger larvae of *Nucella ostrina*, an intertidal dogwhelk, across its
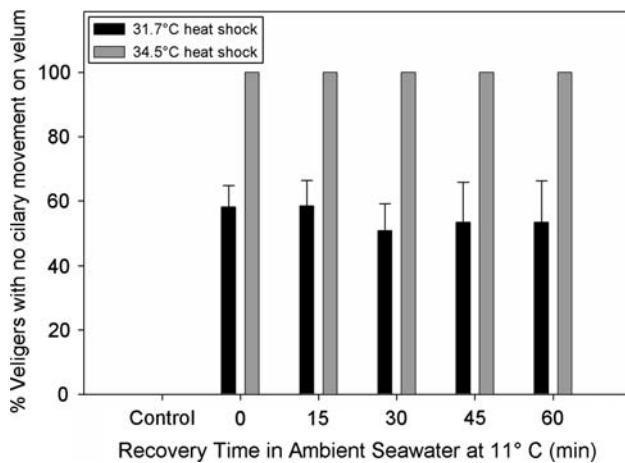
Fig. 2 Recovery experiment conducted with *Nucella ostrina* veligers from Strawberry Hill, OR. The *x-axis* corresponds to the time the veligers spent recovering at 11°C post-1-h heat shock. *Y-axis* is the percent of veligers with no ciliary movement on the velum after time spent recovering. Each *bar* represents the number dead compared to the overall total number of larvae used. The *black bars* correspond to veligers that were heat shocked at 31.7°C, the LT_{50} for this particular site. Whereas, the *light bars* correspond to veligers that were exposed to their lethal temperature of 34.5°C (mean ± standard deviation). No significant difference was detected across recovery time for the LT_{50} temperatures of 31.7°C ($P = 0.1008$) nor for the lethal temperature of 34.5°C ($P = 1$)

biogeographic distribution and measured survivorship in laboratory trials across a range of ecologically relevant temperatures. There were two major findings in this study: (1) *N. ostrina* veligers displayed a sharp change in survivorship within just a few degrees at all sites, and (2) we found a significant relationship between veliger thermal tolerance and latitude.

Larval thermal tolerance

In the thermal trials, there was a rapid, linear increase in mortality occurring over a few degrees of temperature. Specifically, there was only ~3–5°C difference between the temperature at which we first began to see mortality and the temperature where nearly 100% mortality was achieved across all the sites. Given the large-scale distribution of *Nucella ostrina,* a broader range of LT_{50} temperatures might be predicted. However, our data revealed a narrow window of thermal tolerance. For example, we observed a very small gap between survival and mortality, where the LT_{50} temperature for *N. ostrina* veligers collected from Strawberry Hill was 31.7°C when compared to the recorded lethal temperature of 34.5°C. These slight differences in thermal tolerance indicate that there is an abrupt threshold for mortality that could have profound affects on survival where "ecological surprises" of sudden increases in temperature could precipitate mass mortality events (Harley et al. 2006).

While our study is the first to assess thermal tolerance, our observation of the narrow window between tolerance and mortality is consistent with other abiotic stressor studies of *Nucella* that also found broad range of tolerance followed by a sudden decline in survivorship of encapsulated veligers. Although the nature of the egg capsule can mitigate some of the abiotic stresses inherent to life in the intertidal (desiccation stress, osmotic shock, and UV radiation) (Pechenik 1982, 1983; Hawkins and Hutchinson 1988; Rawlings 1990; Russell and Phillips 2009a, b), there are thresholds where the protective capacity of the capsule fails. For example, in a study on desiccation stress, late stage veligers (in the formally *N. emarginata*, now referred to as *N. ostrina*, Marko 1998) could withstand up to 80% water loss from the capsule chamber before suffering substantial mortality (Rawlings 1995). In other studies, it has been shown that capsule wall thickness provides some protection against UV radiation. In a comparative study, the thicker-walled capsules of *N. emarginata* (now referred to as *N. ostrina*) were more resistant to UV stress and protected from UV-A radiation when compared to the thinner-walled lower intertidal species, *N. lamellosa* (Rawlings 1996, Pechenik 1999).

Our finding of an acute increase in *N. ostrina* mortality at elevated temperatures is not isolated within larval biology; similar observations of sudden shifts in survivorship in response to thermal stress have been made in early life history stages of other marine invertebrates. Boon-Niermeijer and Van De Scheur (1984) found that a 1°C increase (39.5–40.5°C) in heat exposure for 3-day-old *Lymnaea stagnalis*, a gastropod mollusk, shifted mortality from 40 to 100%. Similarly, in a non-marine invertebrate, larvae of two species of *Drosophila*, *D. melanogaster* and *D. simulans*, had percent survivorship that shifted from 100% to near zero when exposure temperatures were increased from 37 to 39.5°C (Krebs 1999). Responses of developing embryos to temperature, and the particular temperatures encountered during the normal breeding season, have been most extensively investigated in echinoderms (Andronikov 1975; Strathmann 1987; Fujisawa and Shigei 1990). Purple sea urchin (*Strongylocentrotus purpuratus*) embryos displayed abrupt changes in survival over just a 2°C span for both gastrulae and 4-arm larvae (L. M. Hammond, unpublished results). In an early study on five tropical species of sea urchins, Rupp (1973) found that the upper thermal limits of cleavage were near 34°C, whereas egg fertilization was more thermally resistant and not affected until 36°C, suggesting that larval development would cease if larvae were trapped in flat reef pools or lagoons where temperatures exceed 36°C. Similarly, Sewell and Young (1999) reported that the ability for blastulae and later staged tropical sea urchin larvae (*Echinometra lucunter*) to survive short periods (2 h) of

Fig. 3 Latitudinal comparison of veliger thermal tolerance for *Nucella ostrina*, distribution indicated by *solid black line*, during May–July 2006. *Black dots*, on the graph, represent the calculated LT_{50} for each site with *error bars* representing ±95% confidence intervals. *Y-axis* represents latitude and correlates with the collection sites depicted by *black dots* on the map. The *x-axis* is the temperature at which 50% of the veligers died after a 1-h exposure ($P = 0.0011$, $R^2 = 0.8995$)
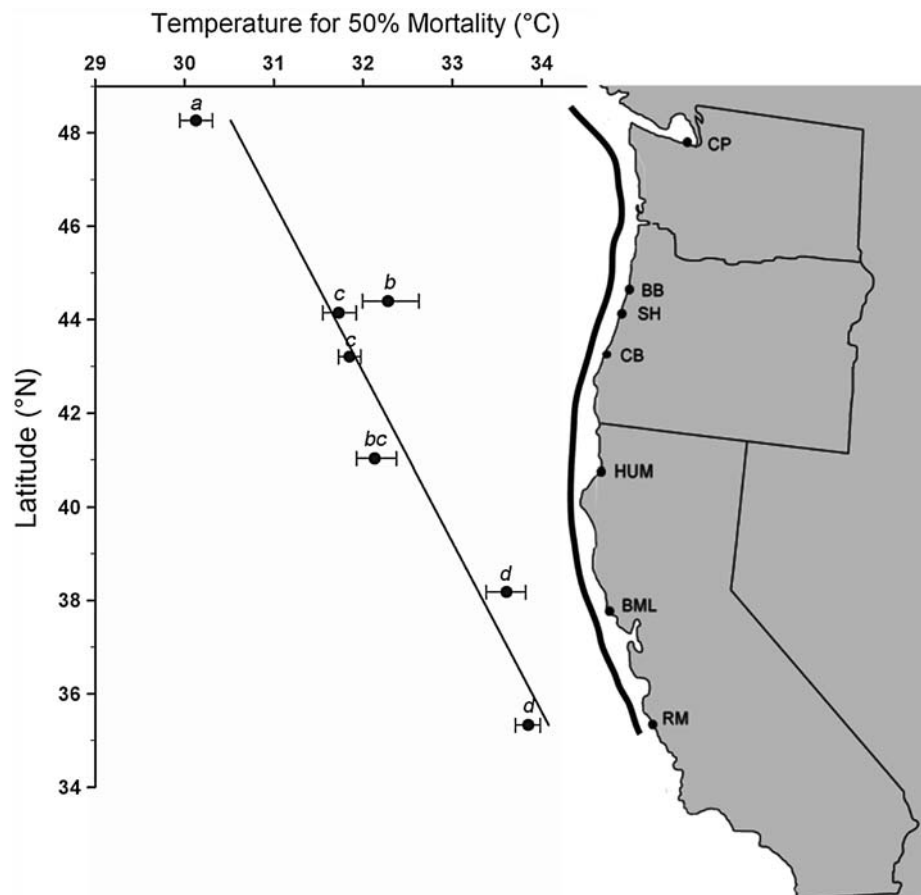
elevated temperatures (4–5°C higher than the 34°C upper limit for normal development) might be important if the larvae are carried to shallow waters of the Caribbean reef flats where seawater temperatures can reach 40°C. In another experiment, significant increases in mortality were observed in the larvae of a brooding tropical coral, *Porites astreoides*, when exposed to slight increases in temperature from 28 to 33°C (Edmunds et al. 2001). Finally, in a polar species, successful larval development was achieved in a 3°C window, from +6 to +9°C, for the sub-Antarctic crab, *Paralomis granulosa* (Anger et al. 2003).

While all the above examples help to explain the importance of understanding how temperature limitations influence early developmental stages of larvae, they also highlight the scarcity of data on the temperature impacts on non-planktonic larvae. From an ecological perspective, this study contributes to our understanding of how conditions in the intertidal might influence larval survival. In a more global context, these data also suggest that increased air and seawater temperatures due to global climate change may also increase mortality during extreme heat events (Hoegh-Guldberg 1999; Pandolfi et al. 2003; Denny et al. 2009).

Relationship of thermal tolerance and latitude

Our data suggest a strong latitudinal relationship between calculated LT_{50} temperature and site. Larvae from more southerly distributed populations were more thermally tolerant than northern populations. For *N. ostrina* veligers collected from Cattle Point, the LT_{50} was 30.1°C when compared to an LT_{50} of 33.9°C of veligers collected at the more southerly location of Rancho Marino Reserve (Table 2). Few other studies have addressed the relationship of biogeography and the physiological tolerances of larval forms. One such study found a modest correlation between thermal tolerance and biogeography for echinopluteus larvae of *Strongylocentrotus purpuratus*. Larvae spawned from Oregon adults ($LT_{50} = 29.7$°C) were more thermally sensitive than those larvae collected from Baja California, Mexico urchins ($LT_{50} = 31$°C) (L. M. Hammond, unpublished results).

In contrast to the limited data on larval forms, the correlation of thermal tolerance with latitude and environment has been documented in adult forms of many marine invertebrates (see review Vernberg 1962; Stillman and Somero 2000; Somero 2005; Sorte and Hofmann 2005; Jansen et al. 2007) and in other ectotherms (e.g., *Drosophila melanogaster*—Hoffmann et al. 2002, mosquitoes—Zani et al. 2005,

Fundulus heteroclitus—Fangue et al. 2006). Similar to our results, Urban (1994) found a correlation between LT_{50} temperature and geographical distribution for adults of 10 bivalve species from Peru and Chile over 22° of latitude.

In summary, the current study showed that *Nucella ostrina* veligers displayed different thermal tolerances as a function of the latitude at which they were collected. The data presented here are a conservative measurement of the upper limits of physiological thresholds of encapsulated larvae. Overall, these data suggest that larval stages of this intertidal invertebrate may not be a hyper-vulnerable life stage (see also Hamdoun and Epel 2007). This observation is further supported by other studies, for example, on an intertidal bivalve which found that early life stages and adults had similar thermal tolerances. The oyster, *Ostreola conchaphila*, brood their young and adults and veliger larvae survive the same lethal temperatures of 38.5–39°C (Brown et al. 2004). However, changing thermal patterns due to climate change may significantly increase mortality during larval development and result in population fragmentation based on the latitudinal timing of low tides and tendency for local adaptation (Sanford et al. 2006).

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