

# Spatial and temporal scales of exposure and sensitivity drive mortality risk patterns across life stages

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**Abstract.** Impacts of increases in extreme heat events under climate change may differ across ontogeny for species with complex life cycles. Different life stages may (1) experience unequal levels of environmental stress that vary across space and time (exposure) and (2) have different stress tolerances (sensitivity). We used a field experiment to investigate whether exposure, sensitivity, and overall mortality risk differed between life stages of a marine foundation species (the mussel *Mytilus californianus*) across thermal conditions that vary in space (habitat, elevation, and site) and time (season) in southern California, USA. We deployed temperature loggers to document habitat-specific exposure patterns, conducted laboratory thermal tolerance assays to calculate sensitivity, and performed field surveys to determine whether risk patterns were reflected in distributions. Exposure to extreme temperatures was highest in solitary habitats and during spring. Juvenile mussels were more sensitive to extreme heat than adults, and sensitivity for both life stages was highest in December and March. Risk was largely seasonal for juveniles but was more temporally variable for adults. Spatial occurrence patterns were congruent with risk assessments for both life stages (i.e., higher occurrence in lower risk habitats). These results highlight the importance of incorporating life stage and temporal dynamics when predicting impacts of climate change.

**Key words:** exposure; habitat; heat wave; life stage; *Mytilus*; sensitivity; warming.

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## INTRODUCTION

Climate change has impacted ecosystems worldwide, resulting in shifts in organismal physiology, species' ranges, and ecosystem functioning (IPCC 2014). Extreme heat events have increased in frequency, intensity, and duration (IPCC 2014), driving declines in population sizes across systems (Kingsolver et al. 2011, Riegl et al. 2011). Whether extreme heat events lead to selective mortality (e.g., Kingsolver 1989, Wegner et al. 2008) or mass mortality (e.g., Ciais et al. 2005, Garrabou et al. 2009, Depczynski et al.

2013) is largely dependent on the level of heterogeneity in mortality risk across space and time (Helmuth and Hofmann 2001). Furthermore, it is becoming increasingly clear that risk may differ greatly across life stages within a species, with large implications for population dynamics (Pandori and Sorte 2019). Increases in extreme heat events are expected to continue and accelerate (Karl and Trenberth 2003, Meehl and Tebaldi 2004, IPCC 2014). Therefore, it is crucial to understand the patterns and processes of mortality risk across life stages within natural populations in order to anticipate alterations in

demographic rates and population trajectories under climate change.

Risk of mortality is a function of both: (1) exposure, the environmental conditions an organism experiences; and (2) sensitivity, the physiological ability of an organism to tolerate environmental conditions (Gilman et al. 2006). Species with multiple life stages—including most invertebrates (Istock 1967)—often utilize different resources and occupy separate habitats across their life stages, influencing their exposure to climatic conditions (Werner and Gilliam 1984, Kingsolver et al. 2011, Pincebourde and Casas 2015). For example, discrete life cycle stages of the hawkmoth, *Manduca sexta*, experience distinct thermal conditions across habitats, which may differ by up to 10°C (Kingsolver et al. 2011). Hawkmoth adults lay eggs on plant leaves, which maintain cooler than ambient temperatures. Eggs then hatch into larvae, whose thermal conditions are governed by ambient (warmer) temperature until they burrow into the cooler soil to pupate (Kingsolver et al. 2011). Similarly, many coastal marine species experience relatively stable sea temperatures as pelagic larvae, then settle into a range of nearshore habitats with more variable conditions (Helmuth and Hofmann 2001, Helmuth et al. 2006, Jurgens and Gaylord 2016, Jurgens and Gaylord 2018).

Thermal exposure can cause mortality when conditions exceed organismal tolerance limits. Previous research has shown that across invertebrates, younger life stages are often more sensitive to thermal stress than older (particularly adult) life stages (Kingsolver et al. 2011, Byrne and Przeslawski 2013, Pandori and Sorte 2019). This variation in responses across life stages can be modulated by multiple factors, including differences in body size (Klockmann et al. 2017), cellular responses to stress (Giudice et al. 1999, Sorte and Hofmann 2005), organismal energy reserves available to offset metabolic cost of stressor tolerance (Kurihara et al. 2004, Cripps et al. 2014), or developmental stage of organs involved in stress tolerance (Pörtner et al. 2004, Pörtner and Knust 2007, Pörtner and Farrell 2008). Given previous research indicating that exposure and sensitivity are likely to differ across life stages, it is important to consider both factors when predicting how populations will respond to future extreme warming events (i.e., risk).

Exposure patterns can also influence sensitivity: heterogeneity in thermal exposure across habitats can lead to variation in sensitivity within a population due to selective mortality (environmental filtering; Kraft et al. 2015) and phenotypic plasticity in thermal tolerance (Bowler 2005). For example, Bowler and Terblanche (2008) reviewed studies of thermal tolerance across insect life stages and found that ontogenetic differences were explained by both environmental filtering (selective mortality following thermal exposure) and innate physiological differences across life stages. When exposure and sensitivity are below thresholds for mortality, the product of their interaction may be acclimation, leading to changes in thermal sensitivity (Pankhurst and Munday 2011). Prior exposure to sub-lethal temperatures has been shown to increase thermal tolerance (and decrease sensitivity) through mechanisms of heat hardening (Bowler 2005), such as increased heat-shock protein production (Gleason and Burton 2013) and changes to membrane stability (Bowler 2005). Thus, it is important to consider the role of exposure in driving both selection and acclimation, yielding increased tolerance in advanced life stages.

Here, we used a field experiment to investigate whether (1) exposure, (2) sensitivity, and, by extension, (3) mortality risk differ across life stages and habitats of a sessile marine invertebrate species likely to encounter high thermal heterogeneity across habitat space and seasons: the California mussel *Mytilus californianus*. Mussels are critical foundation species in rocky intertidal habitats (Suchanek 1992), where they are subjected to both marine (during high tide) and terrestrial (during low tide) conditions. Temperature often sets species' upper limits in intertidal habitats (Connell 1972, Menge and Sutherland 1987, Somero 2002, Vasseur et al. 2014). Within the intertidal zone, thermal conditions can vary at small spatial scales, altering inhabitants' exposure (Werner and Gilliam 1984, Helmuth and Hofmann 2001, Seabra et al. 2011, Jurgens and Gaylord 2016, Jurgens and Gaylord 2018) and potentially sensitivity (Jimenez et al. 2015) to stressful thermal conditions. *M. californianus* has a complex life cycle with pelagic larval stages that metamorphose into sessile benthic juveniles. Although juvenile mussels often settle onto byssal threads of conspecifics (de Nesnera 2016,

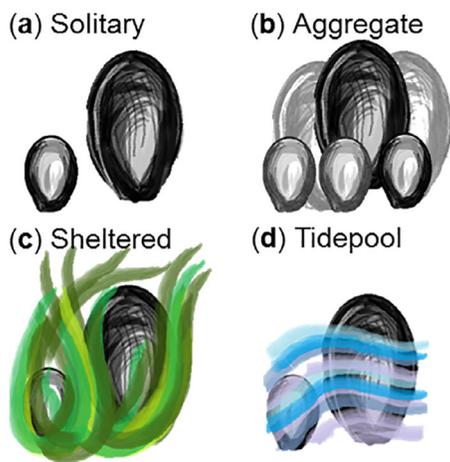


Fig. 1. Habitats mussels occupy in the southern California (USA) rocky intertidal zone. (a) Solitary mussels are not in contact with others, while (b) aggregated individuals are in contact with conspecifics. (c) Sheltered individuals occur under rock or algae. Mussels also occur in (d) tide pools, where they are almost always submerged.

Jurgens and Gaylord 2016, Jurgens and Gaylord 2018), they also occur in a variety of other habitats. For example, solitary mussels have no shade or neighbors (Fig. 1a), while aggregated mussels exist in a 3-dimensional matrix (Fig. 1b), and thermal conditions have been shown to vary by over 5°C between these two habitat types (Jurgens and Gaylord 2018). Additionally, mussels live in sheltered habitats, under rock overhangs or algae (Schiel et al. 2016), with decreased exposure to solar radiation (Fig. 1c). Finally, mussels inhabiting tide pools are never exposed to aerial stressors (Fig. 1d). Since habitats differ in thermal conditions, life stages within them are likely to experience different thermal exposure and effects on sensitivity (via environmental filtering or acclimation), leading to a mosaic of mortality risk (Dowd et al. 2015) that determines the selectivity of extreme heat events.

The objective of this study was to investigate the relative importance of multiple spatial and temporal scales for determining exposure, sensitivity, and mortality risk for *M. californianus*. We hypothesized that exposure to thermal conditions would vary across spatial scales, with increased thermal exposure in less sheltered

habitats and at higher tidal elevations (Helmuth and Hofmann 2001, Seabra et al. 2011, Jurgens and Gaylord 2016, Schiel et al. 2016), and across temporal scales, with season. If thermal conditions differed across space and time, we hypothesized that there would be a negative relationship between exposure to thermal stress and sensitivity (i.e., individuals collected from higher stress habitats and seasons would have lower sensitivity and higher tolerances due to combined effects of environmental filtering and acclimation) and that this relationship would be stronger for adults (which represent a later time point in the life cycle) than juveniles. We also hypothesized that juvenile and adult mussels would occur more frequently in cooler habitats (such as tide pool and sheltered habitats; Bertness and Callaway 1994, de Nesnera 2016). Importantly, this study allows us to move beyond general patterns (across life stages and broad spatial scales) to predict mortality risk at the scales of individuals and to evaluate whether occupancy patterns are markers of selective mortality.

## METHODS

### Experimental approach and study sites

In this study, we tested whether mussel thermal exposure, sensitivity to extreme heat, and habitat associations differed between juvenile and adult mussels across two spatial factors (tide height and habitat type) and one temporal factor (season) at two replicate sites. We defined mussel life stages through the assessment of reproductive maturity (as in Petes et al. 2008). Consistent with preliminary sampling, mussels <20 mm in length did not have mature gonads and were classified as juveniles, and mussels >30 mm in length had mature gonads and were classified as adults (Appendix S1). Measurements of thermal exposure, sensitivity, and habitat associations were conducted at two replicate sites with differing thermal regimes: Crystal Cove State Park (33.5687° N, -117.8351° W) and Little Corona del Mar (33.5881° N, -117.8672° W), located 3.7 km apart in Newport Beach, California, USA, within a common mussel metapopulation (Levinton and Suchanek 1978, Maas et al. 2018). At each site, the average elevation of the lower and upper edges of the mussel zone was measured

and used to define the three tide heights (m above MLLW, mean lower-low water) considered in our experiment: low (0.6 m, lower edge), mid (1.2 m), and high (1.8 m, upper edge). We conducted all measurements at four time points representing seasons (December, March, June, and September) between September 2016 and September 2017, defining seasons as  $\pm 45$  d from the midpoint of the month of quarterly sampling. For example, exposure measurements corresponding to the March sampling include conditions from January 30th to April 29th.

#### *Quantifying exposure to extreme thermal conditions*

To determine whether exposure to thermal stress differed across habitats, we designed and deployed  $N = 3$  temperature monitoring stations at each of the three tide heights at both sites (Appendix S2). Stations were constructed from a galvanized wire mesh structure containing habitat mimics. Thermal conditions in solitary habitats were mimicked by placing iButton temperature loggers (Maxim Integrated, San Jose, California, USA) atop the mesh, while aggregate conditions were mimicked by securing loggers within a torus of plastic Tuffy kitchen scrubber mesh. Sheltered thermal conditions were mimicked by attaching loggers beneath a wire mesh arch covered with white plastic. The entire station was secured to the rock adjacent to a tide pool, where conditions in this fourth habitat type were monitored by loggers attached to the bottom of pools. Loggers recorded temperatures every 30 min and were replaced every two weeks for the one-year duration of the experiment (September 2016–September 2017). Comparisons between temperatures recorded by iButtons differed from those of mussel body temperatures by an average of  $1.3^\circ \pm 0.3^\circ\text{C}$ , similar to the  $\pm 1^\circ\text{C}$  measurement error of the loggers themselves (Appendix S2).

Since our measurements of sensitivity and exposure were focused on conditions during low tide, when temperatures can exceed tolerance limits, we isolated temperatures from our intertidal records where the water level fell below the tide height of temperature-recording stations (Appendix S3). To do this, we used linear regressions between iButton data and meteorological data from the University of California, Irvine

Center for Environmental Biology weather station at the Crystal Cove State Park Research Cottage (<http://128.200.14.200/index.html/>) to interpolate predicted values for missing data (all  $R^2$  values were  $>0.3$ , Appendix S3: Table S1). iButton failure rates were high at the Little Corona del Mar site (Appendix S3: Fig. S1). Therefore, we present only results for all experiments at the Crystal Cove State Park site in the main text, and results from Little Corona del Mar are presented in Appendix S6 of the supplementary material. We conducted Kolmogorov-Smirnov tests to determine whether the distribution of daily maximum 6-h moving average thermal conditions differed across habitats at each tide height and season for each site. To evaluate general trends across sites, we constructed heat maps of temperature data (Appendix S3: Figs. S1, S2).

#### *Thermal sensitivity assays and calculation of $LT_{50}$*

To determine whether sensitivity to thermal extremes differed across mussel life stages habitats, and seasons, we conducted thermal tolerance assays to calculate an  $LT_{50}$  (6-h air temperature exposure that led to 50% mortality) for each life stage (juvenile and adult) of mussels across habitats (solitary, aggregate, sheltered, and tide pool), tide heights, sites, and seasons. We collected  $N = 3$  individuals per life stage  $\times$  habitat  $\times$  tide height  $\times$  season  $\times$  site combination. Within 1 h of collection, we randomly assigned individuals to one of the following treatments: control (air temperatures  $18^\circ\text{--}20^\circ\text{C}$ ),  $32^\circ\text{C}$ ,  $36^\circ\text{C}$ , and  $40^\circ\text{C}$ . These conditions were chosen because they represent points of 100% expected survival (control) and 100% expected mortality ( $40^\circ\text{C}$ , based on our preliminary studies), and thermal conditions experienced by individuals in the field (Appendix S4). These methods are analogous to those used by Sorte et al. (2018, 2019) except that each replicate was run on a different (adjacent) day (i.e.,  $N = 1$  for each of 3 d), reducing pseudoreplication. Mussels were placed in 150-mL plastic tubes with a  $4\text{-cm}^2$  piece of seawater-soaked chamois cloth at the bottom to prevent desiccation and holes in the cap to prevent oxygen depletion. Tubes were placed into 28-L digital water baths and heated from ambient laboratory temperature ( $\sim 22^\circ\text{C}$ ) to treatment temperature in a  $\sim 36$ -min ramp, with a

heating rate of 0.4°C/min (a heating rate similar to that observed in the field, Appendix S4). Thermal conditions in monitoring (no mussel) tubes were recorded at 1-min intervals by Omega HH506RA (Norwalk, Connecticut, USA) logging thermometers for the 6-h exposure duration. Following this heat exposure, mussels were transferred to a running seawater system for an 18-h recovery period at ambient temperature. Survival was assessed through observations of movement and probing (as in Sorte et al. 2018, 2019), followed by dissection to confirm life stage (via visual assessment of gonad development).

As our metric of thermal sensitivity, we calculated  $LT_{50}$  using binomial regressions between 6-h average exposure temperature and proportional survival in the MASS package (Venables and Ripley 2002) for each life stage  $\times$  habitat  $\times$  tide height  $\times$  season  $\times$  site combination (Appendix S4: Fig. S3). To test for differences in thermal tolerance across life stages, habitats, tide heights, seasons, and sites, we used ANOVA followed by Tukey post-hoc tests. To determine whether mussel size (length) was correlated with sensitivity within each life stage and site, we conducted linear regressions and found no relationship (Appendix S7). All statistical analyses were conducted in R Studio (RStudio Team 2015).

#### *Estimating mortality risk under extreme thermal conditions*

We examined patterns of mortality risk across intertidal habitats using the probability of exposure to a daily 6-h average temperature exceeding the sensitivity threshold ( $LT_{50}$ ) of mussels within a particular life stage  $\times$  habitat  $\times$  tide height combination for each season at each site, or  $P(\text{Exposure} > LT_{50})$ . This was assessed by first calculating the daily maximum 6-h moving average temperature for each habitat  $\times$  tide height combination for periods of tidal emersion on each day of station deployment (September 2016–September 2017). Since  $LT_{50}$  values were estimated quarterly, whereas temperatures were measured continuously, we used defined seasons as described above (e.g.,  $LT_{50}$  values from mid-December were used to calculate risk in a cumulative distribution function generated for October 31–January 29). We then calculated the probability of observing a daily maximum 6-h moving average temperature that exceeded the

sensitivity ( $LT_{50}$ ) of juvenile and adult mussels within a given habitat  $\times$  tide height combination at each site. We examined whether risk differed across life stages using a Kruskal-Wallis test, where risk values were pooled across seasons, tide heights, and habitats.

#### *Habitat association surveys*

Habitat associations and population abundances of individuals across life stages, tide heights, habitat types, and sites were documented via field surveys at both sites in each of the four seasons (December 2016–September 2017). We surveyed  $N = 10$  quadrats (0.0625 m<sup>2</sup>) at each of the three tide heights at each site. In each quadrat, we visually estimated the percent cover of each habitat space (solitary, aggregate, sheltered, and tide pool) and the number and life stage (using calipers) of mussels present in each habitat space. It is important to note a distinction between habitat spaces and mussels within habitats: solitary habitat space was defined as area without existing mussels or shelter (overhanging rock or canopy algae), while solitary mussels were defined as mussels not in direct contact with any other mussels (nor in contact with similar aggregations of the gooseneck barnacles, *Pollicipes*). Similarly, aggregate habitat space was defined as area with existing mussel (or *Pollicipes*) aggregations, while aggregated mussels were defined as mussels within aggregate habitat space. Sheltered habitat space was defined as overhanging rock or canopy algal cover. When they occurred in sheltered and tide pool habitats, both solitary mussels and mussel aggregates were classified as occurring in sheltered or tide pool habitats, regardless of aggregations or lack thereof. To compare habitat spaces and thermal records, we considered both unsheltered and sheltered solitary habitat space as solitary habitat, and unsheltered aggregate habitats as aggregate habitat. Thus, to summarize, mussels were characterized primarily by the most important determinant of thermal exposure—either tide pool or shelter—first, with aggregate and solitary designations secondary for non-tide pool or unsheltered mussels.

We characterized both the distribution of habitat space, as well as mussels' occurrence across habitats, by calculating the average proportion of space (percent cover in each quadrat) comprising

each habitat across tide heights for each site. To summarize occurrence patterns, we examined the average abundance of juvenile and adult mussels across each habitat and tide height combination. We also calculated the standardized percent difference (SPD) between the proportion of juvenile or adult mussels within a given habitat and the proportion of space available for a given habitat (Appendix S5; as in de Nesnera 2016).

## RESULTS

Exposure to extreme thermal conditions (defined as daily maxima of 6-h moving average temperatures measured by data loggers) differed

significantly across space (tide heights and habitats) and time (seasons) at both sites (K-S tests,  $P < 0.0125$ ; Appendix S7; Fig. 2 and Appendix S6: Fig. S1). At Crystal Cove State Park (Fig. 2a), exposure to extreme temperatures was highest in the high intertidal: median daily thermal maxima increased from the low ( $\sim 18^\circ\text{C}$ ) to the high ( $\sim 20^\circ\text{C}$ ) intertidal zone, where temperature exposure also varied across habitats (K-S tests,  $P < 0.0125$ ). The most pronounced differences occurred at the high and mid tide heights, where solitary habitats were significantly warmer than the other habitats. Tide pool habitats were coolest, where median daily maximum temperatures were  $\sim 2.33^\circ\text{C}$  cooler than solitary habitats. Additionally, there were significant

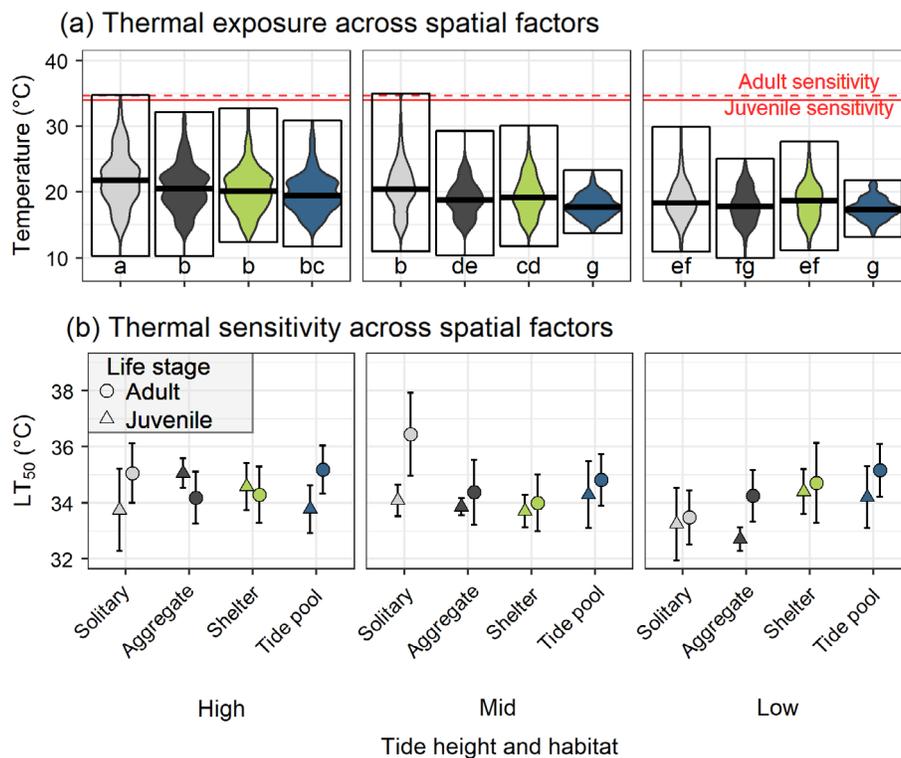


Fig. 2. Distributions of daily thermal maxima (a) differ significantly across spatial factors at Crystal Cove State Park (Kruskal-Wallis tests followed by post-hoc Dunn tests with Bonferroni Correction, see Appendix S7). Additionally, sensitivity to extreme heat events (b) varies across life stages of *Mytilus californianus* (ANOVA,  $F = 25.77$ ,  $P < 0.001$ ) but not across tide heights or habitats at the Crystal Cove site. Juvenile and adult mussels are exposed to conditions which exceed their sensitivity limits (shown in [a] as red solid and dashed lines, respectively) in solitary habitats. Values presented in (a) are daily maxima of 6-h moving average temperatures recorded by loggers in habitat mimics, while values presented in (b) are the average  $\pm$  SE of  $LT_{50}$  (temperature lethal to 50% of individuals) for juvenile (triangles) and adult (circles) mussels subjected to 6-h thermal challenges summarized across seasons.

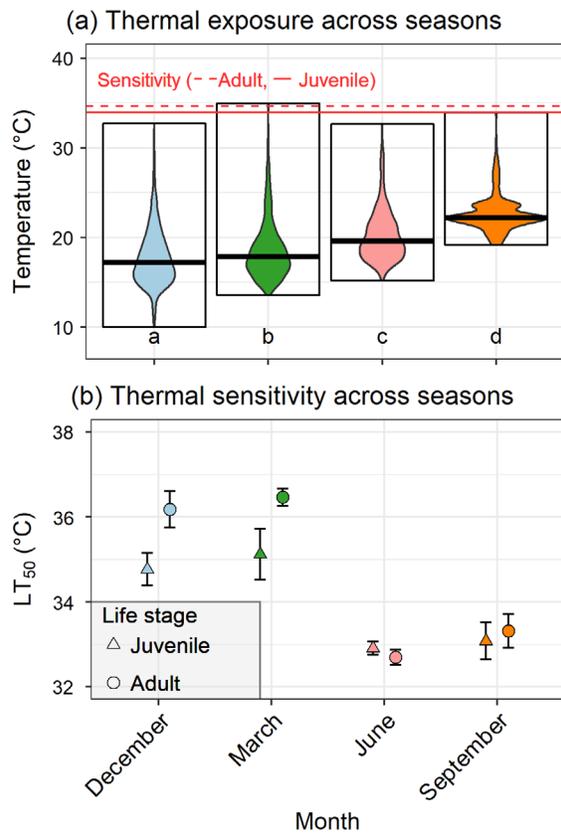


Fig. 3. Exposure (a) and sensitivity (b) to extreme heat events varies across seasons at Crystal Cove State Park (California, USA). Exposure (daily thermal maxima) was highest in the time surrounding the March sampling, where thermal conditions exceeded sensitivity limits for both juvenile and adult mussels. Across life stages, *Mytilus californianus* is less sensitive to extreme heat events (higher temperature lethal to 50% of individuals,  $LT_{50}$ ) in December and March than in June and September (ANOVA,  $F = 34.85$ ,  $P < 0.01$ ). Values presented are the average  $\pm$  SE of  $LT_{50}$  for juvenile (triangles) and adult (circles) mussels subjected to 6-h thermal challenges, summarized across tide heights and habitats.

differences in exposure across 50 of 66 pairwise comparisons between tide height  $\times$  habitat combinations (Appendix S7). Median thermal conditions were hottest in the 90-d period encompassing the March sampling, while conditions surrounding the December sampling were coolest (Fig. 3a).

We investigated patterns of thermal sensitivity of juvenile and adult mussels to extreme heat events across space (four intertidal habitats at three tide heights) and time (four seasons) and found that sensitivity varied significantly between life stages (ANOVA,  $F_{1,81} = 25.77$ ,  $P < 0.01$ ) and seasons (ANOVA,  $F_{3,81} = 34.85$ ,  $P < 0.01$ ). Juvenile mussels died at lower temperatures (indicating higher sensitivity) than adult mussels across most habitats (Fig. 2b) and seasons (Fig. 3b). Seasonally, thermal sensitivity was lowest ( $LT_{50}$  was highest) during the winter and spring and highest ( $LT_{50}$  was lowest) during the summer and fall (Fig. 3b). There were no significant differences in thermal sensitivity across habitats at either site (Appendix S7), and sensitivity differed by tide height at Little Corona del Mar (where sensitivity was greater at lower tide heights; ANOVA,  $F_{2,81} = 5.24$ ,  $P = 0.01$ ) but not at the Crystal Cove site (ANOVA,  $F_{2,81} = 1.39$ ,  $P = 0.26$ ). Integrating measurements of exposure and sensitivity, we found that mortality risk was dependent on both spatial and temporal scales. Mussels were predicted to experience conditions which exceeded their sensitivity limits in solitary habitats in the high and mid-intertidal zone (Fig. 2a) and in the time surrounding March sampling (Fig. 3a). These spatial and temporal patterns were consistent across life stages.

While all habitat types were present across all tide heights, juvenile and adult mussels occurred most frequently in aggregate and sheltered habitats (Fig. 4). Despite solitary habitat representing the largest proportion of available space, few juvenile and adult mussels occurred in the solitary habitat. However, occupancy was greater than availability for aggregate habitat for both life stages and across all tide heights. The coolest sheltered and tide pool habitats represented 12% and 5% of space, while 27% and 13% of mussels were observed in these habitats, respectively (averaging across tide heights and, for mussel counts, life stages). Mussels were most abundant at lower tide heights; at the high tide height, 89% of available habitat was solitary, and <1% of mussels were observed in this warmest habitat.

## DISCUSSION

Our results highlight the importance of including life stage and seasonal variance in order to

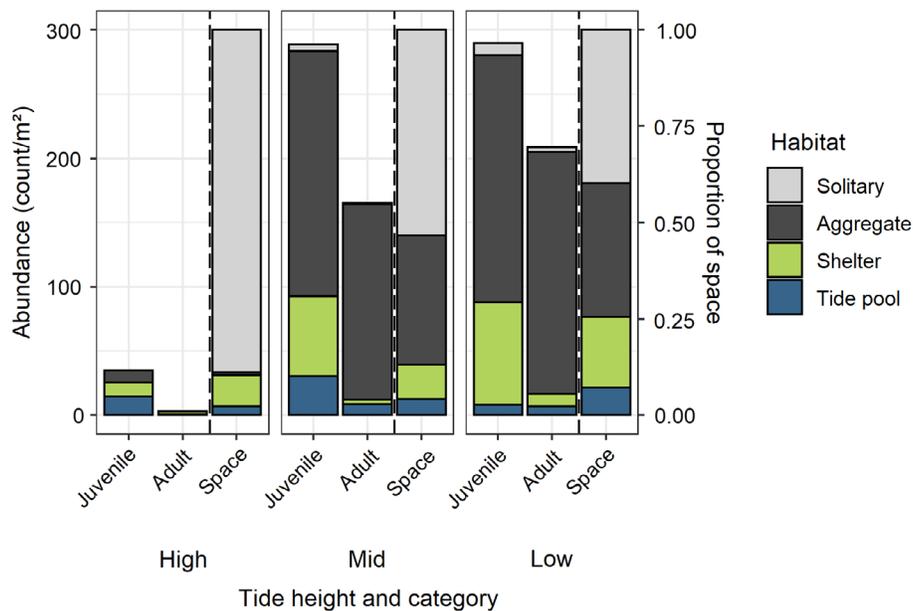


Fig. 4. Abundance of juvenile and adult mussels (two bars in each group to the left of the dashed vertical lines) and proportion of space available (rightmost bar in each group) across habitats (colors, as shown on legend) and tide heights (groups of 3 bars) at Crystal Cove State Park (California, USA). Values are averages across  $N = 30$  quadrats. Juvenile and adult mussels do not occupy habitats in direct relationship to their availability; instead, mussels are most abundant in sheltered and aggregate habitats.

predict the impacts of extreme heat events. In this study, we investigated the interplay between exposure, sensitivity, and risk of encountering conditions which exceed organismal tolerances. Our results demonstrate that exposure differed across both space (habitats and tide heights) and time (seasons). More specifically, we found that exposure to extreme temperatures was highest in the high intertidal, and in solitary habitats, especially during the summer and fall seasons. While exposure patterns differed significantly across small spatial scales, sensitivity was most influenced by seasonal trends in exposure to high heat conditions. Sensitivity was highest ( $LT_{50}$  values were lowest) in December and March, where juvenile mussels were more sensitive than adult mussels. Mortality risk estimates reflected the importance of both spatial and temporal factors and were most strongly driven by variation in exposure across seasons and habitats. The importance of spatial scale was reflected in occurrence patterns: juvenile and adult mussels were most abundant in low-exposure habitats, such as aggregates of conspecifics and habitats with algal

or rock shelter from solar radiation. Together, these results suggest that spatial and temporal factors combine to influence mortality risk.

We found evidence of heterogeneity in exposure to extreme temperatures across small-scale habitats in space and time. In space, higher tide heights had higher aerial temperatures, (Connell 1972, Helmuth 1998, 1999), which are associated with higher body temperatures across intertidal taxa (Denny et al. 2006). Additionally, exposure differed across habitats at small spatial scales, where sheltered and tide pool habitats were cooler than solitary and aggregate habitats (Fig. 2a). Our results are consistent with prior studies, which have shown that mussel aggregations (Jurgens and Gaylord 2016) and macroalgal cover (Schiel et al. 2016) play a role in stress amelioration and that exposure to high temperatures was highest in the summer and fall (Helmuth et al. 2006, Jurgens and Gaylord 2016). Temporal trends can vary across geographical scales, as intertidal thermal conditions are governed by the interplay between air temperature and the timing of low tide, both of which vary across

seasons. In southern California (USA), air temperatures are highest in the times around December and March sampling, when low tides occur during midday. Seasonal variation in thermal conditions can affect population demography and community interactions. For example, the upper tide height limits of sea stars (*Pisaster ochraceus*) are determined by seasonal variations in thermal conditions, with probably impacts on their mussel *M. californianus* prey (Pincebourde et al. 2008, Wallingford and Sorte 2019).

Across habitats and seasons, we found that juvenile mussels were more sensitive to temperature extremes than adult mussels, consistent with results of our recent synthesis which spanned marine invertebrate species (Pandori and Sorte 2019). However, our results do not strongly support the hypothesis that greater thermal exposure is associated with increased thermal tolerance, as previously shown by Bowler (2005). Instead, in our temporal analysis, we found that sensitivity was highest (tolerance was lowest) during the season of highest thermal exposure (Fig. 3). In addition, within each season, sensitivity did not differ significantly among small-scale habitats for either site and differed by tide height only at Corona del Mar, a pattern that we were unable to fully explore (by calculating mortality risk) due to incomplete temperature data. While prior exposure can increase tolerance via acclimation, environmental stress can also lead to increased metabolic costs (Jansen et al. 2007) with reduced energy available to support tolerance mechanisms (Fitzgerald-Dehoog et al. 2012). Increased metabolic cost also increases resource requirements, and food availability varies across seasons: in the Southern California Bight, surface productivity is highest in the spring and lower in all other seasons (Hayward and Venrick 1998, Mantyla et al. 2008). Given that thermal exposure is highest, and food availability is lowest, during the periods surrounding March and June sampling, it is possible that metabolic trade-offs influenced sensitivity patterns observed in our study.

A key limitation of previous studies is their sole focus on exposure or sensitivity. Here, we integrate exposure and sensitivity to predict mortality risk. From this integration, we discovered that risk patterns vary in time as well as in space, as indicated by high mortality risk in the summer

and fall seasons, when both sensitivity and exposure to extreme heat were highest. In southern California, mussel recruitment is highest in the spring and early summer (Suchanek 1981), and mussels reach the juvenile stage 4–8 months after settlement (Seed 1969, Blanchette et al. 2007). Our juvenile mortality risk estimates (where 1–2% of days exceed  $LT_{50}$ ) are lower than field measurements of juvenile mortality (de Nesnera 2016 reports 70–92%). There are several drivers of mortality that were not included in our risk estimate, including exacerbation of thermal stress by desiccation, dislodgement by waves, and community interactions (e.g., competition and predation; Suchanek 1978, 1981).

While solitary habitat was most abundant at our sites, mussels, regardless of life stage, most commonly occurred in aggregate or sheltered habitats. Mussel occurrence patterns could arise due to two main mechanisms: recruit habitat choice and environmental filtering. *Mytilus* recruits exhibit behaviors such as cue recognition (Petersen 1984, Morgan 2001) that modulate settlement patterns among small-scale habitats (Morgan 2001). After settlement, *M. californianus* recruits and juveniles exhibit habitat shifts from algal association to mussel bed association, which promote survival and growth (de Nesnera 2016). Mussel distributions at many scales can also be determined by thermal conditions which may exceed tolerance limits, resulting in selective or mass mortality events, which can influence adult distributions at site-level scales (Johnson and Geller 2006). If environmental filtering (Kraft et al. 2015) played a role in establishing distribution patterns across habitats, we might expect that adult mussels living in a hotter habitat would be less sensitive to thermal extremes. We found no evidence for an inverse relationship, with neither juveniles nor adults. This finding suggests that any environmental filtering related to differential juvenile tolerance is not distinguishable from the baseline mortality of younger life stages or that any selective mortality occurred in the recruit stage, before mussels reached threshold size for inclusion in our study. Overall, our occurrence data suggest that, cumulatively, spatial differences in thermal exposure manifest in distribution patterns.

Our study demonstrates that the risk of encountering conditions which exceed tolerance limits

varies across temporal scales and small spatial scales. These results occur via both differences in exposure (thermal conditions experienced) and sensitivity (lethal thermal tolerance limits) over time. We found that thermal conditions exceed tolerance limits more for juvenile mussels than adults, and more so in the period surrounding the March sampling. Given that mussels in solitary habitats in the mid- to high intertidal zone encountered conditions which exceed their sensitivity limits, our results highlight an increasing risk of selective mussel mortality as both global average temperature and the occurrence of extreme heat events increase (IPCC 2014). Fortunately, the great majority of mussels occur in habitats of lower exposure, such as aggregates and sheltered habitat, making the likelihood of such mass mortality events relatively low. However, as mussels decline in southern California (USA), mussel bed cover and depth are decreasing (Smith et al. 2006), resulting in higher exposure to increased temperatures. This trend suggests that locally, the availability of aggregate habitat will decrease, and solitary habitat will increase, potentially leading to an amplifying feedback of increasing risk and mortality. Since foundation species create thermal refugia for a diverse assemblage of associated species (Helmuth et al. 2006, de Nesnera 2016, Jurgens and Gaylord 2016), declines in foundation species across ecosystems (Smith et al. 2006, Sorte et al. 2018), coupled with warming global climate (IPCC 2014), could result in increasing seasonal mass mortality events in coastal habitats.

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### DATA AVAILABILITY

All data are available in Dryad: <https://doi.org/10.15146/R3C39D>. Subsequent R code for analysis is available on GitHub: [https://github.com/lmpandori/Mussel\\_Habitat\\_Risk](https://github.com/lmpandori/Mussel_Habitat_Risk).

### SUPPORTING INFORMATION

Additional Supporting Information may be found online at: <http://onlinelibrary.wiley.com/doi/10.1002/ecs2.3552/full>