Check for updates

# Differential survival of *Ilyanassa obsoleta* to water temperature and association with the non-native red alga *Gracilaria vermiculophylla*

Timothy S. Lee · Amy E. Fowler · Jessica R. Largen · Jonathan P. Russo · Zackary J. Schlegel · Dawson K. Wright · April M. H. Blakeslee

**Abstract** Along the U.S. east coast, the widespread non-native red alga *Gracilaria vermiculophylla* provides habitat for an array of macroinvertebrates, including the eastern mudsnail *Ilyanassa obsoleta*. Though *I. obsoleta* tolerates a wide temperature range, increases in summer water temperatures may enhance mortality; furthermore, the presence of non-native algae in rising seawater temperatures could exacerbate harmful conditions. We tested how the presence or absence of *G. vermiculophylla* influenced snail mortality across a range of summer temperatures over a 3-week period. We found that *I. obsoleta* survived the longest in the lowest temperature (27 °C), followed by the medium (32 °C), and lastly the highest (36 °C) where all snails died within 2 days. Mortality was also higher and faster for snails in the presence versus absence of *G. vermiculophylla*. We suspected dissolved oxygen became very low at the higher temperatures with *G. vermiculophylla*; thus we conducted a laboratory-based dissolved oxygen experiment. We found that *G. vermiculophylla* degraded and oxygen declined faster at the highest temperature treatment, thereby creating anoxic conditions. Altogether, our results demonstrate that *G. vermiculophylla* could enhance anoxic conditions at high summer temperatures, potentially leading to enhanced faunal mortality.

**Keywords** Climate change · Invasive · Northwest Atlantic · Seaweed · Oxygen

T. S. Lee (✉) · J. R. Largen · J. P. Russo · Z. J. Schlegel · D. K. Wright · A. M. H. Blakeslee
Department of Biology, East Carolina University, Greenville, NC, USA
e-mail: tslee@uncg.edu

T. S. Lee
Department of Biology, University of North Carolina at Greensboro, Greensboro, NC, USA

A. E. Fowler
Department of Environmental Science and Policy, George Mason University, Fairfax, VA, USA

## Introduction

Coastal marine environments are vulnerable to numerous stressors as a result of human-induced global change (Harley et al., 2006), including rapid seawater warming. Globally, over 70% of the world's coastlines are significantly warming, and the sea surface temperature of all coastal basins is expected to rise by 1 °C between 2015 and 2050 (Lima & Wethey, 2012; Varela et al., 2023). Rising temperatures can alter the composition of native

communities by reducing native species biodiversity, increasing species homogeneity, and enhancing the spread of invasive species (Bianchi et al., 2019).

Seawater warming can also influence species distribution shifts—in either positive or negative directions. Some distributions may increase for species with physiological capacities to persist in rapidly changing environments, while others may decline because increased water temperatures reduce oxygen supply and may exceed a species' upper heat limit and threshold for maximum growth (Fujiwara et al., 2019). For example, following a 35-year monitoring study of 150 fish and invertebrate species along the Gulf of Mexico, Fujiwara et al., (2019) found that over half the species experienced increases in occupancy probability, while ~20% experienced declines. Increases in seawater temperature can also intensify the occurrence and distribution of harmful algal blooms (e.g., *Alexandrium* Halim 1960, and *Karenia* G. Hansen & Moestrop 2000 spp.) that enhance fish and invertebrate mortalities due to oxygen depletion and release of algal toxins (Karlson et al., 2021). Finally, rising water temperatures and warming events like marine heat waves may negatively impact reproduction; for example, Shanks et al., (2020) found winter spawning intensities of coastal invertebrates to be significantly lower following a marine heat wave in 2015 (known as the "warm blob") off the coast of Oregon, USA.

Along with temperature, species introductions are another major stressor on native biodiversity and ecosystem function (Simberloff et al., 2013). Examples of impactful invasive species on native communities include the European green crab *Carcinus maenas* Linnaeus, 1758; the Mediterranean blue mussel *Mytilus galloprovincialis* Lamarck, 1819; the "killer algae" *Caulerpa taxifolia* (M. Vahl) C. Agardh 1817; and many other examples (Ruesink & Collado-Vides, 2006; Gregory & Quijon, 2011; Lockwood & Somero, 2011; Ravaglioli et al., 2022). Indeed, algae have important roles in marine ecosystems as both habitat and food, and many are key ecosystem engineers (Gribben et al., 2009; Bellgrove et al., 2017; Pocklington et al., 2018). Introductions of marine algae can therefore induce shifts in native algal diversity and composition, as well as associated macroinvertebrates (Gillis & Chalifour, 2010; Thomsen, 2010; Thomsen et al., 2012; Foster et al., 2019).

Rising seawater temperatures can also influence the impact and success of introduced algae. For example, structure-forming non-indigenous macroalgae, such as *Undaria pinnatifida* (Harvey) Suringar, 1873 in New Zealand, have been shown to tolerate a wider range of salinities and temperature than native algae, while also generating higher photosynthetic yields than native species (Bollen et al., 2016). Another example involves the extreme warming events along the coasts of Baja California from 2014 to 2016, which triggered major declines in a native alga, *Macrocystis pyrifera* (Linnaeus) C. Agardh, 1820, resulting in communities that became dominated by invasive species, including *Sargassum horneri* (Turner) C. Agardh, 1820, and *U. pinnatifida* macroalgae (Félix-Loaiza et al., 2022). Finally, rising seawater temperatures in the northwestern Mediterranean have caused native seagrass coverage to decrease, allowing a non-native macroalga with a higher thermal tolerance, *Halimeda incrassata* (J.Ellis) J.V. Lamouroux, 1816, to thrive and outcompete seagrass for light and nutrition (Marx et al., 2021).

In the Mid-Atlantic and southeastern regions of the United States, temperature shifts are expected to impact the distributions and interactions of non-native algae with their associated invertebrate communities. One prominent algal invader to this region is the red macroalga *Gracilaria vermiculophylla* (Ohmi) Papenfuss, 1967, which is native to the Northwestern Pacific. In its native range, *G. vermiculophylla* is found from the northern Sea of Japan to the East China Sea and south toward the central Kuroshio Current (Kim et al., 2010; Krueger-Hadfield et al., 2017). This macroalga can tolerate a wide range of environmental stressors, including but not limited to extreme temperatures, low salinities, and low light exposure (Rueness, 2005, Phooprong et al., 2009, Nejrup & Pedersen 2012, Sotka et al., 2018). In addition, *G. vermiculophylla* has invaded nearly every temperate coastline in the northern hemisphere since its hypothesized introduction in the early 20th century with the movement of *Magallana gigas* (Thunberg, 1793) oysters (Thomsen et al., 2006; Krueger-Hadfield et al., 2017). From Virginia to Georgia, *G. vermiculophylla* has predominantly invaded soft-sediment estuarine habitats (Thomsen et al., 2009; Byers et al., 2012; Ramus et al., 2017), and unlike some native algae in the region, *G. vermiculophylla* grows rapidly and can attain large biomasses (Thomsen et al., 2009).

The spread of *G. vermiculophylla* in some coastal habitats has increased primary production, provided novel structural complexity, and increased secondary production by providing shelter, refuge, and substrate for macroinvertebrates (Nyberg et al., 2009, Thomsen, 2010, Byers et al., 2012, Thomsen et al., 2013, Guidone et al., 2014, Ramus et al., 2017, Keller et al., 2019, Haram et al., 2020, , Lee et al. in revision). Studies have also indicated that *G. vermiculophylla* may be associated with a greater diversity and abundance of gastropods than native algae and may provide refuge, shelter, and habitat for these organisms from thermal stresses (Thomsen, 2010). However, at high water temperatures, *G. vermiculophylla* may induce anoxic events, reducing biomass and percent cover of native algae and increasing mortality of seagrasses and invertebrates (Ramus et al., 2017; Keller et al., 2019).

Co-occurring with *G. vermiculophylla* in the western Atlantic is the eastern mudsnail *Ilyanassa obsoleta* Say, 1822, a common and abundant gastropod in the region (Guidone et al., 2014). Few studies have investigated the co-occurrence of *G. vermiculophylla* and *I. obsoleta* in field or laboratory settings, and those few have primarily focused on *I. obsoleta* egg deposition preference. For example, Guidone et al., (2014) demonstrated that *I. obsoleta* prefers depositing eggs on *G. vermiculophylla* over native substrates (Thomsen et al., 2013; Guidone et al., 2014). In contrast, Harmon & Allen, (2018) found that *I. obsoleta* preferred depositing eggs on native eelgrass and suggested that its egg deposition preferences may vary across latitudinal gradients, depending on geomorphology and foundational species composition. To date, however, no research has investigated how the survival of Nassariidae Iredale, 1916 (1835) gastropods co-occurring with *G. vermiculophylla* may vary with rising seawater temperature.

To address the question of *I. obsoleta* survivability in habitats occupied by non-native macroalga, we conducted a survival experiment across three seawater temperatures—representing moderate to extreme summer temperatures in coastal North Carolina—to determine whether *I. obsoleta* survival was affected by the presence or absence of *G. vermiculophylla*. Moreover, because *I. obsoleta* is an important first-intermediate host species of digenean trematodes, we also took data on infection status to determine whether parasitic infection played a role in snail survival; this is because past work has shown that temperature can enhance the pathology associated with trematode infection in infected snail hosts (e.g., Paull & Johnson, 2011). During our experiment, we also observed female *I. obsoleta* to lay egg capsules at our lowest temperature treatment, and therefore, we also examined whether the presence of *G. vermiculophylla* influenced the number of egg capsules laid and any preference for egg deposition on *G. vermiculophylla* versus bare substrate. Finally, to determine whether high water temperature in combination with *G. vermiculophylla* may have impacted dissolved oxygen concentrations in our treatments, we conducted a laboratory-based dissolved oxygen experiment in the presence or absence of *G. vermiculophylla*. Our data help to discern what impact rising seawater temperature, non-native macroalgae, and changing oxygen levels may have on the survival and egg-laying preference of an abundant native gastropod species in the western Atlantic.

## Methods

### Study species

The eastern mudsnail *Ilyanassa obsoleta* is a highly abundant gastropod species in estuarine habitats throughout eastern North America from the Gulf of Saint Lawrence, Canada to Northern Florida, forming densities as high as 8000 individuals/m2 (Dimon, 1902; Abbott, 1974; Curtis & Hurd, 1983; Harmon & Allen, 2018). These gastropods primarily live in soft-sediment habitats, although they are also observed on coarser sediments such as sand, shell fragments, and eelgrass (Dimon, 1902). The ecological and evolutionary success of *I. obsoleta* in achieving high densities is often attributed to the snail's ability to use a wide range of resources for its nutrition, including detritus, carrion, and benthic microflora (Curtis & Hurd, 1979, 1981; Cranford, 1988). In addition to a versatile diet, *I. obsoleta* has wide thermal (0–30 °C) and salinity (1 –35 PSU) tolerances (Fofonoff et al. 2018). *Ilyanassa obsoleta* also serves as a first-intermediate host to nine species of digenean trematodes (Blakeslee et al., 2012). The life cycles of these parasites typically require two to three host organisms, and, for most digenean species, begin with *I. obsoleta* grazing on the feces of definitive hosts that contains

the eggs of the parasite (Combes et al., 1994, Rohde, 2005). An infected *I. obsoleta* is castrated and parasitized for life (Blakeslee et al. 2020). Parasitism alters behavior and physiology of *I. obsoleta*, as it negatively impacts feeding rates and survivability under thermal stresses (Curtis & Hurd, 1983).

## Experiment

We used temperature logger data collected from Beaufort, NC, USA (Asch, pers. obs.; Blakeslee, pers. obs.) during the summers of 2019 and 2020 (May–September) to establish three temperature treatments for this study. The low temperature (27 °C) was determined from the overall average temperature recorded continuously from May 1–September 3, 2019 (Asch 2019: unpub. data); the medium (32 °C) and high (36 °C) temperatures were determined based on the average and peak temperatures, respectively, recorded from August 5–14, 2020 (Blakeslee, unpub. data) for loggers that were directly exposed to the mud where *I. obsoleta* were collected for our experiment (see below). We performed two experimental trials, as described below.

We ran our first trial from February 2–22, 2021. We used three ThermoFisher Scientific (Waltham, MA) Heratherm™ General Protocol Microbiological Incubators, one for each temperature treatment. We used lights on a 12:12 h light cycle in each incubator. Two days prior to running the experiment, we collected > 300 *I. obsoleta* from Curtis Perry Park in Beaufort, NC, USA (Lat: 34.709731, Long: − 76.632494) because prior research (Moore et al., in review) found a high abundance of snails and a moderate infection prevalence (10% infection) at this site. We attempted to standardize snail size as much as possible during these collections (average shell length = 15.4 mm, standard deviation = 1.11 mm). One day prior to running the experiment, we collected *Gracilaria vermiculophylla* from the University of North Carolina Wilmington Center for Marine Science in Wilmington, NC (Lat: 34.140212, Long: − 77.863701) in the intertidal zone at low tide. This location was selected due to the widespread distribution of the alga in this region year-round (Freshwater et al., 2006, Lee pers. obs). Algae and snails were housed in 36.83 × 22.22 × 24.46 cm Kritter Keeper® Aquaria and were acclimated to laboratory conditions

for 2 days, using 30 PSU seawater made from Instant Ocean® Sea Salt at ambient room temperature (20 °C). We selected this salinity because it is a non-stressful salinity for both species.

Three-hundred snails were haphazardly assigned to either of two habitats (with *G. vermiculophylla* (henceforth "algae") and no *G. vermiculophylla* (henceforth "bare") and one of three temperatures such that there were 50 snails for each habitat x temperature combination. Snails were individually placed into separate grids of a MroMax® 18-Grid Electronic Component Storage Box (fixed-grid), which is an effective experimental housing for invertebrate survival experiments (Tepolt et al. 2020, Blakeslee et al. 2021). *Gracilaria vermiculophylla* was washed in fresh water to induce osmotic shock to remove any associated organisms and macro-epiphytes (Fowler et al. 2016, Lee et al., in review). Next, 2.5 g (wet weight) of the alga was added to every other grid, and the density and structural complexity of each algal frond was standardized by eye as best as possible. We filled each grid with 30 PSU seawater and added a single pellet of Aqueon® Cichlid Pellet as food for the snails and covered each box with their respective lid while ensuring boxes were not airtight. The 18-grid boxes were haphazardly assigned to the three temperature treatments, such that there were 100 snails per incubator.

To assess the potential influence of desiccation on snail mortality with and without algae, we replicated one low tide each day. Snail survival was checked twice daily for 21 days at 9:00 and 15:00, respectively. After checking for mortality at 9:00, we moved all surviving snails and algae to a new, dry storage compartment. At 15:00, after checking for mortality, we re-filled all the grids with 30 ppt seawater kept in the incubators at the assigned temperature treatment and fed each snail one Aqueon® Cichlid Pellet. If a snail had died, we measured its shell length (from operculum to the spiral) and dissected snail gonad tissues for trematode infection status; if parasitized, we identified the trematode to species level, using approaches in Blakeslee et al., (2012). At each mortality check, we rotated the 18-grid boxes to different shelves of the incubator. Additionally, throughout the experiment, we checked the structural integrity of *G. vermiculophylla*. If *G. vermiculophylla* was fragmenting or starting to decompose, we replaced it with the same standard biomass (2.5 g).

The second 21-day trial ran from February 23–March 15, 2021. We collected > 300 new *I. obsoleta* and *G. vermiculophylla* from the same locations used in Trial 1 and housed them using the same methodology. Like Trial 1, we attempted to standardize snail size as much as possible (average shell length = 15.35 mm, standard deviation = 0.95 mm). For Trial 2, we re-assigned each incubator to a different temperature treatment. Otherwise, our approach for collecting data in Trial 2 was identical to Trial 1.

During Trial 1, we also observed *I. obsoleta* depositing eggs in the low temperature treatment. As a result, during Trial 2, we took egg count data during each mortality check. To ensure we could obtain accurate counts without double-counting, we scraped eggs off the walls of the grid boxes and/or replaced *G. vermiculophylla* if they were covered with eggs.

### Dissolved oxygen data

At the end of Trial 1 and Trial 2, we found rapid mortality in the high temperature treatments with algae (see "Results" section). We hypothesized that this may be the result of anoxic conditions induced by high temperatures and algal degradation in this stressful environment (Bermejo et al., 2020). Though we attempted to control for algal degradation as much as possible by replacing algae and seawater during our experiment, it was clear that algae in the high temperature treatment were degrading quickly, often showing signs of bleaching. As a result, we examined the impact of temperature and *G. vermiculophylla* presence/absence on dissolved oxygen in the same grids in the same containers used in the trials above. For this experiment, we used the same experimental setup as described above (i.e., algae and bare habitats and the three temperature treatments), except in these trials we did not include snails. Our two trials lasted five days (October 17–21, 2022; October 24–28, 2022). We chose a 5-day experimental period because, per our *Results*, the high temperature treatment resulted in high mortality within this time period. We collected data twice per day, at 8:00 and 16:00. We measured dissolved oxygen using a YSI® (Yellow Springs, OH, USA) Pro20 Dissolved Oxygen Meter. Unlike the snail survival experiment, we did not replace water daily because we were aiming to observe the trends of dissolved oxygen through time.

### Statistical analyses

To analyze our survival data, we used the Cox proportional hazards model (CPHM), which uses number of days survived as the response variable (Cox, 1972; Therneau & Grambsch, 2000), to determine which sets of variables best explained snail survival. For our experiment, these factors included habitat type: algae or bare, temperature: low, medium, or high, infection status: yes or no, snail size (shell length in mm), trial: 1 or 2, and the following interactions: habitat*temperature, habitat*infection status, temperature*infection status. These interaction terms were included based on their likely biological significance and as a result of preliminary statistical runs. Pilot runs showed that *I. obsoleta* survival significantly differed between Trials 1 and 2. Henceforth, we ran a CPHM separately for each trial. For each trial, we created different sets of CPHM models with different combinations of predictors using the R packages *survival* and *survminer* and used AICc with the *aictab* function in the R package *AICcmodavg* (Mazerolle, 2017; R Core Team, 2023) to determine which set of predictors best explained *I. obsoleta* survival. During pilot runs, we eliminated snail size as a predictor from our CPHM models, as it was not found to influence survival; this is likely because we attempted to standardize snail size as much as possible prior to running our experiment.

Based on the predictors that best explained *I. obsoleta* survival from the AICc results for each trial, we created Kaplan–Meier Curves to visualize *I. obsoleta* survival through time with temperature and habitat type as factors affecting survival in Trial 1 and temperature for Trial 2 (see *Results*). We also created temperature-response curves and calculated an $LT_{50}$ for each trial, or the temperature with 50% *I. obsoleta* mortality.

Based on our AICc results from each trial, we then performed several univariate analyses. In Trial 1, we used a Kruskal–Wallis test (Kruskal & Wallis, 1952) for overall significance and a Bonferroni correction method (Sedgwick, 2012) for pairwise comparisons to determine the effect on *I. obsoleta* survival in six categories (low-algae; low-bare; medium-algae; medium-bare; high-algae; high-bare). We also used a 2-tailed t-test to determine survivability differences between infected and uninfected *I. obsoleta*. For Trial 2, we

used a Kruskal–Wallis with Bonferroni correction to assess differences in *I. obsoleta* survivability among the three temperature treatments. For this trial, we did not assess survivability differences between infected and uninfected across the temperature, as infection status did not show up as a predictor in the top model and was not significant (see *Results*). To assess *I. obsoleta*'s egg deposition preference between algae and bare surface, we also analyzed egg counts in the low temperature algae treatment (number of eggs that were laid on the algae itself or on the wall of the container) using a paired *t*-test.

For dissolved oxygen, we ran a series of Generalized Linear Mixed Models (GLMM) using the R package *lme4* with dissolved oxygen as the response variable and the following predictors: temperature (low, medium, and high), habitat (algae or bare), trial (1 or 2), and time (AM or PM: AM = 8:00, PM = 16:00) as fixed effects, and "day" as a random effect (day 1, day 2, day 3, day 4, and day 5). We used the Gaussian family. We also ran AICc with the *aictab* function in the package *AICcmodavg* to determine which sets of predictors best explained the differences we observed in dissolved oxygen values. Based on our AICc results, we plotted the differences of dissolved oxygen between the following habitat*temperature interaction categories: low and algae, low and bare, medium and algae, medium and bare, high and algae, high and bare. We also used a Kruskal–Wallis test to determine the overall significance of the differences of dissolved oxygen levels across all six categories and used a Bonferroni correction method for pairwise comparisons. We used R 4.2.2 for all our data analyses (R Core Team, 2023).

## Results

For Trial 1, we found that temperature, habitat, and the habitat*temperature interaction were significant predictors of *Ilyanassa obsoleta* survival (Tables 1, S1-2). *Ilyanassa obsoleta* survival was greatest in the low (27 °C) temperature treatment for both habitats, with 96% and 92% surviving in algae and bare habitat, respectively, by Day 21 (Fig. 1A). For the medium (32 °C) temperature treatment, *I. obsoleta* survival was much lower, with no snails surviving the length of the experiment in the algae habitat (all snails had perished by Day 7 at 15:00), and only 10% survived in the bare habitat by Day 21 (Fig. 1B). For the high (36 °C) temperature treatment, all *I. obsoleta* had perished by Day 2 at either 9:00 (algae habitat) or 15:00 (bare habitat) (Fig. 1C). For Trial 2, we found that temperature alone was the sole significant predictor of *I. obsoleta* survival (Tables 2, S3–5), and hence we plotted Kaplan–Meier Curves for the three temperature treatments only. For the low temperature treatment, 60% of *I. obsoleta* survived by 15:00 on Day 21, while for the medium temperature, only 1% survived by 15:00 on Day 21. For the high temperature, all *I. obsoleta* perished by 9:00 on Day 2 (Fig. 2).

From Trial 1, we found that the $LT_{50}$ for the algae habitat was lower (27.53 °C) than the $LT_{50}$ for the bare habitat (29.62 °C) (Fig. 3A). In addition, infection status was a marginally significant additive predictor in the top model (Table 1), so we also calculated the $LT_{50}$ for infected ($n = 20$) versus uninfected *I. obsoleta* ($n = 280$) and fitted a logistic curve. We found that the $LT_{50}$ for infected *I. obsoleta* was lower (27.38 °C) than the $LT_{50}$ for uninfected *I. obsoleta* (29.49 °C) (Fig. 3B). In Trial 2, we calculated $LT_{50}$ for overall *I. obsoleta* across all temperature treatments because temperature alone was the sole

**Table 1** Trial 1's comparisons of *I. obsoleta* survival based on Cox proportional hazards model (CPHM) selection using AICc

temp, temperature (low, medium, high); habitat, habitat type (algae or bare); infected, infection status (yes or no)

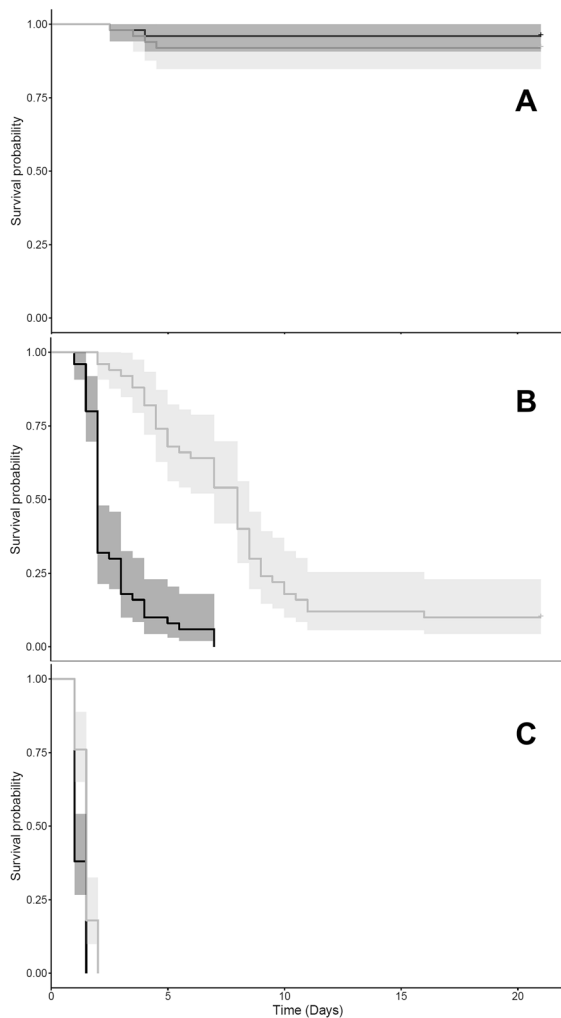| Model | K | AICc | ΔAICc | AICc Wt | Cumulative Wt |
|---|---|---|---|---|---|
| temp*habitat + infected | 6 | 1588.28 | 0 | 0.58 | 0.58 |
| temp*habitat | 5 | 1588.95 | 0.67 | 0.42 | 1 |
| temp + habitat | 3 | 1599.88 | 11.6 | 0 | 1 |
| temp + habitat + infected | 4 | 1600.16 | 11.88 | 0 | 1 |
| infected*habitat + temp | 6 | 1602.42 | 14.14 | 0 | 1 |
| temp*infected + habitat | 6 | 1602.42 | 14.14 | 0 | 1 |
| temp | 2 | 1664.6 | 76.32 | 0 | 1 |
| habitat | 1 | 2109.9 | 521.62 | 0 | 1 |

**Fig. 1** Survival probability of *I. obsoleta* in Trial 1 (21 days) was dependent on the interaction of temperature and habitat (Tables 1, S1–2). **A** = low (27 °C) temperature, **B** = medium temperature (32 °C), and **C** = high temperature (36 °C). Black = algae, gray = bare. Lines have been fitted from the Cox proportional hazard models, and shaded areas are 95% confidence intervals from the Kaplan–Meier survival analysis

significant predictor in the top performing model (Tables 2, S3–5). For Trial 2, the $LT_{50}$ was 27.4 °C for *I. obsoleta* across all temperature treatments (Fig. 3C).

For univariate analyses of Trial 1's habitat*temperature interaction, we found that the survival of *I. obsoleta* among groups was significantly different (Kruskal–Wallis: df = 5, $P < 0.001$; Fig. 4). We observed the greatest survival in low temperature algae habitat ($\mu = 20.29$, SE = 0.49 days), followed by low temperature bare ($\mu = 19.61$, SE = 0.67 days), medium temperature bare ($\mu = 8.33$, SE = 0.71 days), medium temperature algae ($\mu = 2.59$, SE = 0.21 days), high temperature bare ($\mu = 1.47 \pm 0.05$ days), and high temperature algae ($\mu = 1.19$, SE = 0.03 days) (Fig. 4). We did not find any significant differences in the survival between infected and uninfected snails in Trial 1 (Figure S1).

We found that survivability for Trial 2 decreased with increasing temperature, with greatest survivability in low temperature ($\mu = 15.06$, SE = 0.78 days), followed by medium ($\mu = 2.23$, SE = 0.24 days) and high ($\mu = 0.995$, SE = 0.005 days); survivability in low temperature was significantly higher than medium temperature ($P < 0.001$), while the survivability between medium and high were not significantly different (Figure S2).

For egg counts in Trial 2 in the low temperature algae treatment, we did not detect a significant difference ($P > 0.05$) (Figure S3); however, cumulative egg counts throughout the duration of the experiment was greater on *G. vermiculophylla* than on the plastic grid wall in the algae habitat (Fig. 5).

For the dissolved oxygen experiment, in the top performing model, temperature, habitat type, and the interaction of temperature*habitat were significant predictors (Tables S6–7). We observed
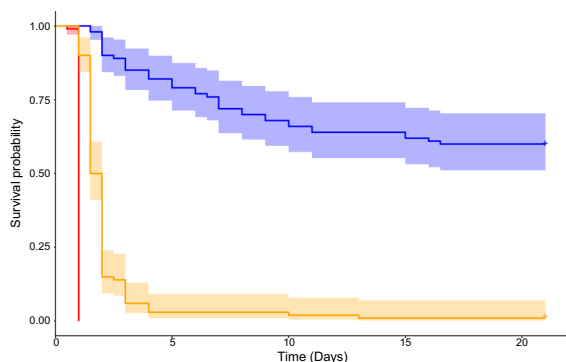
**Table 2** Trial 2's comparisons of *I. obsoleta* survival based on CPHM selection using AICc

| Model | K | AICc | ΔAICc | AICc Wt | Cumulative Wt |
|---|---|---|---|---|---|
| temp | 2 | 1993.19 | 0 | 0.29 | 0.29 |
| temp + habitat | 3 | 1993.64 | 0.44 | 0.23 | 0.52 |
| temp + habitat + infected | 4 | 1993.79 | 0.6 | 0.22 | 0.74 |
| infected*habitat + temp | 5 | 1995.67 | 2.47 | 0.08 | 0.82 |
| temp*infected + habitat | 6 | 1995.79 | 2.6 | 0.08 | 0.9 |
| temp*habitat | 5 | 1996.51 | 3.32 | 0.06 | 0.96 |
| temp*habitat + infected | 6 | 1996.94 | 3.75 | 0.04 | 1 |
| habitat | 1 | 2446 | 452.81 | 0 | 1 |

temp, temperature (low, medium, high); habitat, habitat type (algae or bare); infected, infection status (yes or no)

**Fig. 2** Survival probability of *I. obsoleta* in Trial 2 (21 days) was dependent on temperature alone (Tables 2, S3–5). Blue = low (27 °C) temperature treatment, orange = medium (32 °C) temperature, and red = high temperature (36 °C). Lines have been fitted from the Cox proportional hazard models, and shaded areas are 95% confidence intervals from the Kaplan–Meier survival analysis



**Fig. 3** Proportional survival of *I. obsoleta* in **A** Trial 1 (red = algae, blue = bare): $LT_{50}$ for algae = 27.53 °C, $LT_{50}$ for bare = 29.62 °C; **B** between infected (red; n = 20) and uninfected (blue; n = 280) in Trial 1: $LT_{50}$ for infected = 27.38 °C, $LT_{50}$ for uninfected = 29.49 °C; **C** Trial 2 across temperature: $LT_{50}$ = 27.4 °C. Black dashed lines represent the 50% mortality and their corresponding $LT_{50}$

the highest oxygen level at low temperature bare ($\mu = 3.43$, SE = 0.04 mg/lit), followed by medium temperature bare ($\mu = 2.88$, SE = 0.06 mg/lit), high temperature bare ($\mu = 2.65$, SE = 0.03 mg/lit), low temperature algae ($\mu = 1.03$, SE = 0.12 mg/lit), medium temperature algae ($\mu = 0.68$, SE = 0.06 mg/lit), and high temperature algae ($\mu = 0.06$, SE = 0.07 mg/lit). Using the Bonferroni correction method, we found that dissolved oxygen was significantly different ($P < 0.05$) between all pairs of temperature*habitat interaction categories (with higher dissolved oxygen levels in bare habitats for all temperature treatments), except for medium*algae and high*algae (Figure S4).

## Discussion

Sea surface temperatures around the globe are warming rapidly. The coupling of temperature rise and the expansion of invasive species can be harmful to the fitness and survival of native species. In our study, we examined the potential interactive influence of sea water temperature and an invasive alga, *Gracilaria vermiculophylla*, on the survival and reproductive output of a native mudsnail, *Ilyanassa obsoleta*. Our experimental results can serve as a baseline for understanding how native macroinvertebrates co-occurring with *G. vermiculophylla* may be impacted by climate change in the North Atlantic, as seawater temperature
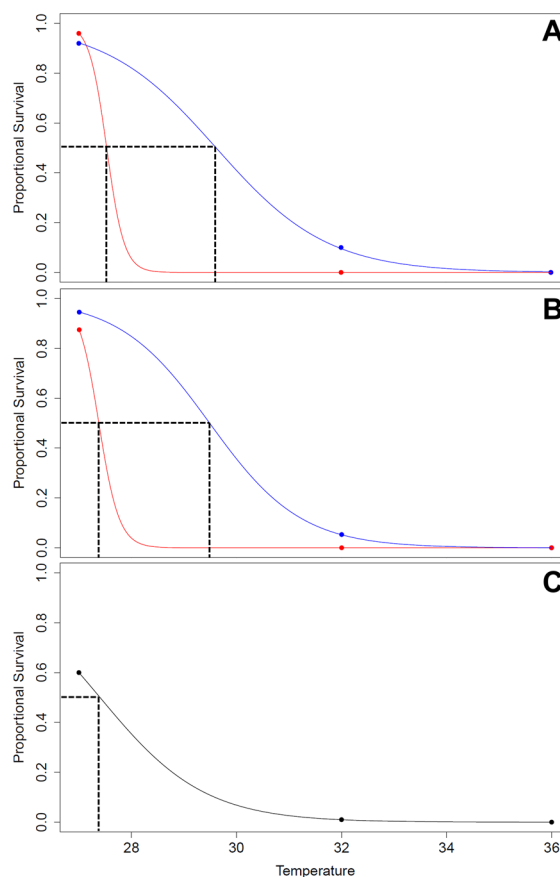
continues to rise and enhance growth and expansion of invasive seaweeds like *G. vermiculophylla*.

### The influence of temperature on *Ilyanassa obsoleta* survival

We found the mortality rate of *I. obsoleta* to be highest in the warmest water temperature treatment (Figs. 1, 2, 3). This observation for decreased survivability with increasing water temperature has also been observed in experimental studies with other snail species (e.g., Raut et al., 1992). For example, freshwater snails, including *Pomacea canaliculata* Lamarck, 1828, have been found to exhibit faster
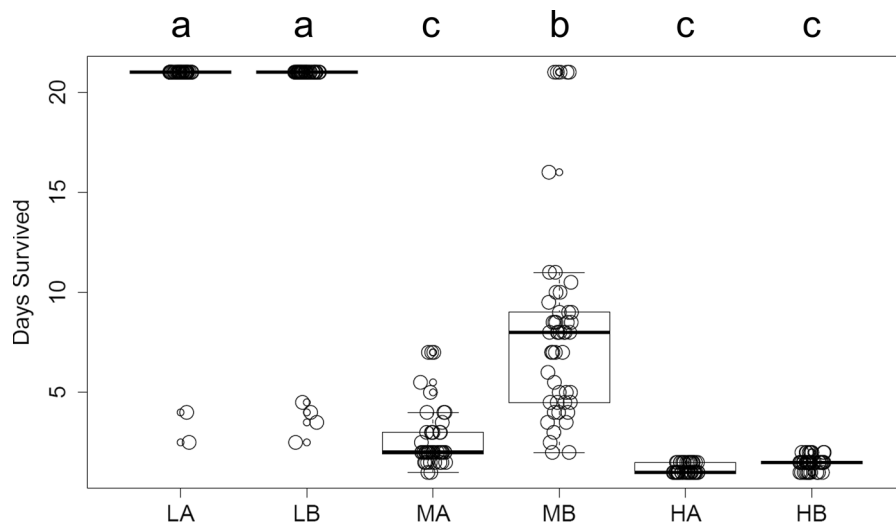
**Fig. 4** Number of days survived by individual *I. obsoleta* in Trial 1 by habitat and temperature interaction. LA, low temperature (27 °C), algae; LB, low temperature, bare; MA, medium temperature (32 °C), algae; MB, medium temperature, bare; HA, high temperature (36 °C), algae; HB, high temperature, bare (df = 5, $P < 0.001$). Same letters above the graph indicate that those categories are not statistically significant in pairwise comparisons. Error bars = SE, black circle = number of days each snail survived (jittered)

growth at higher temperatures, but decreased survival. In particular, at 15 and 20 °C, these snails experienced no mortality, but at 25, 30, and 35 °C, they grew 2–3 mm longer than the snails at 15–20 °C, but with enhanced mortality (Seuffert & Martin 2013). Parashar & Rao, (1988) also observed that the freshwater planorbid snail *Gyraulus convexiusculus* T. Hutton, 1849 experienced the highest growth rate at the highest temperature treatment (35 °C), but also experienced highest survival at lower temperatures, and their peak survival times differed based on life stage. In marine environments, however, it appears that many snails are frequently exposed to high water and air temperatures, and hence have evolved heat tolerance plasticities, such as the tropical snail *Echinolittorina malaccana* (R.A. Philippi, 1847), which is capable of modifying their $LT_{50}$ (Brahim & Marshall, 2020). Another marine snail, *Chlorostoma funebralis* A. Adams, 1855, has evolved higher thermal limits (the maximum temperature at which their heart function will cease), with some populations of *C. funebralis* reaching maximum temperatures of 40 °C (Gleason & Burton, 2013). While aquatic snails in the wild are frequently exposed to temperatures as high as 35–40 °C, it is important to note that these temperatures do induce major physiological stress and

undoubtedly increase mortality. However, snails may be able to respond in their natural environments by seeking refuge from stressful conditions. In our study, snails did not have such an opportunity to seek refuge from thermal stress. Thus, to better understand their heat tolerance plasticity in nature, future studies could examine snails in the field, where they would receive natural water exchange through changing tides and could seek refuge by burying in the mud or sheltering in habitats that help prevent desiccation.

**The interaction of temperature and *G. vermiculophylla* presence on snail survival and dissolved oxygen**

During our first trial, we found that *I. obsoleta* survival was lower and that snails perished faster in treatments at higher temperatures in the presence of *G. vermiculophylla* (Figs. 1, 3A, 4; Tables 1, S1–2). Higher seawater temperature can induce algal degradation, and subsequent degradation could lead to anoxic conditions. For example, in a study from northeast Brazilian coastal reefs, Sassi et al., (1988) found that algal decomposition resulted in seawater completely devoid of oxygen over a 10-h period. Specific to *G. vermiculophylla*, Bermejo et al., (2020)
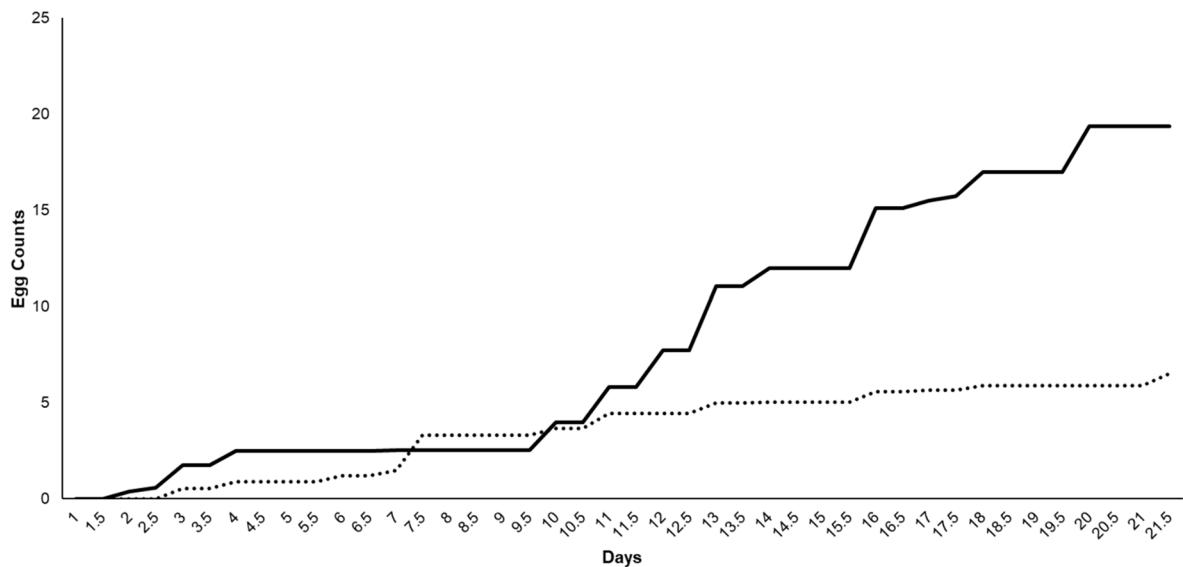
**Fig. 5** Cumulative egg count for Trial 2, low temperature algae habitat (solid line = eggs on *G. vermiculophylla*, dashed line = eggs on the grid wall)

found that during *G. vermiculophylla* blooms in estuaries of Ireland, higher temperatures increased stress on the seaweed, and also increased degradation. These high rates of decomposition increased bacterial growth, thereby leading to anoxic conditions (Bermejo et al., 2020).

Past work has shown that under rising seawater temperature, invasive seaweeds may release toxic exudates that are then harmful to native fauna. For example, in Europe, exudates released by the invasive red alga, *Asparagopsis armata* Harvey, 1855, have been shown to negatively affect the neurophysiology, digestive glands, and the native *M. galloprovincialis*' muscular system (Vieira et al., 2021). Like other macroalgae, *G. vermiculophylla* also exudates toxic compounds at stressful conditions; in particular, *G. vermiculophylla* releases prostaglandins as a wound-activated production (Hammann et al., 2016). Compared to their native counterparts, the non-native *G. vermiculophylla* thalli produce significantly higher concentrations of eicosatetraenoids, a chemical that is released as a wounding of thalli through decay or predation (Hammann et al., 2016). This not only makes non-native *G. vermiculophylla* less palatable to herbivores, but as the algae decay with increasing seawater temperature, they can create anoxic conditions, while also releasing increasing concentrations of toxins.

Such toxins deter herbivores and increase macroinvertebrate mortality.

In our study, we observed clear degradation of *G. vermiculophylla* and a milky liquid on the surface of the water in the medium and high temperature treatments. Such an observation of a milky substance following algal degradation has been described by Bermejo et al., (2020) as the result of bacterial growth, which then causes a reduction in dissolved oxygen in the water. Following these observations in our trials, we set up a dissolved oxygen experiment to determine how the presence of *G. vermiculophylla* affected oxygen levels across our temperature treatments. In all temperature treatments, we found oxygen levels were significantly lower in habitats with *G. vermiculophylla* than without (Figure S4, Tables S6–7). Thus, it is likely that the combination of temperature stress plus low levels of dissolved oxygen in the medium and higher temperature treatments resulted in high mortality of *I. obsoleta*. However, we acknowledge that in a controlled laboratory setting, the snails likely experienced higher than natural mortality, as their experimental habitats had limited water flow. We attempted to limit this impact by changing water daily; however, it is very likely that the snails experienced anoxia to a greater level due to a lack of oxygen-rich water in the experiment. Though our study did not completely replicate natural conditions, it is

likely that in the wild, these snails may be exposed to high temperatures, algal degradation, and low dissolved oxygen during the hottest parts of the summer and during heat waves, especially in very shallow mud flats at low tide or within pools in the upper parts of the intertidal zone at low tide.

The influence of infection status on snail survival

*Ilyanassa obsoleta* serves as first-intermediate host to nine species of trematodes in its range in the Northwest Atlantic (Curtis et al., 2000). These trematode species can induce a major cost on their snail hosts, since they lead to complete castration and are an energetic strain (Cheng et al., 1983; Pearson & Cheng, 1985; Sullivan et al., 1985). Due to this strong impact on snail fitness, we also assessed survivability between infected and uninfected *I. obsoleta* to determine whether infected snails would be more likely to die at a faster rate than uninfected snails. Across all snails (all temperature treatments and habitats), we identified no impact of infection status on a snail's survival (Figure S1). However, when we examined the influence of infection and temperature in our $LT_{50}$ plots, we found as temperature increased, infected *I. obsoleta* perished faster than those that were uninfected (Fig. 3B). Other investigations have shown that higher temperatures increase parasitic cercariae production: for instance, the trematode parasite *Ribeiroia ondatrae* (Price, 1931) Price, 1942 had a four times higher fecundity in their snail host *Planorbella trivolvis* Say, 1817 at 26 °C compared to 17 °C (Paull & Johnson, 2011). In addition, Studer et al., (2010) found that transmission of the trematode cercarial stage from the first to second intermediate host was greatest at temperatures between 20 and 25 °C, while transmission decreased at temperatures > 30 °C, and < 20 °C. Studer et al., (2010) also observed increased mortality within the second intermediate host at temperatures > 30 °C. These studies indicate that while higher temperatures may induce greater parasite fecundity, the successful transmission of trematodes with multi-host life cycles may also be negatively impacted at temperatures > 30 °C due to increasing mortality of their hosts. We similarly observed that higher temperatures had a stronger impact on *I. obsoleta* survival

in infected individuals; however, our sample size of infected individuals was much lower ($n = 20$) than uninfected ($n = 280$) individuals, which may have affected our results. It would be important to assess this question in a future study with a greater number of infected individuals, as the patterns we observed may become stronger with a higher sample size in the infected group.

The influence of *G. vermiculophylla* on *I. obsoleta* egg capsule counts and location

During Trial 1, we observed *I. obsoleta* snails to lay egg capsules in our low temperature treatment. As a result, we counted the number of egg capsules laid in the two habitats (algae or bare) and the number of egg capsules laid on the algae vs bare plastic walls during Trial 2. We found no significant differences in the number of egg capsules laid in the algae versus bare treatments (Figure S3). However, we noticed that the cumulative trend of eggs being laid over time was faster on *G. vermiculophylla* versus the bare treatment (Figure S1). Guidone et al., (2014) found that *I. obsoleta* preferred depositing eggs on *G. vermiculophylla* versus other substrate types and even preferred depositing eggs on the non-native algae versus native algae. Guidone et al., (2014) also noted that thick layers of egg masses on *G. vermiculophylla* did not hamper growth of the non-native algal thalli, while it slowed the growth of the native alga *Ceramium virgatum* Roth, 1797. In our study, *I. obsoleta* did not lay egg capsules in any of the medium or high temperature treatments, suggesting a strong influence of temperature on reproduction in our laboratory experiment. In the high temperature treatment, *I. obsoleta* perished rapidly, while in the medium temperature, some individuals survived the entire duration of the experiment. Sastry, (1971) noted that *I. obsoleta* fecundity can increase with higher temperatures, but an optimal temperature is required that enhances fecundity without leading to greater temperature-induced stress on reproduction and survival.

Differences detected during Trials

In Trial 1, we identified a significant interaction between temperature and habitat (presence/absence of *G. vermiculophylla*) on *I. obsoleta* survival, while in Trial 2, only temperature was significant. The two-week difference in collection timing for the snails and the algae, as well as the time of year the study was carried out, could have played a role in the differences we observed between the two trials. Past studies have indicated that *G. vermiculophylla* store high nitrogen concentrations in winter months, which can enhance their growth in summer months when light availability is optimal but nitrogen is limited (Abreu et al., 2011). In our experiment, though we acclimated both *I. obsoleta* and *G. vermiculophylla* to a non-stressful temperature (20 °C) in the laboratory prior to running the experiments, these species were exposed to warm temperature treatments more quickly than they would in natural environments, where they may be able to acclimate to gradually rising water temperature from winter to summer months. Future studies assessing invertebrate survivability could be implemented in summer months with macroalgae thalli from warm seawater temperatures.

The life stage of *G. vermiculophylla* could be another factor influencing the different results in our two trials. It is possible that the different collection timing of *G. vermiculophylla* may have resulted in differing compositions of gametophytes and tetrasporophytes. In non-native habitats, 90–100% of *G. vermiculophylla* populations are tetrasporophytes, while in native habitats, gametophytes and tetrasporophytes comprise ~40 and ~60% of thalli, respectively (Lees et al., 2018). While we did not control for algal life stage in this study, non-native *G. vermiculophylla* populations are tetrasporophyte-dominated (Krueger-Hadfield et al., 2017), and for *Gracilaria* spp., these two life stages differ in ecological performance. For example, Fonseca Faria & Plastino, (2024) found that for *Gracilaria tenuifrons* (C.J.Bird & E.C.Oliveira) Fredericq & Hommersand, 1989, tetrasporophytes experienced greater growth at a higher temperature (30 °C), while a lower temperature (25 °C) resulted in higher growth of unfertilized female gametophytes. The differing composition of unfertilized *G. vermiculophylla* female gametophytes between those collected for Trials 1 and 2 may have led to differences in *I. obsoleta* survivability because a higher composition of gametophytes could increase algal decay and anoxia. While we were not able to quantify the rate of decay or bacterial growth between trials, such factors could be considered for future studies assessing invertebrate survivability coupled with rising seawater temperatures in the presence or absence of invasive macroalgae.

## Conclusions

In some systems, non-native *G. vermiculophylla* can increase the abundance of native free-living macroinvertebrates compared to native foundational species, due to the alga's complex three-dimensional structure (Thomsen, 2010; Thomsen et al., 2013). However, this potential benefit could be hampered by rising seawater temperatures. Large blooms of *G. vermiculophylla* during high seawater temperature events may induce anoxia (Martínez-Lüscher & Holmer 2010), and thus lead to higher levels of mortality among native macroinvertebrates, including co-occurring species like *I. obsoleta*. However, it is possible that native macroinvertebrates associated with *G. vermiculophylla*, even during low-oxygen conditions and high temperature events, may have evolved physiological, behavioral, and molecular mechanisms to survive such conditions, as high water and air temperatures at low tide in intertidal environments occur regularly for many species (Wright et al., 2010). In the Northwest Atlantic, the long-lasting coupling effects of high seawater temperature and *G. vermiculophylla* presence on native macroinvertebrate communities requires further monitoring to better understand how human-induced climate change may alter marine community composition and structure in future.

**Data availability** All data are available upon reasonable request. Supplementary figures and tables are enclosed.

## Declarations

**Conflict of interest** Not applicable.

**Open Access** This article is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons licence, and indicate if changes were made. The images or other third party material in this article are included in the article's Creative Commons licence, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons licence and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this licence, visit http://creativecommons.org/licenses/by/4.0/.

## References

Abbott, R. T., 1974. American Seashells; The Marine Molluska of the Atlantic and Pacific Coasts of North America, 2nd ed. Van Nostrand Reinhold, New York:

Abreu, M. H., R. Pereira, A. H. Buschmann, I. Sousa-Pinto & C. Yarish, 2011. Nitrogen uptake responses of *Gracilaria vermiculophylla* (Ohmi) Papenfuss under combined and single addition of nitrate and ammonium. Journal of Experimental Marine Biology and Ecology 407: 190–199. https://doi.org/10.1016/j.jembe.2011.06.034.

Bellgrove, A., P. F. McKenzie, H. Cameron & J. B. Pocklington, 2017. Restoring rocky intertidal communities: lessons from a benthic macroalgal ecosystem engineer. Marine Pollution Bulletin 117: 17–27. https://doi.org/10.1016/j.marpolbul.2017.02.01.

Bermejo, R., M. MacMonagail, S. Heesch, A. Mendes, M. Edwards, O. Fenton, K. Knöller, E. Daly & L. Morrison, 2020. The arrival of a red invasive seaweed to a nutrient over-enriched estuary increases the spatial extent of macroalgal blooms. Marine Environmental Research 158: 104944. https://doi.org/10.1016/j.marenvres.2020.104944.

Bianchi, C. N., A. Azzola, M. Bertolino, F. Betti, M. Bo, R. Cattaneo-Vietti, S. Cocito, M. Montefalcone, M. Morri, A. Oprandi, A. Peirano & G. Bavestrello, 2019. Consequences of the marine climate and ecosystem shift of the 1980–90s on the Ligurian Sea biodiversity (NW Mediterranean). The European Zoological Journal 86: 458–487. https://doi.org/10.1080/24750263.2019.1687765.

Bollen, M., C. A. Pilditch, C. N. Battershill & K. Bischof, 2016. Salinity and temperature tolerance of the invasive alga *Undaria pinnatifida* and native New Zealand kelps: implications for competition. Marine Biology 163: 1–14. https://doi.org/10.1007/s00227-016-2954-3.

Blakeslee, A. M., I. Altman, A. W. Miller, J. E. Byers, C. E. Hamer & G. M. Ruiz, 2012. Parasites and invasions: a biogeographic examination of parasites and hosts in native and introduced ranges. Journal of Biogeography 39: 609–622. https://doi.org/10.1111/j.1365-2699.2011.02631.x.

Blakeslee, A. M., D. L. Pochtar, A. E. Fowler, C. S. Moore, T. S. Lee, R. B. Barnard, K. M. Swanson, L. C. Lukas, M. Ruocchio, M. E. Torchin, A. W. Miller, G. M. Ruiz & C. K. Tepolt, 2021. Invasion of the body snatchers: the role of parasite introduction in host distribution and response to salinity in invaded estuaries. Proceedings of the Royal Society B 288: 20210703. https://doi.org/10.1098/rspb.2021.0703.

Brahim, A. & D. J. Marshall, 2020. Differences in heat tolerance plasticity between supratidal and intertidal snails indicate complex responses to microhabitat temperature variation. Journal of Thermal Biology 91: 102620. https://doi.org/10.1016/j.jtherbio.2020.102620.

Byers, J. E., P. E. Gribben, C. Yeager & E. E. Sotka, 2012. Impacts of an abundant introduced ecosystem engineer within mudflats of the southeastern US coast. Biological Invasions 14: 2587–2600. https://doi.org/10.1007/s10530-012-0254-5.

Cheng, T. C., J. T. Sullivan, K. H. Howland, T. F. Jones & H. J. Moran, 1983. Studies on parasitic castration: soft tissue and shell weights of *Ilyanassa obsoleta* (Mollusca) parasitized by larval trematodes. Journal of Invertebrate Pathology 42: 143–150. https://doi.org/10.1016/0022-2011(83)90055-1.

Combes, C., A. Fournier, H. Moné & A. Théron, 1994. Behaviours in trematode cercariae that enhance parasite transmission: patterns and processes. Parasitology 109: S3–S13. https://doi.org/10.1017/S0031182000085048.

Cox, D. R., 1972. Regression models and life-tables. Journal of the Royal Statistical Society: Series B 34: 187–202. https://doi.org/10.1111/j.2517-6161.1972.tb00899.x.

Cranford, P. J., 1988. Behaviour and ecological importance of a mud snail (*Ilyanassa obsoleta*) population in a temperate macrotidal estuary. Canadian Journal of Zoology 66: 459–466. https://doi.org/10.1139/z88-065.

Curtis, L. A. & L. E. Hurd, 1979. On the broad nutritional requirements of the mud snail, *Ilyanassa* (Nassarius) *obsoleta* (Say), and its polytrophic role in the food web. Journal of Experimental Marine Biology and Ecology 41: 289–297. https://doi.org/10.1016/0022-0981(79)90137-0.

Curtis, L. A. & L. E. Hurd, 1981. Nutrient procurement strategy of a deposit-feeding estuarine *neogastropod*, *Ilyanassa obsoleta*. Estuarine, Coastal and Shelf Science 13: 277–285. https://doi.org/10.1016/S0302-3524(81)80026-6.

Curtis, L. A. & L. E. Hurd, 1983. Age, sex, and parasites: spatial heterogeneity in a sandflat population of *Ilyanassa obsoleta*. Ecology 64: 819–828. https://doi.org/10.2307/1937205.

Curtis, L. A., J. L. Kinley & N. L. Tanner, 2000. Longevity of oversized individuals: growth, parasitism, and history in an estuarine snail population. Journal of the Marine Biological Association of the United Kingdom 80: 811–820. https://doi.org/10.1017/S0025315400002782.

Dimon, A. C., 1902. Quantitative study of the effect of environment upon the forms of *Nassa obsoleta* and *Nassa*

*trivittata* from Cold Spring Harbor, Long Island. Biometrika 2: 24–43. https://doi.org/10.2307/2331499.

Félix-Loaiza, A. C., L. M. Rodríguez-Bravo, R. Beas-Luna, J. Lorda, E. de La Cruz-González & L. Malpica-Cruz, 2022. Marine heatwaves facilitate invasive algae takeover as foundational kelp. Botanica Marina 65: 315–319. https://doi.org/10.1515/bot-2022-0037.

Fofonoff, P.W., G.M. Ruiz, B. Steves, A.H. Hines & J.T. Carlton, 2018. National exotic marine and estuarine species information system. Retrieved from http://invasions.si.edu/nemesis/.

Fonseca Faria, A. V. & E. M. Plastino, 2024. Effects of temperature on isomorphic haploid-diploid phases of *Gracilariopsis tenuifrons* (Gracilariales, Rhodophyta). Phycologia 63: 3–10. https://doi.org/10.1080/00318884.2023.2278381.

Foster, A. D., H. L. Spalding, T. E. Cox, F. F. La Valle & J. Philippoff, 2019. The invasive green alga *Avrainvillea* sp. transforms native epifauna and algal communities on a tropical hard substrate reef. Phycological Research 67: 164–169. https://doi.org/10.1111/pre.12359.

Fowler, A. E., A. M. Blakeslee, J. Canning-Clode, M. F. Repetto, A. M. Phillip, J. T. Carlton, F. C. Moser, G. M. Ruiz & A. W. Miller, 2016. Opening Pandora's bait box: a potent vector for biological invasions of live marine species. Diversity and Distributions 22: 30–42. https://doi.org/10.1111/ddi.12376.

Freshwater, D. W., F. Montgomery, J. K. Greene, R. M. Hamner, M. Williams & P. E. Whitfield, 2006. Distribution and identification of an invasive *Gracilaria* species that is hampering commercial fishing operations in southeastern North Carolina, USA. Biological Invasions 8: 631–637. https://doi.org/10.1007/s10530-005-1809-5.

Fujiwara, M., F. Martinez-Andrade, R. D. Wells, M. Fisher, M. Pawluk & M. C. Livernois, 2019. Climate-related factors cause changes in the diversity of fish and invertebrates in subtropical coast of the Gulf of Mexico. Communications Biology 2: 403. https://doi.org/10.1038/s42003-019-0650-9.

Gillis, C. A. & M. Chalifour, 2010. Changes in the macrobenthic community structure following the introduction of the invasive algae *Didymosphenia geminata* in the Matapedia River (Québec, Canada). Hydrobiologia 647: 63–70. https://doi.org/10.1007/s10750-009-9832-7.

Gleason, L. U. & R. S. Burton, 2013. Phenotypic evidence for local adaptation to heat stress in the marine snail *Chlorostoma* (formerly Tegula) *funebralis*. Journal of Experimental Marine Biology and Ecology 448: 360–366. https://doi.org/10.1016/j.jembe.2013.08.008.

Gregory, G. J. & P. A. Quijón, 2011. The impact of a coastal invasive predator on infaunal communities: assessing the roles of density and a native counterpart. Journal of Sea Research 66: 181–186. https://doi.org/10.1016/j.seares.2011.05.009.

Gribben, P. E., J. E. Byers, M. Clements, L. A. McKenzie, P. D. Steinberg & J. T. Wright, 2009. Behavioural interactions between ecosystem engineers control community species richness. Ecology Letters 12: 1127–1136. https://doi.org/10.1111/j.1461-0248.2009.01366.x.

Guidone, M., C. Newton & C. S. Thornber, 2014. Utilization of the invasive alga *Gracilaria vermiculophylla* (Ohmi)

Papenfuss by the native mud snail *Ilyanassa obsoleta* (Say). Journal of Experimental Marine Biology and Ecology 452: 119–124. https://doi.org/10.1016/j.jembe.2013.12.016.

Hammann, M., M. Rempt, G. Pohnert, G. Wang, S. M. Boo & F. Weinberger, 2016. Increased potential for wound activated production of Prostaglandin E2 and related toxic compounds in non-native populations of *Gracilaria vermiculophylla*. Harmful Algae 51: 81–88. https://doi.org/10.1016/j.hal.2015.11.009.

Haram, L.E., E.E. Sotka & J.E. Byers, 2020. Effects of novel, non-native detritus on decomposition and invertebrate community assemblage. Marine Ecology Progress Series 643: 49–61. https://doi.org/10.3354/meps13335.

Harley, C. D., A. Randall Hughes, K. M. Hultgren, B. G. Miner, C. J. Sorte, C. S. Thornber, L. F. Rodriguez, L. Tomanek & S. L. Williams, 2006. The impacts of climate change in coastal marine systems. Ecology Letters 9: 228–241. https://doi.org/10.1111/j.1461-0248.2005.00871.x.

Harmon, E. A. & J. D. Allen, 2018. Predator-induced plasticity in egg capsule deposition in the mud snail *Tritia obsoleta*. Marine Ecology Progress Series 586: 113–125. https://doi.org/10.3354/meps12368.

Karlson, B., P. Andersen, L. Arneborg, A. Cembella, W. Eikrem, U. John, J. Joy West, K. Klemm, J. Kobos, S. Lehtinen, N. Lundholm, H. Mazur-Marzec, L. Naustvoll, M. Poelman, P. Provoost, M. De Rijcke & S. Suikkanen, 2021. Harmful algal blooms and their effects in coastal seas of Northern Europe. Harmful Algae 102: 101989. https://doi.org/10.1016/j.hal.2021.101989.

Keller, E. L., S. K. Berke, C. N. Needham & C. R. Salerno, 2019. A double-edged sword: infaunal responses to *Agarophyton vermiculophyllum* in the Mid-Atlantic United States. Estuaries and Coasts 42: 1924–1937. https://doi.org/10.1007/s12237-019-00608-z.

Kim, S. Y., F. Weinberger & S. M. Boo, 2010. Genetic data hint at a common donor region for invasive Atlantic and pacific populations of *Gracilaria vermiculophylla* (Gracilariales, Rhodophyta). Journal of Phycology 46: 1346–1349. https://doi.org/10.1111/j.1529-8817.2010.00905.x.

Krueger-Hadfield, S. A., N. M. Kollars, A. E. Strand, J. E. Byers, S. J. Shainker, R. Terada, T. W. Greig, M. Hammann, D. C. Murray, F. Weinberger & E. E. Sotka, 2017. Genetic identification of source and likely vector of a widespread marine invader. Ecology and Evolution 7: 4432–4447. https://doi.org/10.1002/ece3.3001.

Kruskal, W. H. & W. A. Wallis, 1952. Use of ranks in one-criterion variance analysis. Journal of the American Statistical Association 47: 583–621. https://doi.org/10.1080/01621459.1952.10483441.

Lees, L. E., S. A. Krueger-Hadfield, A. J. Clark, E. A. Duermit, E. E. Sotka & C. J. Murren, 2018. Nonnative *Gracilaria vermiculophylla* tetrasporophytes are more difficult to debranch and are less nutritious than gametophytes. Journal of Phycology 54: 471–482. https://doi.org/10.1111/jpy.12746.

Lima, F. P. & D. S. Wethey, 2012. Three decades of high-resolution coastal sea surface temperatures reveal more than warming. Nature Communications 3: 704. https://doi.org/10.1038/ncomms1713.

Lockwood, B. L. & G. N. Somero, 2011. Invasive and native blue mussels (genus *Mytilus*) on the California coast: the role of physiology in a biological invasion. Journal of Experimental Marine Biology and Ecology 400: 167–174. https://doi.org/10.1016/j.jembe.2011.02.022.

Martínez-Lüscher, J. & M. Holmer, 2010. Potential effects of the invasive species *Gracilaria vermiculophylla* on Zostera marina metabolism and survival. Marine Environmental Research 69: 345–349. https://doi.org/10.1016/j.marenvres.2009.12.00.

Marx, L., S. Flecha, M. Wesselmann, C. Morell & I. E. Hendriks, 2021. Marine macrophytes as carbon sinks: comparison between seagrasses and the non-native alga *Halimeda incrassata* in the Western Mediterranean (Mallorca). Frontiers in Marine Science 8: 746379. https://doi.org/10.3389/fmars.2021.746379.

Mazerolle, M. M. J., 2017. Package 'AICcmodavg'. R package 281.

Nejrup, L. B. & M. F. Pedersen, 2012. The effect of temporal variability in salinity on the invasive red alga *Gracilaria vermiculophylla*. European Journal of Phycology 47: 254–263. https://doi.org/10.1080/09670262.2012.702225.

Nyberg, C. D., M. S. Thomsen & I. Wallentinus, 2009. Flora and fauna associated with the introduced red alga *Gracilaria vermiculophylla*. European Journal of Phycology 44: 395–403. https://doi.org/10.1080/09670260802592808.

Parashar, B. D. & K. M. Rao, 1988. Effect of temperature on growth, reproduction and survival of the freshwater planorbid snail, *Gyraulus convexiusculus*, vector of echinostomiasis. Hydrobiologia 164: 185–191. https://doi.org/10.1007/BF00008458.

Paull, S. H. & P. T. Johnson, 2011. High temperature enhances host pathology in a snail–trematode system: possible consequences of climate change for the emergence of disease. Freshwater Biology 56: 767–778. https://doi.org/10.1111/j.1365-2427.2010.02547.x.

Pearson, E. J. & T. C. Cheng, 1985. Studies on parasitic castration: occurrence of a gametogenesis-inhibiting factor in extract of *Zoogonus lasius* (Trematoda). Journal of Invertebrate Pathology 46: 239–246. https://doi.org/10.1016/0022-2011(85)90064-3.

Phooprong, S., H. Ogawa & K. Hayashizaki, 2009. Photosynthetic and respiratory responses of Gracilaria vermiculophylla (Ohmi) Papenfuss collected from Kumamoto, Shizuoka and Iwate, Japan. Journal of Applied Phycology 20: 743–750. https://doi.org/10.1007/s10811-007-92539.

Pocklington, J. B., S. R. Jenkins, A. Bellgrove, M. J. Keough, T. D. O'Hara, P. E. Masterson-Algar & S. J. Hawkins, 2018. Disturbance alters ecosystem engineering by a canopy-forming alga. Journal of the Marine Biological Association of the United Kingdom 98: 687–698. https://doi.org/10.1017/S0025315416002009.

R Core Team, 2023. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria [retrieved from https://www.R-project.org/].

Ramus, A. P., B. R. Silliman, M. S. Thomsen & Z. T. Long, 2017. An invasive foundation species enhances multifunctionality in a coastal ecosystem. Proceedings of the National Academy of Sciences 114: 8580–8585. https://doi.org/10.1073/pnas.1700353114.

Raut, S. K., M. S. Rahman & S. K. Samanta, 1992. Influence of temperature on survival, growth and fecundity of the freshwater snail *Indoplanorbis exustus* (Deshayes). Memórias Do Instituto Oswaldo Cruz 87: 15–19. https://doi.org/10.1590/S0074-02761992000100003.

Ravaglioli, C., L. Benedetti-Cecchi, I. Bertocci, E. Maggi, M. Uyà & F. Bulleri, 2022. The role of environmental conditions in regulating long-term dynamics of an invasive seaweed. Biological Invasions 24: 1175–1187. https://doi.org/10.1007/s10530-021-02680-8.

Rohde, K., 2005. Marine Parasitology. CSIRO publishing. Collingwood, Victoria, Australia. https://doi.org/10.1071/9780643093072.

Rueness, J., 2005. Life history and molecular sequences of *Gracilaria vermiculophylla* (Gracilariales, Rhodophyta), a new introduction to European waters. Phycologia 44: 120–128. https://doi.org/10.2216/0031-8884(2005)44[120:LHAMSO]2.0.CO;2.

Ruesink, J. L. & L. Collado-Vides, 2006. Modeling the increase and control of *Caulerpa taxifolia*, an invasive marine macroalga. Biological Invasions 8: 309–325. https://doi.org/10.1007/s10530-004-8060-3.

Sassi, R., M. B. B. Kutner & G. F. Moura, 1988. Studies on the decomposition of drift seaweed from the northeast Brazilian coastal reefs. Hydrobiologia 157: 187–192. https://doi.org/10.1007/BF00006971.

Sastry, A. N., 1971. Effect of temperature on egg capsule deposition in the mud snail *Nassarius obsoletus* (Say). Veliger 13: 339–341.

Sedgwick, P., 2012. Multiple significance tests: the Bonferroni correction. Bmj. https://doi.org/10.1136/bmj.e509.

Seuffert, M. E. & P. R. Martín, 2013. Juvenile growth and survival of the apple snail *Pomacea canaliculata* (*Caenogastropoda*: *Ampullariidae*) reared at different constant temperatures. SpringerPlus 2: 1–5. https://doi.org/10.1186/2193-1801-2-312.

Shanks, A. L., L. K. Rasmuson, J. R. Valley, M. A. Jarvis, C. Salant, D. A. Sutherland, E. I. Lamont, M. A. H. Hainey & R. B. Emlet, 2020. Marine heat waves, climate change, and failed spawning by coastal invertebrates. Limnology and Oceanography 65: 627–636. https://doi.org/10.1002/lno.11331.

Simberloff, D., J. L. Martin, P. Genovesi, V. Maris, D. A. Wardle, J. Aronson, F. Courchamp, B. Gali, E. Garcia-Berthou, M. Pascal, P. Pysek, R. Sousa, E. Tabacchi & M. Vilà, 2013. Impacts of biological invasions: what's what and the way forward. Trends in Ecology and Evolution 28: 58–66. https://doi.org/10.1016/j.tree.2012.07.013.

Sotka, E.E., A.W. Baumgardner, P.M. Bippus, C. Destombe, E.A. Duermit, H. Endo, B.A. Flanagan, M. Kamiya, L.E. Lees, C.J. Murren, M. Nakaoka, S.J. Shainker, A.E. Strand, R. Terada, M. Valero, F. Weinberger & S.A. Krueger-Hadfield, 2018. Combining niche shift and population genetic analyses predicts rapid phenotypic evolution during invasion. Evolutionary Applications 11: 781–793. https://doi.org/10.1111/eva.12592.

Studer, A., D. W. Thieltges & R. Poulin, 2010. Parasites and global warming: net effects of temperature on an intertidal

host–parasite system. Marine Ecology Progress Series 415: 11–22. https://doi.org/10.3354/meps08742.

Sullivan, J. T., T. C. Cheng & K. H. Howland, 1985. Studies on parasitic castration: castration of *Ilyanassa obsoleta* (*Mollusca*: *Gastropoda*) by several marine trematodes. Transactions of the American Microscopical Society 104: 154–171. https://doi.org/10.2307/3226423.

Tepolt, C.K., A.M.H. Blakeslee, A.E. Fowler, J.A. Darling, M.E. Torchin, A.W. Miller & G.M. Ruiz, 2020. Strong genetic structure in a widespread estuarine crab: A test of potential versus realized dispersal. Journal of Biogeography 47: 2532–2542. https://doi.org/10.1111/jbi.13919.

Therneau, T. M. & P. M. Grambsch, 2000. Testing proportional hazards. In: Modeling Survival Data: Extending the Cox Model. Statistics for Biology and Health. Springer, New York, NY. pp. 127–152. https://doi.org/10.1007/978-1-4757-3294-8_6.

Thomsen, M. S., K. J. McGlathery & A. C. Tyler, 2006. Macroalgal distribution patterns in a shallow, soft-bottom lagoon, with emphasis on the nonnative *Gracilaria vermiculophylla* and *Codium fragile*. Estuaries and Coasts 29: 465–473. https://doi.org/10.1007/BF02784994.

Thomsen, M. S., K. J. McGlathery, A. Schwarzschild & B. R. Silliman, 2009. Distribution and ecological role of the non-native macroalga *Gracilaria vermiculophylla* in Virginia salt marshes. Biological Invasions 11: 2303–2316. https://doi.org/10.1007/s10530-008-9417-9.

Thomsen, M. S., 2010. Experimental evidence for positive effects of invasive seaweed on native invertebrates via habitat-formation in a seagrass bed. Aquatic Invasions 5: 341–346. https://doi.org/10.3391/ai.2010.5.4.02.

Thomsen, M. S., T. De Bettignies, T. Wernberg, M. Holmer & B. Debeuf, 2012. Harmful algae are not harmful to everyone. Harmful Algae 16: 74–80. https://doi.org/10.1016/j.hal.2012.01.005.

Thomsen, M. S., P. A. Stæhr, L. Nejrup & D. R. Schiel, 2013. Effects of the invasive macroalgae *Gracilaria vermiculophylla* on two co-occurring foundation species and associated invertebrates. Aquatic Invasions 8: 133–145. https://doi.org/10.3391/ai.2013.8.2.02.

Varela, R., M. de Castro, J. M. Dias & M. Gómez-Gesteira, 2023. Coastal warming under climate change: global, faster and heterogeneous. Science of the Total Environment 886: 164029. https://doi.org/10.1016/j.scitotenv.2023.164029.

Vieira, H. C., A. C. Rodrigues, S. F. Pires, J. M. Oliveira, R. J. Rocha, A. M. Soares & M. D. Bordalo, 2021. Ocean warming may enhance biochemical alterations induced by an invasive seaweed exudate in the mussel *Mytilus galloprovincialis*. Toxics 9: 121. https://doi.org/10.3390/toxics9060121.

Wright, J. T., J. E. Byers, L. P. Koukoumaftsis, P. J. Ralph & P. E. Gribben, 2010. Native species behaviour mitigates the impact of habitat-forming invasive seaweed. Oecologia 163: 527–534. https://doi.org/10.1007/s00442-010-1608-2.

**Publisher's Note** Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.