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ORIGINAL PAPER

Marine heatwaves as selective filters on the behaviour of native and non-native invertebrates

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Abstract Climate change is associated with an increase in heatwave events, extended periods of unusually high temperatures compared to seasonal or local averages. Marine invertebrates may be particularly vulnerable to the effects of heatwaves, especially in transitional waters that support a complex community of native and non-native animals while exhibiting unique physical–chemical characteristics tied to tidal dynamics. Understanding whether and how heatwaves impact wildlife, particularly non-native species, is thus crucial for predicting and mitigating their combined effects on ecosystems. In this study, we experimentally examined the behavioural responses to heatwaves of two Mediterranean nudibranch species: the native *Cratena peregrina* (N = 54) and the non-native *Godiva quadricolor* (N = 76). By applying a within-subject design, we compared the alertness to external stimuli, spatial information gathering, and risk-avoidance behaviour of wild individuals temporarily held in captivity from both species (two populations each) and exposed them to simulated heatwaves (ranging from 18 to 32 °C). Both species exhibited reduced risk aversion as temperature increased, while alertness remained stable. Native individuals decreased spatial information gathering at higher temperatures, whereas non-native individuals sustained consistent levels. These different behavioural responses suggest distinct strategies for coping with thermal stress: non-native individuals maintained high levels of spatial information gathering, likely favouring dispersal, while native individuals adopted energy-conserving behaviours. Our results challenge prevailing assumptions about the resilience of invasive species and underscore the necessity to integrate both short-term behavioural and physiological responses into climate change models that assess the impacts of global warming on biodiversity and ecosystem resilience.

Keywords Heat stress · Climate change · Biological invasions · Spatial information gathering · Transitional environments · Nudibranch · Animal behaviour

Introduction

Global warming is one of the most evident consequences of climate change (Gleckler et al. 2012; Moore and Schindler 2022). By intensifying pressure on both natural and human systems, current levels of global warming are increasing environmental variability, worsening the ongoing biodiversity crisis in both ectothermic and endothermic animals (e.g.

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Hughes 2000; Messina et al. 2025; Corregidor Castro et al. 2025). Aquatic ecosystems are expected to be strongly affected by global warming, particularly through the increase in marine heatwaves' intensity, duration, and frequency in the coming years (Oliver et al. 2021).

Marine heatwaves are defined as prolonged periods of anomalously high sea surface temperatures, i.e. exceeding historical averages (Hobday et al. 2018). The ecological impacts of heatwaves are determined by factors such as their duration, intensity, and the organisms' ability to withstand thermal stress during abrupt environmental changes, leading to mass mortality, shifts in species distributions, and potentially promoting the introduction and establishment of non-native species, ultimately influencing the structure and function of biological communities (Arias-Ortiz et al. 2018; Madeira et al. 2018; Bayne 2017; Hulme 2017; Monteiro et al. 2023; Sanford et al. 2019; Smith et al. 2023; Messina et al. 2025; Corregidor-Castro et al. 2025). These events are typically described on broad spatial scales (e.g. biogeographical provinces or ecoregions), relying on multi-decadal historical baselines of sea surface temperature from open, physically homogeneous marine systems (Hobday et al. 2016). However, such an approach often overlooks the fine-scale and highly dynamic nature of environments such as lagoons, estuaries, and coastal basins, where temperature fluctuations can be more abrupt, less predictable, and strongly modulated by local forcing.

Low thermal inertia environments, such as transitional waters, are particularly vulnerable to rapid temperature fluctuations, and could act as ecological traps due to their quick response to rising temperatures (Vinagre et al. 2018). As such, transitional environments may serve as early indicators of climate change (Madeira et al. 2018, 2012; Vinagre et al. 2018). Strong temperature gradients from tidal cycles favour heat-tolerant individuals, but this adaptation may entail significant energetic costs (Armstrong et al. 2019; Helmuth et al. 2006a, b). Even thermally tolerant species in unstable environments risk exceeding their thermal limits during heat waves extreme temperature fluctuation events, leading to intense selective pressures and the adoption and eventually evolution of adaptive strategies (Lockwood et al. 2010; Somero 2010). Transitional environments are also well-known hot-spots of non-native species (more than 50 species, Boon et al. 2023; Macali et al. 2024), and the combined impact of heat waves and biological invasions can intensify competition and further disrupt the ecological balance (Hulme 2017).

While heat waves and non-native species pose a significant threat to local biodiversity, phenotypic plasticity within populations can boost a certain degree of resilience, increasing the chances of survival in the face of rapid environmental changes. Phenotypic plasticity can facilitate species persistence in their original habitat by reducing the risk of extinction in climate change scenarios (Bonamour et al. 2019). The ability to respond quickly to rapid and unpredictable environmental changes is crucial for the survival of organisms, as is their ability to adapt to continuously changing environments (Lapiedra et al. 2017). Behaviour represents an animal's first line of defence against environmental variation, as it represents the most immediate response compared to other adaptive strategies that an organism can employ (Tuomainen and Candolin 2011). However, not all organisms interact with the social and physical environment in the same way. Non-native species, in particular, tend to display marked behavioural differences compared to native species, often characterized by higher aggression levels, high levels of exploratory behaviour, and low risk-aversion (e.g. Chapple et al. 2012; Macali et al. 2024). This set of traits, which are part of the so-called "invasive syndrome", is thought to facilitate their success in colonizing new habitats, enhancing their spread and competition with local species.

Our study aimed to uncover potential differences in the behavioural responses of Mediterranean native and non-native nudibranchs to thermal stress in transitional environments, thereby providing insights into climate change's evolutionary and ecological implications for biological invasions. Among the organisms inhabiting transitional environments, ectotherms, whose physiology and behaviour are strongly influenced by environmental temperature, are particularly vulnerable to rising temperatures (Collins et al. 2020). Marine molluscs are potentially good models for studying human-induced environmental changes, and the interactions between sources of alteration, for example, biological invasions and climate change (Madeira et al. 2018). In this study, we compared alertness, the ability to quickly respond to disturbances when startled (Macali et al. 2024), spatial

information gathering, and risk aversion of native and non-native nudibranchs experimentally exposed to simulated heat waves. We hypothesised that non-native and native nudibranchs would differ in their response to rising temperatures. We predicted that non-native individuals would show responses consistent with an invasive syndrome, namely higher spatial information gathering and lower risk-aversion at both normal and increased temperatures.

Materials and methods

Animals and housing

The species under study were the non-native *Godiva quadricolor* (Barnard, 1927) and the native *Cratena peregrina* (Gmelin, 1791). *G. quadricolor*, which is native to the southern coastal environments of the Indian Ocean, was introduced to the Mediterranean Sea about twenty years ago (Cervera et al. 2010). It now exhibits a clumped distribution in the Mediterranean region, primarily in transitional environments such as small coastal lakes. *C. peregrina* is a native species of the Mediterranean Sea, where its widespread distribution also encompasses habitats colonized by *G. quadricolor* (e.g., Macali et al. 2024).

We collected individuals of both species on the Tyrrhenian side of the Mediterranean Sea from two different sites per species: the Nassa Channel of Orbetello Lake (Italy, Tuscany, Orbetello (GR); 42°25′59″'N-11°09′30″'E, hereafter referred to as site NAT1) (N = 30) and the Miseno Lake channel (Italy, Campania, Bacoli (NA); 40°47′33″N 14°04′39″E, hereafter referred to as site NAT2) (N = 24) for *C. peregrina*, as well as Torrefumo Lake (Italy, Campania, Bacoli (NA); 40°47′20″N 14°03′17″E, hereafter referred to as site NON-NAT1) (N = 40) and the Roman Channel of Sabaudia Lake (Italy, Lazio, Sabaudia (LT); 41°14′50″N-13°02′16″E, hereafter referred to as site NON-NAT2) (N = 36) for *G. quadricolor*. Considering the tendency of *G. quadricolor* to prey on other nudibranchs, including *C. peregrina*, and to avoid any predatory effects on the behaviour of the native species, we selected sampling sites where the two species were not in syntopy.

Immediately after sampling, the animals were placed in individual plastic jars within a thermally insulated container to prevent temperature fluctuations and were oxygenated using an oxygenation pump. They were then transported to the Ichthyogenic Experimental Marine Centre of the University of Tuscia (CISMAR), where the experiments took place. Here, each individual was photographed on a Petri dish positioned on graph paper for length measurement (from the centre of the head to the tip of the tail). Each animal was given a unique identifier and housed individually in 10 × 10 cm trays that floated in two identical 1000 l tanks filled with aerated seawater (salinity 35 ‰), initially maintained at 18 °C. One tank served as the "Control group," while the other was designated as the "Heat-wave group" (Table 1). Both groups were kept under the same salinity and photoperiod conditions. Individuals of both species were randomly assigned to each group. Animals were fed daily: *C. peregrina* with *Eudendrium* sp. and *G. quadricolor* with *Mytilus* sp. The experimental phase began after a 5-day acclimatization period.

Experimental setup

To accurately inform the experimental conditions, we relied on a fine-scale, site-specific temperature dataset (described in detail in the Appendix, Fig. 4). This approach allowed us to reproduce thermal patterns closely aligned with the actual environmental conditions experienced by organisms in transitional coastal

Table 1 Experimental group composition for 54 individuals of native *C. peregrina* and 76 individuals of non-native *G. quadricolor*

Species	Classification	Sampling code	Sampling site	N. ind. in Control group	N. ind. in Heat-wave group
C. peregrina	native	NAT1	Orbetello lake	4	20
		NAT2	Miseno lake	10	20
G. quadricolor	non-native	NON-NAT1	Torrefumo lake	10	30
		NON-NAT2	Sabaudia lake	10	26

systems, typically overlooked by broad-scale marine heatwave definitions.

Initially, all animals were acclimated to a water temperature of 18 °C for five days. Then, in the "Heat-wave group", the water temperature was gradually increased to 27 °C in the course of 24 h using two 300-W heaters, which was maintained for three days. The temperature was subsequently raised to 32 °C for another 24 h during an additional three days. The entire experiment lasted a total of 11 days (Fig. 1). Throughout the same period, the control group was maintained at a constant temperature of 18 °C. Throughout the experimental period, we measured a number of behavioural responses related to spatial information gathering, risk aversion, and alertness to external stimuli, while also monitoring morphometric parameters associated with health status as well as the mortality rate for each group.

Behavioural assays

Individuals were tested multiple times: at the same baseline temperature for animals in the "Control group", and multiple times at different temperatures in the case of the animals included in the "Heat-wave group" (twice per each temperature). Overall, every individual was tested for a total of six times (Fig. 1). Replicates (i.e. tests of the same individual at the same temperature) were carried out with a one-day interval to minimize manipulation stress. In each replicate, three behavioural assays were performed consecutively without interruptions: "Locomotion measurement," "Spontaneous behaviour," and "Response to disturbance", described in detail below. Animals were removed from their floating containers using a 50 mL Falcon tube and individually transferred into separate glass bowls—90 mm in diameter for the native species and 150 mm for the non-native species. These diameters were selected to be approximately three times the average body length of the species. The bowls were positioned under a GoPro Hero 11 camera mounted on a tripod. The cameras were operated remotely to avoid influencing the animals. We monitored eight individuals at a time. After a 15-min acclimatization period, behavioural observations began. At the end of the test, each animal was returned to its housing tray.

Locomotion measurement

The "Locomotion measurement" was designed to observe the animals' movement in undisturbed conditions within the experimental arenas. Such movement behaviour reflects their propensity to gather information from the environment, find a shelter, locate food, and seek mates (Harvey et al. 2022; Smith et al. 2023). During heat waves, behavioural changes could compromise these abilities, increasing their vulnerability to predation and negatively impacting overall health and fitness.

We collected data on the distance (m) swam by each individual, average speed (m/s), and the percentage of time spent near the tank's edge (thigmotaxis) (Table 2). Thigmotaxis is a proxy for risk-aversion propensity because it quantifies the time spent near protective structures, thereby aiding in the identification of shelters and reducing exposure to predators, and also a propensity to escape from dangers (Macali et al. 2024). Video recordings were made in time-lapse mode, capturing one frame every 5 s over a

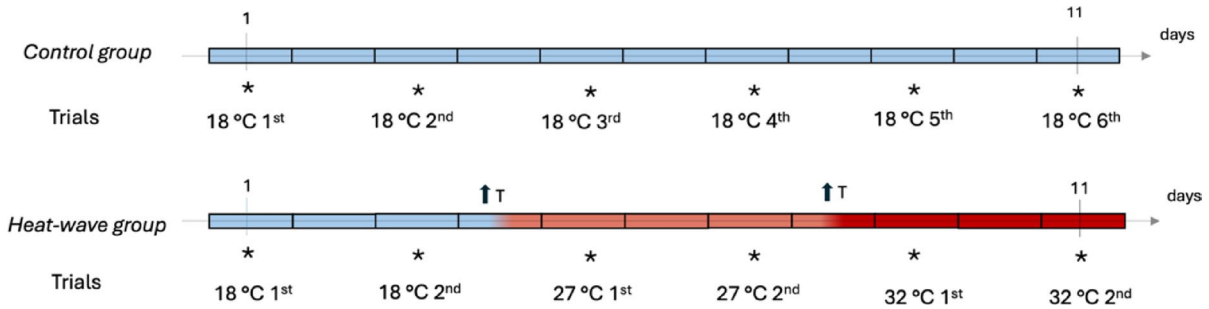

Fig. 1 Timeline of behavioural tests for the Control and Heat-wave groups. Asterisks (*) indicate the days on which photographs were taken for morphometric measurements

Table 2 Summary of the behavioural tests conducted in the study and the parameters measured for each test for 54 individuals of native *C. peregrina* and 76 individuals of non-native *G. quadricolor*

Tests	Time	Behaviours	Operational definition	Unit
Locomotion measurement	1 h	*Distance*	Total distance travelled by the animal during the test	m
		Average speed	Average speed at which the animal moved during the test	m/s
		Thigmotaxis	Percentage of time spent near the tank's edge	%
Spontaneous behaviour	5 min	*Crawling*	Movement along the tank	s
		Folding	Animal curls into a U-shape	frequency
		Rearing	The animal lifts the front part of its body off the substrate	frequency
		Veering	The animal changes direction by 180 degrees	frequency
Response to disturbance	5 min	*Cerata extension*	The animals extends its cerata outwards	s

60-min recording period. The images collected were compiled into a 30-s video at a frame rate of 24 fps and analysed using Tracker Video Analysis and Modelling Tools v. 6.1.1 (Open-Source Physics; available at https://physlets.org/tracker/). The software calibration was based on graph paper placed beneath the glass tank. We tracked the animals point by point, following the movement of their heads, which allowed us to extrapolate the distance travelled by each individual. The average speed was calculated by dividing the total distance by a time conversion factor of 120, reflecting the 24 × time-lapse speedup at 1 frame per 5 s.

Spontaneous behaviour and response to disturbance

The test consisted of two distinct phases. In the pre-stimulus phase, we video-recorded and quantified the frequency and duration of the following behaviours while the animal remained undisturbed for 5 min (24fps) (Table 2): (i) crawling along the tank, which relates to gathering of environmental information, foraging, and seeking shelter; (ii) folding, in which the animal curls into a U-shape as a defensive measure against predators; (iii) rearing, where the animal lifts the front part of its body off the substrate, indicating a response to harmful stimuli; (iv) veering, when the animal changes direction by 180 degrees.

In the second phase, we analysed how a threatening stimulus affected the studied species under varying temperature conditions to further assess the impact of heat waves on behavioural responses to potential threats. Immediately after the conclusion of the first test, we simulated a disturbance by gently applying a soft plastic stick (10 × 3 × 0.1 mm) to the median dorsal region of the animal. We then filmed for 5 min after the stimulation, measuring (v) the time taken for the cerata to return to their relaxed state (Table 2). We only considered this variable in this phase since preliminary analyses showed that none of the other behaviours were affected by the stimulus. Aeolid nudibranchs use cerata as a defensive mechanism against predators (Aguado and Marin 2007; Faulkner 2020). These structures exhibit active movement and extension in response to various stimuli, which have been proven to be a reliable behavioural endpoint for measuring attentiveness to external stimuli (Macali et al. 2024). To quantify all behavioural variables listed in Table 2, we employed the Behavioural Observation Research Interactive Software (BORIS) (Friard and Gamba 2016).

Mortality rate and morphometric parameters

We monitored the variation in body length and mortality rates of the nudibranchs throughout the experimental phase to evaluate their physiological capacity to respond to heat waves. We also carried out daily measurements of the animal's body length. The photographs used to assess the body length of the animals were analysed using ImageJ software v 1.53 (Abràmoff 2004). Given the observed body length reduction in the experimental "Heat wave group", we calculated the percentage of body shortening during each experimental phase in comparison to the preceding phase using the formula "$shortening = \frac{Length_{\{27°C\}} - Length_{\{18°C\}}}{Length_{\{27°C\}}} \times 100\varepsilon$. This measure will be referred to as shortening henceforth. At the

beginning of each test day, any deceased individuals were removed from the experimental setup.

Statistical analyses

All statistical analyses were conducted using R software (The R Foundation for Statistical Computing, version 4.4.0). The accepted significance level was ≤ 0.05.

Behavioural analysis

We conducted a Principal Component Analysis (PCA) to reduce the dimensionality of the behavioural data and identify the primary components that explained most of the observed variance. The PCA was performed using an *oblimin* rotation along with the '*psych*' package (Revelle and Revelle 2015). To evaluate the adequacy of the data for PCA, we performed the Kaiser–Meyer–Olkin (KMO) test (0.56) and Bartlett's test of sphericity ($X^2 = 565.5$; $p < 0.001$) and calculated the determinant of the correlation matrix (0.39) (Field 2024), identifying the principal components that accounted for the variance). The components derived from the PCA were used in the subsequent steps of the analysis.

In a second step, we investigated whether heatwaves triggered different behavioural responses between the native and the non-native species. We fitted restricted maximum-likelihood linear mixed-effect models (LMM, R package '*lme4*'(Bates et al. 2014) with each of the three PCA components as dependent variable, body length, group ("Control group" vs "Heat-wave group"), trial, and the interaction between species and temperature as fixed factors. Since animals were tested multiple times (twice per temperature in Heat-wave group and six times at the same temperature for the Control group), we added individual identity nested within sampling site as random factor. Analyses were first performed on the whole dataset; when the interaction between species and temperature was significant, we ran post-hoc analyses on subsets of data including only one species at a time, with each PCA component as the dependent variable, body length, group ("Control group" vs "Heat-wave group"), trial, and temperature as fixed factors, and individual identity nested within sampling site as random effect. When the interaction between temperature and species was not significant, the effects of the individual fixed variables were analysed separately using Tukey post-hoc tests with '*emmeans*' function from the R package '*rstatix*' (Kassambara 2023). Visual inspection of residual plots did not reveal any obvious deviations from homoscedasticity or normality.

Mortality rate and morphometric parameters

First, we compared the reduction in body length of the animals in the "Heat-wave group" and the "Control group" with a t-test. We evaluated the impact of temperature on body length variation during the experiment by fitting a linear mixed-effects model (LMM) that included an interaction between the fixed factors, temperature and species, along with the random factors trial number and individual identity nested within the sampling site. The analysis was performed using the "*lmer*" function from the R package '*lme4*' (Bates et al. 2014). For significant interactions, post-hoc tests were performed on species-specific datasets, using LMMs in which shortening was the dependent variable, temperature was the fixed factor, and individual identity nested within sampling site served as the random effect. A survival analysis was carried out with a Kaplan–Meier curve, using the R packages '*ggplot2*' (Wickham and Wickham 2016), and '*survival*' (Therneau 2020).

Results

Behavioural assays

The PCA identified three main components (TC1, TC2 and TC3, Table 3) that together explained 65% of the variability in the behavioural data. Specifically, the First Component (TC1) accounted for 29.89% of the variation, and was associated with distance moved, crawling, and veering (Fig. 2, Table 3). Since these behavioural variables reflect the amount of exploratory movement in the animal's surroundings, we refer to this component as Spatial information gathering. The Second Component (TC2) explained 20.83% of the variation and was associated with thigmotaxis, folding, and veering (Fig. 2, Table 3). Since these behavioural variables reflect self-protecting tendencies, we refer to this component as Risk aversion. The Third Component

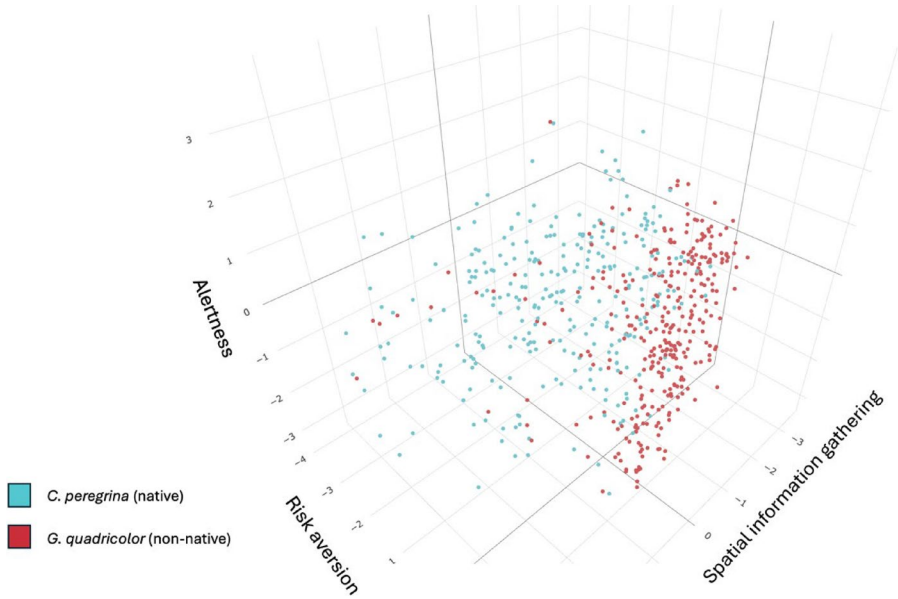

Fig. 2 3D plot illustrating the three principal components, and their relationship to the original variables for the native species *Cratena peregrina (Cp)* and the non-native species *Godiva quadricolor (Gq)*. The first component (TC1) represents spatial information-gathering behaviours, characterized by *distance*, *crawling*, and *veering*, while the second component (TC2) indicates risk-averse behaviours, encompassing *folding*, *veering*, and *thigmotaxis,* and the third component (TC3) characterized by rearing and cerata extension

(TC3) accounted for 14.25% of the variation, and was associated to rearing and cerata extension (Fig. 2, Table 3). These behavioural variables are underscored by the attention given to external stimuli, so we refer to this component as Alertness.

The increase in temperature induced different responses between the native and non-native species regarding spatial information (temperature*species: Sum Sq = 11.63, F = 12.58, $p < 0.001$; Fig. 3; Table A3). Spatial information gathering decreased with rising water temperature in the native species *C. peregrina* (Sum Sq = 3.05, F = 4.43, $p < 0.05$, Fig. 3, Table 4, Table 5), whereas it did not change for the non-native species *G. quadricolor* (Sum Sq = 0.26, F = 0.24, $p = 0.62$) (Fig. 3; Table 4, Table 5). Increasing temperature affected both species similarly in terms of risk aversion (temperature: Sum Sq = 23.896, F = 46.98, $p < 0.001$; Fig. 3; Table 4, Table 5), with all individuals expressing more risk-prone behaviours in warmer water (18 °C-32°C: $\beta = 0.87 \pm 0.12$, $t = 7.35$, $p < 0.001$, Fig. 3, Table 5). Alertness did not change in either species in response to increasing temperatures, although individuals of *G. quadricolor* tended to decrease alertness, while individuals of *C. peregrina* remained stable (temperature*species: Sum Sq = 4.54, F = 5.30, $p = 0.022$; *C. peregrina*: Sum Sq = 0.09, F = 0.09, $p = 0.76$; G. quadricolor: Sum Sq = 2.50, F = 3.16, $p = 0.08$; Fig. 3; Table 5).

Table 3 PCA loadings of behaviours in the Locomotion measurement, Spontaneous behaviour and Response to disturbance tests for 54 individuals of native *C. peregrina* and 76 non-native *G. quadricolor* tested at 18 °C, 27 °C, and 32 °C

Behaviours with significant contributions to each component are highlighted in bold font

	First component (TCI) *Spatial information gathering*	Second component (TCII) *Risk aversion*	Third component (TCIII) *Alertness*
Eigenvalue	2.092	1.458	0.997
Variance explained (%)	29.893	20.832	14.251
Distance (log-transformed)	**0.536**	−0.07	0.131
Thigmotaxis	0.270	**−0.629**	0.252
Crawling	**0.482**	0.356	−0.154
Folding (log-transformed)	−0.356	**0.493**	0.077
Rearing	0.260	0.237	**0.472**
Veering	**0.408**	**0.409**	0.032
Cerata extension (log-transformed)	−0.213	0.07	**0.815**

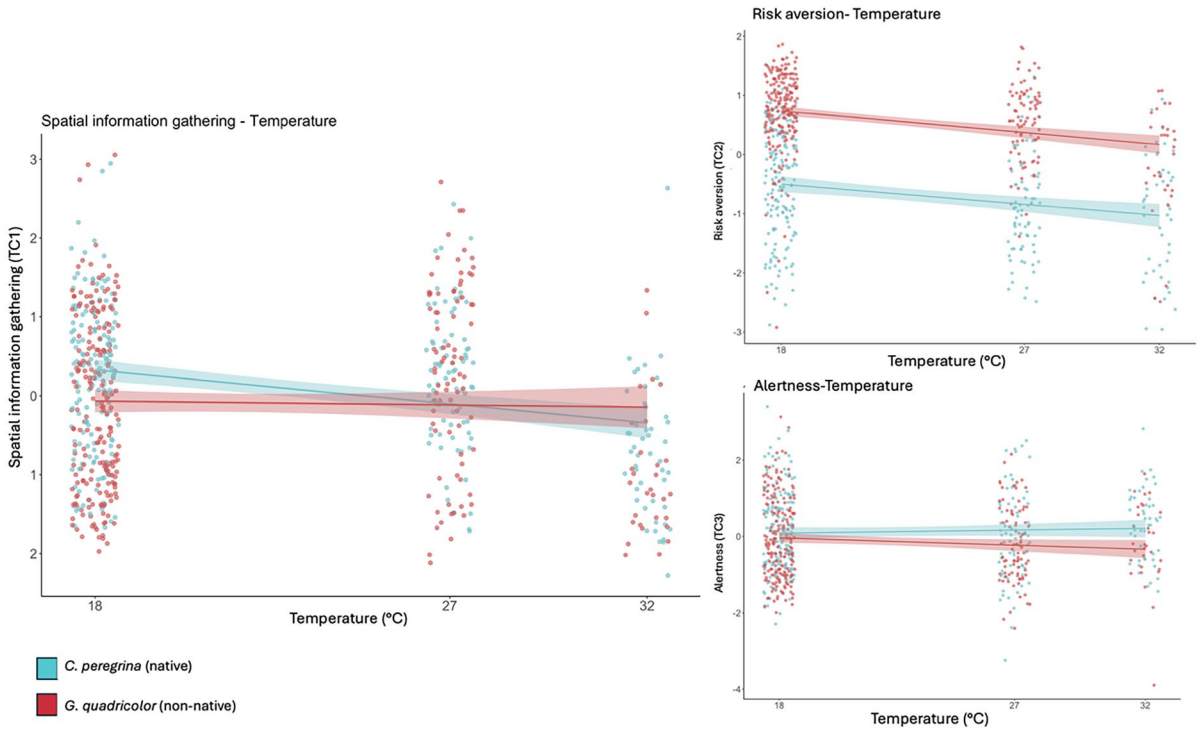

Fig. 3 Relationship between water temperature and spatial information gathering (**a**), risk aversion (**b**), and alertness (**c**) as measured across three behavioural assays for the native species *Cratena peregrina* and the non-native species *Godiva quadricolor*. Shown is the prediction line with 95% confidence band (grey shading) from linear model for visual representation and jittered raw data points for native and non-native species. TC1, TC2 and TC3 stand for the three composite variables obtained through the PCA. Data points are jittered with a width of 0.6

Table 4 Model results for each component identified by the PCA in relation to body length of the individual, experimental group (heat wave vs control), temperature, species, (Cp vs Gq), and the interaction between temperature and species, for individuals of native *C. peregrina* and non-native *G. quadricolor*

	Full model				
	Fixed effects	Sum Sq	df	F	*p*
TC1 (Spatial inf. gathering)	Body length	10.65	208.47	11.50	< 0.001
	Group (C-HW)	0.08	172.13	0.083	0.77
	Temperature	1.72	598.81	18.56	0.17
		20.94	411.95	22.62	**< 0.001**
	Temperature*Species Species (Gq)	11.63	524.47	12.58	**< 0.001**
TC2 (Risk aversion)	Body length	0.743	231.19	1.46	0.22
	Group (C-HW)	2.03	167.03	4.00	0.478
	Temperature	23.90	598.65	46.98	**< 0.001**
	Species (Gq)	9.82	464.40	19.31	**< 0.001**
	Temperature*Species	0.01	578.63	0.015	0.90
TC3 (Alertness)	Body length	1.85	239.43	2.15	0.14
	Group (C-HW)	0.15	157.74	0.17	0.67
	Temperature	1.02	597.92	1.19	0.27
	Species (Gq)	2.84	359.05	3.31	0.06
	Temperature*Species	4.617	535.68	5.38	0.02

P values in bold font indicate the significant effect of the specific predictor and/or interaction on the considered dependent variable

Table 5 (a) Outcomes for both species (native *C. peregrina* and non-native *G. quadricolor*) of the linear model for the rotation score. We performed the analysis only when the interaction between Species and Temperature was statistically significant. (b) Results of the pairwise Tukey-post hoc analysis on the fixed effect significant in full method, we considered body length as a covariate in temperature (as factor) contrast. *P* value in bold font indicate the significant effect of the specific predictor on the considered dependent behavioural variable

(a)		*Cratena peregrina* (native)				*Godiva quadricolor* (non-native)			
	Fixed effects	Sum Sq	df	F	*p*	Sum Sq	df	F	*p*
TC1 (Spatial inf. gathering)	Body length	18.09	278	26.22	< 0.001	2.49	124.82	2.30	0.13
	Group (C-HW)	0.20	278	0.29	0.58	0.22	90.27	0.21	0.64
	Temperature	3.05	278	4.43	< 0.05	0.26	318.57	0.24	0.62
TC3 (Alertness)	Body length	0.19	86.44	0.20	0.65	1.44	139.68	1.82	0.17
	Group (C-HW)	0.15	68.67	0.16	0.68	0.77	88.69	0.97	0.32
	Temperature	0.06	266.22	0.06	0.79	2.71	317.81	3.43	0.06

(b)	Tukey post-hoc tests					
	Contrast	Estimate	SE	df	*t*	*p*
TC2 (Risk aversion)	18–32 °C	0.856	0.11	598	7.212	**< 0.001**

Mortality rate and morphometric parameters

A decrease in body length was observed in the "Heat-wave group" (native: $t = -9.81$, $p < 0.001$; non-native: $t = -5.92$, $p < 0.00$;)Fig. 5), but not in the "Control group" (native: $t = -0.92$, $p = 0.374$; non native: $t = -1.97$, $p = 0.064$; Fig. 5). We also observed a higher mortality in the non-native species compared to the native species (Fig. 6; Table 6), both in the "Control group" (Cp = 7.14%; Gq = 20%) and in the "Heat wave group" (Cp = 57.5%; Gq = 85.71%) (Fig. 6 in the Appendix; Table 6).

Discussion

In this study, we examined the response strategies used by sympatric native and non-native nudibranchs to cope with rapid temperature increases caused by a simulated heat wave. Neither species showed changes in alertness; while both displayed decreased risk-aversion as temperatures rose. Further, non-native individuals maintained high levels of spatial information gathering despite the rising thermal stress, while native individuals gradually reduced it. These contrasting strategies may allow

Table 6 Number of dead animals throughout the experiment for each of the experimental groups Heatwaves and Control. The columns refer to the temperature and the trial number (e.g., 18 1st = 18 degrees, 1st trial)

Specie	Classification	Sampling site	Control group					
			18_1st	18_2nd	18_3rd	18_4th	18_5th	18_6th
C. peregrina	Native	NAT1	0	0	0	0	0	0
		NAT2	0	0	1	0	0	0
G. quadricolor	Non-native	NON-NAT1	0	2	1	0	0	0
		NON-NAT2	0	0	0	0	1	0
Specie	Classification	Sampling site	Heatwave group					
			18_1st	18_2nd	27_1st	27_2nd	32_1st	32_2nd
C. peregrina	Native	NAT1	0	1	0	1	3	4
		NAT2	0	0	0	1	4	9
G. quadricolor	Non-native	NON-NAT1	0	2	5	12	7	4
		NON-NAT2	0	1	0	2	5	10

both species to cope with short-term heat stress, though with different survival outcomes. The general expectation regarding species loss due to heatwaves often indicates thermotolerance, while frequently overlooking species' capacity for behavioural adaptation to thermal stress. Although heatwaves are expected to drive population declines (Wernberg et al. 2013; Oliver et al. 2017; Garrabou et al. 2009; Gillanders et al. 2011), even closely related species can exhibit highly divergent responses to heat stress (Leung et al. 2019).

When considering the interplay between biological invasion and global warming, native species are generally assumed to be more vulnerable to extreme temperatures than non-native species (e.g., Smale et al. 2019; He et al. 2022; Raymond et al. 2022; Ma et al. 2023). However, while some non-native species thrive under elevated temperatures, others show greater vulnerability than their native counterparts. Non-native bivalves such as *Corbicula fluminea* and *Dreissena polymorpha* exhibit life-history traits that favour dispersal and rapid colonization of new environments, but face higher mortality under prolonged heat stress compared to sympatric native species due to metabolic constrains (McMahon 2002). Similarly, non-native freshwater snails (*Pomacea canaliculata*) and fish like *Oncorhynchus mykiss* experience substantial physiological stress and reduced acclimation abilities under extreme temperatures (Seuffert and Martin 2017; Myrick and Cech 2000). Conversely, native species that have evolved in thermally-variable environments often exhibit more effective thermoregulatory behaviours that enhance their ability to avoid thermal stress (Schulte 2015). These findings suggest that, despite the common belief in greater resilience, not all non-native species could gain advantages under extreme thermal conditions. Physiological limitations and maladaptive behavioural responses may hinder their success during increasingly frequent marine heatwaves, potentially allowing native species to maintain a competitive edge in certain ecosystems. Although these general patterns offer a broad framework for understanding how species respond to heat stress, direct experimental evidence is essential to assess how specific populations react under controlled conditions.

Behavioural trade-offs and heat stress

At 18°C, non-native nudibranchs showed lower spatial information gathering and higher risk aversion than native individuals, possibly indicating an earlier colonization strategy that prioritized habitat assessment over risk-prone behaviours (e.g. Eccard et al. 2023). This strategy could later facilitate the emergence of distinct behavioural phenotypes that are better suited to high-density environments and intraspecific competition (Grabowska et al. 2019). While the invasive syndrome theory typically predicts high levels of aggressiveness and low risk aversion in established populations, it often overlooks the initial stages of colonization, which can be extremely rapid (e.g., Perkins et al. 2013). This entails a lack of accurate information about the traits expressed by pioneers in earlier stages, which are generally characterized by behavioural phenotypes that favour cautious behaviour (e.g., Myles-Gonzalez et al. 2015; Lapiedra et al. 2018). Unfortunately, the precise arrival dates for the populations we studied remain unknown, although their presence at one sampling site has been reported since 2008 (Macali et al. 2013). It cannot be ruled out that the extreme environmental variability of these habitats, such as seasonal salinity fluctuations, has caused periodic local extinctions and recolonizations, challenging the assumption that these populations are recent arrivals.

During the simulated heatwave, both species showed decreased risk aversion. This change in behaviour may serve as an adaptive strategy to manage increased physiological stress under extreme temperatures. Elevated temperatures impose significant metabolic costs, potentially leading individuals to prioritize immediate thermoregulatory needs. Among ectotherms, thermal stress increases activity and risk-taking behaviours, possibly to secure resources or alleviate physiological strain (Killen et al. 2012; Ebbesson and Braithwaite 2012; Culumber 2020; Gutierrez et al. 2023; Messina et al. 2025). Animals often face behavioural trade-offs between thermoregulation and predation risk (Glass et al. 2021; White et al. 2020; Pereira and Vitule 2019; Mameri et al. 2020; Spence-Jones et al. 2025). When physiological adaptations fall short of coping with heat waves, behavioural responses can become crucial in mitigating thermal stress (Leung et al. 2019), as individuals reallocate resources based on modified risk

perception (Sokolova et al. 2012). Our findings suggest that the two species adopted different information gathering strategies in response to environmental stress. Non-native nudibranchs engaged in proactive information-seeking behaviours, while native species relied on more energy conserving responses. These differences likely stem from their evolutionary histories and the selective pressures they have encountered. Non-native species colonizing new habitats experience strong selection for exploratory traits (Shine 2011), which provide adaptive advantages in dynamic environments (Chapple et al. 2012; Macali et al. 2024). By limiting their movements, native nudibranchs seem to cope better with simulated extreme heat, as evidenced by their higher survival rates. Minimizing metabolic costs may be the most effective approach for native species, allowing them to tolerate heat stress while waiting for the cooler waters to return with the next high tide (Stillman and Somero 2000). This strategy has been observed in various intertidal organisms, where reduced movement during thermal extremes helps lower metabolic demands and ultimately enhances survival rates (Helmuth et al. 2006a, b; Denny et al. 2009; Miller et al. 2014). However, it cannot be ruled out that the higher mortality rate observed in the non-native species may not solely stem from the increased energetic costs associated with continuous spatial information gathering, but rather from the inefficacy of this behaviour in mitigating thermal stress. In our experimental set-up, since animals were in captivity, they were not able to employ successfully an escape strategy to find better conditions. In the wild, this could be indeed the best solution for non-native individuals that possibly are not equipped to face the extreme change in temperature, or not equipped in the same way as native ones. Transitional environments, characterized by steep ecological gradients and abrupt physico-chemical fluctuations, provide a selective landscape in which behavioural strategies such as spatial information gathering can significantly influence population persistence and establishment success (Macali et al. 2024). In these highly dynamic systems, species exposed to strong selective pressures may develop phenotypic traits that enhance their ability to cope with thermal stress, facilitating population expansion even amid the increasing frequency of extreme heatwaves. Increased spatial information gathering could allow individuals to locate thermally favourable microhabitats, enhancing survival and overall resilience. Thus, the ability to adjust behavioural responses dynamically to sudden environmental changes may serve as a key mechanism for the persistence and range expansion of non-indigenous species in the context of ongoing climate change. Further investigations testing whether populations of the same species inhabiting more thermally stable environments show reduced behavioural plasticity compared to those in transitional habitats are recommended. Additionally, comparative analyses of native and non-native species across multiple transitional ecosystems may provide deeper insights into the role of environmental variability in shaping behavioural adaptation and invasion success.

Implications for climate change resilience

As climate change exacerbates the frequency and intensity of extreme thermal events, understanding the interplay between species-specific behavioural and physiological responses will be crucial in predicting future shifts in community structure within transitional ecosystems. While several phylogeographic studies have inferred range expansions in nudibranchs based on larval dispersal (King et al. 2019), our understanding of how adult individuals respond to rapid climatic fluctuations remains limited. Previous studies mainly captured long-term trends rather than short-term responses of benthic adults. Only a few studies have explored how adult nudibranchs react to acute environmental stressors like marine heatwaves (Armstrong et al. 2019), with a negative correlation between baseline thermal tolerance and plasticity, suggesting limited adaptability to sudden temperature increases in some species. Organisms typically react to abiotic changes over much shorter timeframes than the longer evolutionary scales often considered in climate change projections. These responses can occur within hours (Hofmann and Todgham 2010) or even several months through acclimatization (Pörtner, 2002), reflecting the critical role of rapid adaptive responses for survival. Marine heatwaves place significant and unpredictable pressure on populations and communities, reshaping them on much shorter timescales than traditionally expected, underscoring the need to better integrate short-term behavioural and physiological responses into climate change models (Harvey et al. 2022).

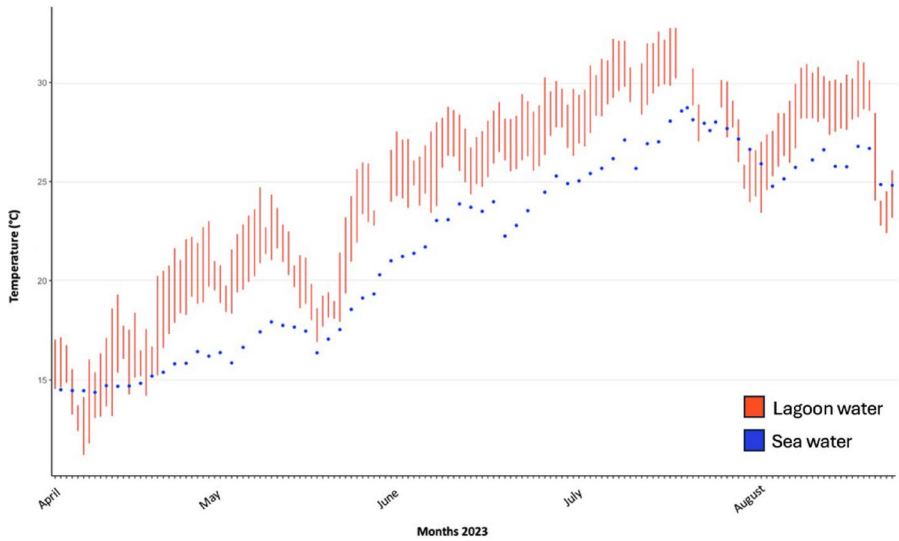

Fig. 4 Red lines: daily water temperature (°C) recorded at NAT1 (Orbetello Lagoon); blue dots: sea temperature measured 1 km outside of the channel connecting the lagoon to the marine environment (data from https://www.esa.int/Applications/Observing_the_Earth/Copernicus)

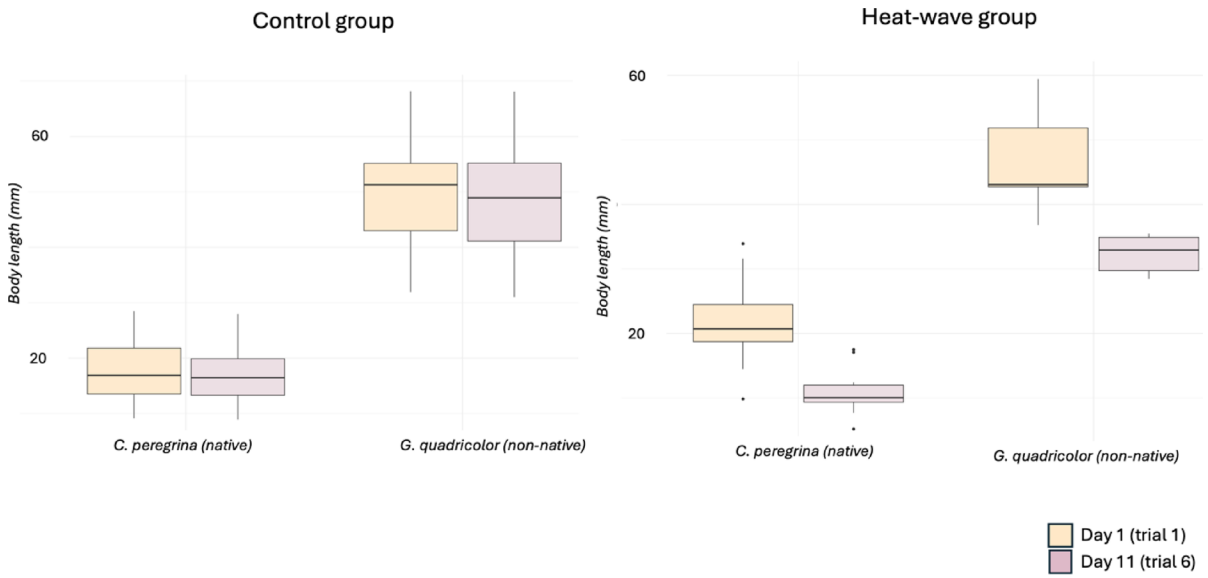

Fig. 5 Boxplot showing the variation in body length during the experimental phase. Body length is reported for day 1 (beige) and day 11 (violet) for both native *C. peregrina* and non-native *G. quadricolor* across the control and heat wave groups

Our results emphasize the importance of quantitatively examining biogeographic patterns in environmental variables at scales relevant to organisms and forecasting the impacts of climate change across species ranges. While physiological adaptation alone may not fully mitigate the effects of acute thermal stress, our results highlight the central role of behavioural strategies, particularly those related to information gathering and risk perception, in helping organisms to cope with extreme conditions. These behavioural responses—such as seeking cooler habitats or reducing activity—complement physiological processes and represent a critical component of an organism's survival toolkit. Our findings suggest that, especially for non-native species, behavioural traits, such as spatial information gathering and risk

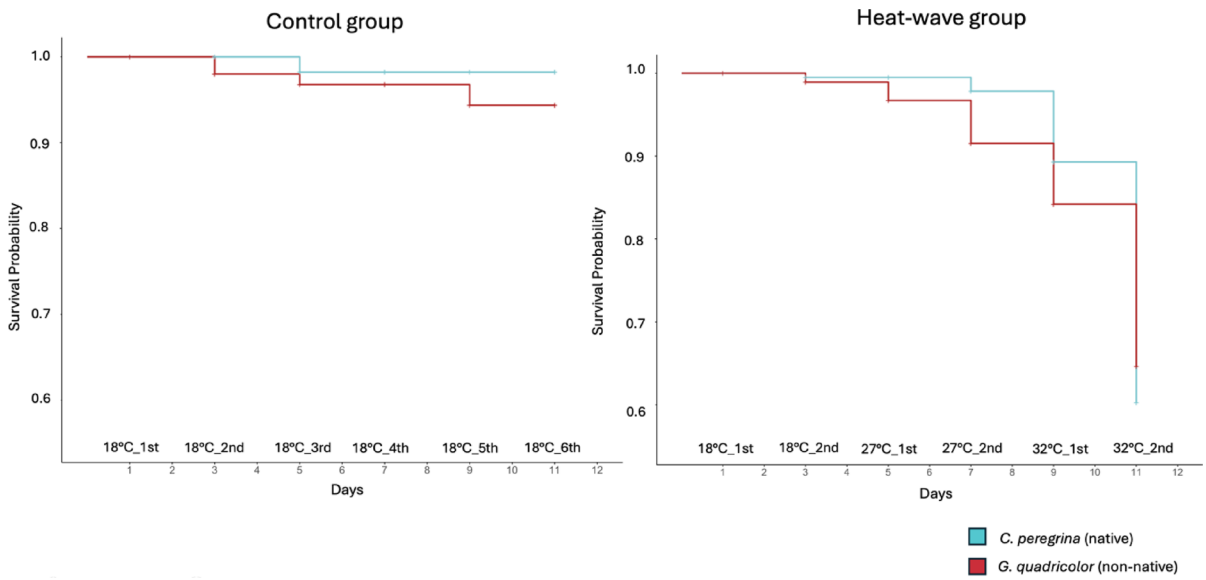

Fig. 6 Kaplan–Meier survival rate graphic plot for the four different group tested for both species. In light blue *C. peregrina* (native) and in red *G.quadricolor* (non-native)

avoidance are extremely important in novel or disturbed environments, while native species may adopt more conservative, energy-saving strategies that help them cope with predictable environmental fluctuations. By highlighting the interaction between these adaptive processes, we provide insights into how species may cope with the challenges of climate change and how transitional environments can act as critical hotspots for studying evolutionary and ecological responses, enabling species to thrive in increasingly unpredictable and extreme conditions.

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Declarations

Conflict of interest The authors declare no conflict of interest.

Appendix

Identification of suitable experimental temperatures

To replicate the temperature conditions experienced by Mediterranean nudibranchs, we monitored temperature data from the National Environmental Protection Agency (ARPA) for our sampling site NAT1 and the adjacent portion of the sea during the period

from April to August 2023, when both species were present. We calculated the temperature differences between the lagoon and the sea at the same time of day to determine the shifts experienced by organisms inhabiting the connecting channel during tidal oscillations. During high tide, they were exposed to colder seawater (21.5 °C ± SD), while during low tide, they remained in warmer lagoon waters (25.8 °C ± SD) (Fig. 4). We selected 18 °C as the control temperature, which corresponds to the temperature recorded at the time of sampling at NAT1, NAT2, and INV2. The experimental temperatures included 27 °C, which was the average environmental temperature typically experienced by the organisms during summer high tides, and 32 °C, the maximum recorded temperature in the lagoon, as the highest experimental condition (Figs. 4, 5, 6, Tables 3, 4, 5, 6).

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