Science of the Total Environment 806 (2022) 150943

Contents lists available at ScienceDirect

Science of the Total Environment

journal homepage: www.elsevier.com/locate/scitotenv

Evolutionary constraints on physiology confound range shift predictions of two nacellid limpets

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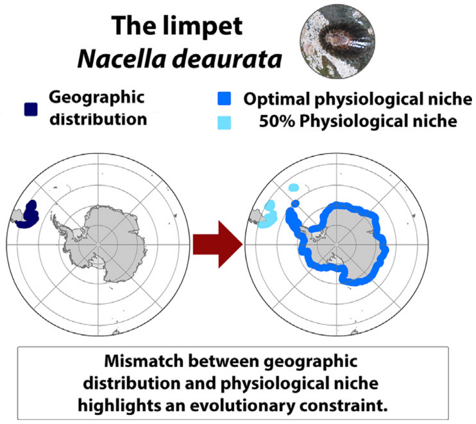
HIGHLIGHTS

- Thermal physiological tolerances of *N. deaurata* were mismatched to experienced environment.
- A cold climate legacy makes *N. deaurata* vulnerable to climate change.
- *N. deaurata* physiology suggests it is suited to "invade" the Southern Ocean.
- This study shows how evolutionary constraints can confound macrophysiological expectations.

GRAPHICAL ABSTRACT



ARTICLE INFO

Article history:
Received 27 May 2021
Received in revised form 8 October 2021
Accepted 8 October 2021
Available online 14 October 2021

Editor: Rafael Mateo Soria

Keywords:
Evolutionary constraint
Niche conservation
Cold climate legacy
Macrophysiology
Climate transitions
Redistribution

ABSTRACT

Physiological comparisons are fundamental to quantitative assessments of the capacity of species to persist within their current distribution and to predict their rates of redistribution in response to climate change. Yet, the degree to which physiological traits are conserved through evolutionary history may fundamentally constrain the capacity for species to adapt and shift their geographic range. Taxa that straddle major climate transitions provide the opportunity to test the mechanisms underlying evolutionary constraints and how such constraints may influence range shift predictions. Here we focus on two abundant and shallow water nacellid limpets which have representative species on either side of the Polar front. We test the thermal thresholds of the Southern Patagonian limpet, *Nacella deaurata* and show that its optimal temperatures for growth (4 °C), activity (-1.2 to -0.2 °C) and survival (1 to 8 °C) are mismatched to its currently experienced annual sea surface temperature range (5.9 to 10 °C). Comparisons with the congeneric Antarctic limpet, *N. concinna*, reveal an evolutionary constraint on *N. deaurata* physiology, with overlapping thermal capacities, suggesting that a cold climate legacy has been maintained through the evolution of these species. These physiological assessments predict that the South American range of *N. deaurata* will likely decline with continued warming. It is, however, one of the first species with demonstrated physiological capacity to successfully colonize the cold Southern Ocean. With the expected increase in opportunities for transport within high southern latitudes, *N. deaurata* has the potential to establish and drive ecological change within the shallow Southern Ocean.

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https://doi.org/10.1016/j.scitotenv.2021.150943

1. Introduction

One of the greatest challenges of our time is to successfully predict future patterns of biodiversity in the face of climate change (Pennisi, 2005; IPCC, 2021). Physiological studies have emerged as powerful tools for predicting changes in species geographic distributions, highlighting species capacities to persist within their current range and their predicted rates of redistribution through climate matching (Sunday et al., 2012; Burrows et al., 2019). Clear macrophysiological principles have been described that underlie the evolution of physiological capacity across latitude, altitude and depth zones (Gaston et al., 2009; Spicer et al., 2019).

The ability to predict the redistribution of species is particularly important for oceanic regions that have been historically isolated by climate transitions, such as by the steep temperature gradients, often caused by transitions between water masses and currents (Hayden and Dolan, 1976). Our study focuses on one of the earth's major climate transitions, between South America and the Southern Ocean. Ectotherms within the Southern Ocean have evolved narrow, stenothermal, physiologies that allow them to cope with the constant cold but have limited heat tolerance, making them vulnerable to predicted rates of warming (e.g. Somero, 2010; Peck, 2015). These cold physiologies are expected to be absent from species that have evolved north of the Polar front with broader physiological tolerance (eurythermal), which will act as a barrier to colonisation of the Southern Ocean by non-native species. The evolution of thermal tolerance windows (Sunday et al., 2012) and the rate of warming will therefore determine the likelihood of species replacing any that are lost due to warming and the maintenance of ecosystem function (Somero, 2010). The opportunities for species to cross these barriers are projected to increase with climate change, as oceanographic barriers weaken (Duffy et al., 2017) and a rise in ship traffic provides additional vectors for transport (McCarthy et al., 2019). This redistribution of species is expected to drive impacts in communities that have been isolated over evolutionary timescales (Duffy et al., 2017; Frenot et al., 2005; Morley et al., 2020).

However, departures from these macrophysiological predictions can occur as physiological capacity is constrained through the evolution of closely related taxa (Bennett et al., 2021), with similar body plans and ecological niches (Angilletta et al., 2002). Representative species on either side of climate transitions, which share a common ancestor, provide fundamental starting points for investigations into key traits that may be constrained. They allow assessment of the degree to which niches are conserved through evolutionary history (Bennett et al., 2021; Wiens et al., 2010) and how these constraints can confound predictions of geographic range shifts. Here we take advantage of a marked climate transition between the nearshore benthic ecosystems of Southern Chile and the Antarctic Peninsula. In both provinces these assemblages are often dominated by closely related species from the Nacellidae family of limpets (Picken, 1980; González-Wevar et al., 2017).

The separation of the South American and Southern Ocean nacellids occurred around 12.5 Ma (million years ago) with a mitochondrial DNA divergence of around 7.0% (González-Wevar et al., 2017). Quaternary radiation of the South American clade of *Nacella* 1 Ma resulted in the evolution of *N. deaurata* (González-Wevar et al., 2017). Since this most recent diversification *N. deaurata* has been subject to 100,000 year glacial cycles that dominated the Earth's climate in the second half of the Pleistocene, repeatedly covering much of the high latitude shallows with ice (Zachos et al., 2001). Ice cover is thought to have forced many species into refugia (Barnes and Kulinsky, 2010, Fernández Iriarte et al., 2020) and the periodicity of these glacial cycles likely drove speciation within shallow water species (González-Wevar et al., 2011).

Here we investigate evolutionary constraints on thermal physiological capacity through a suite of experiments on nacellid limpets. We measure chronic (survival and "scope for growth" over 2 months) and acute (muscle exhaustion through duration tenacity, and feeding activity through radula rasping rates, over weeks) thermal challenges in *N. deaurata*. Through physiological comparisons with published data from the related Antarctic limpet, *N. concinna* (Morley et al., 2012, 2014; Navarro et al., 2020), we test if the physiology of *N. deaurata* is consistent with the expectations based on its currently experienced environment or if there is evidence of a deep-time climate legacy. Through these comparisons we establish the vulnerability of *N. deaurata* within its current range and assess its suitability to establish within a warming Southern Ocean (McCarthy et al., 2019; Cárdenas et al., 2018; Hughes et al., 2020).

2. Methods

2.1. Sampling and collection site

Individuals of the Southern Patagonian limpet (*Nacella deaurata*) were collected by SCUBA divers from the subtidal zone (5 to 10 m deep) or in the intertidal (0.5 m deep) at Punta Carrera, Strait of Magellan, Punta Arenas, Chile (53° 35′ S, 70° 55′ W). Experiments were conducted between November and January. Experimental temperature and salinity conditions were selected to match average summer temperatures recorded by a continuously recording datalogger (STAR ODDI: DST CTD), deployed for 2 years at 10 m depth (August 2016–August 2018) in Faro San Isidro, Magellan Strait (5 km from the collection site of *N. deaurata*). Temperature at this location varied between 5.88 and 9.95 °C, with an annual mean of 7.86 ± 0.16 °C varying between 7.1 and 9.62 °C in summer, with a mean of 8.12 ± °C. Salinity varied between 22.1 and 30.7 psu, with an annual mean of 29.52 ± 0.24 psu. Aquaria were monitored daily, and any moribund limpets were removed each day to monitor mortality rates through time and between aquaria and treatments.

2.2. Scope for growth

Sixty adult limpets were collected with a mean shell length of 35.4 ± 0.2 mm and a mean dry tissue weight of 475.6 ± 16.5 mg. The specimens were transported to the laboratory of the Center FONDAP-IDEAL, Punta Arenas, Chile. To reduce any field or collection differences between individuals, the limpets were randomly distributed into individual 4-liter aquaria for sixty days at 8 °C and 30 psu (similar to summer field conditions), with constant aeration and with a permanent food supply (biofilm grown on glass plates). Half the collection (thirty) of these limpets were used to measure the scope for growth as described below, while the other thirty were exposed to identical treatments and surviving limpets were used to measure mucus production at the end of this experiment (Table 1).

Immediately after this sixty-day period at 8 °C, thirty of these limpets were divided into five temperature treatments (Table 1) for measurement of the scope for growth with 6 individuals per treatment. One treatment (control temperature) was held stable at an endpoint temperature of 8 °C. Treatments with endpoints of 4 and 11 °C were chosen as they span the minimum and maximum sea surface temperature experienced in the Magellanic region. A high temperature of 14 °C was chosen to simulate a future climate scenario in the Magellanic region. Temperature treatments of 1 and 4 °C enabled comparisons with an average current summer sea surface temperature experienced in the shallows on the western Antarctic Peninsula

Table 1
The number of individual *N. deaurata* used in both chronic and acute experiments. For the acute (weeks) experiments each individual was only measured once.

Experiment: parameters	Shore height	Experimental design	Number of individuals
Scope for growth: Ingestion rate Absorption rate Absorption efficiency Oxygen consumption	Subtidal	Chronic – 2 months Each individual was repeat sampled at day 10, 20, 30, 40, 50 and 60.	At day 0: 1 °C (*n* = 6), 4 °C (*n* = 6), 8 °C (n = 6), 11 °C (n = 6), 14 °C (n = 6).
Scope for growth: Mucus Production	Subtidal	Chronic – 2 months Initial *n* = 30. Measured at day 60.	At day 60: 1 °C (n = 5), 4 °C (*n* = 4), 8 °C (*n* = 5), 11 °C (*n* = 3), 14 °C (*n* = 2).
Duration tenacity	Subtidal	Acute – weeks Each field fresh individual was measured once.	-1.1 °C (*n* = 12) 0.1 °C (n = 10) 4.1 °C (*n* = 13) 8.1 °C (*n* = 12) 10.0 °C (n = 12) 12.1 °C (n = 12) 13.2 °C (*n* = 10)
Duration tenacity	Intertidal	Acute – weeks Each field fresh individual was measured once.	-1.0 °C (*n* = 14) 0.3 °C (*n* = 15) 4.1 °C (n = 12) 8.5 °C (n = 12) 12.0 °C (*n* = 9) 14.1 °C (n = 12)
Duration tenacity	Subtidal	Acute – weeks Initial *n* = 60 Individuals were incubated at 8.5 °C for 2 months. Each individual was measured once.	0.1 °C (n = 10) 4.2 °C (n = 10) 8.5 °C (n = 10) 12.3 °C (n = 10) 16 °C (n = 9)
Feeding rate	Subtidal	Acute – weeks Each field fresh individual was measured once.	0.1 °C (n = 16) 3.6 °C (n = 16) 8.2 °C (*n* = 19) 12.6 °C (*n* = 16) 14.2 °C (n = 16)
TOTAL			358

(1 °C) and future projected summer maxima (4 °C). Temperature was either increased or decreased gradually (0.5 °C day^{-1}) from 8 °C, until the endpoint temperatures were reached (1, 4, 11 and 14 °C), and thus each temperature endpoint was reached at different times. These experimental endpoint temperatures were maintained for sixty days during which time physiological measurements were carried out every ten days. In each aquarium, sea water (same temperature and salinity (30 psu)) was partially changed (50%) every two days.

To provide biofilm for the limpets to feed on, three hundred glass plates of 140 × 140 mm were maintained in racks and incubated for twenty five days in a continuous seawater flow system (Marine Research Centre Laredo of the Magellan University) from the Strait of Magellan, which allowed the growth of primary biofilm on each plate. Potential food on these plates was evaluated every ten days by scraping all adhered materials from the upper surfaces of each of five replicate plates per treatment. The collected material was filtered onto pre-weighed Whatman GF/C glass fiber filter, washed with 3% ammonium formate, dried to constant weight, and then ashed at 450 °C for 3 h to calculate the organic matter content.

One glass plate was placed horizontally in the bottom of each 4 L aquaria, one for each limpet, with the biofilm facing upwards. Two plates, in containers without limpets, were run as controls. Biofilm was still visible on the plates after ten days, indicating that food supply was not limiting. Every ten days plates were removed and the material remaining on them was scraped off and analysed as described above to measure remaining biofilm. The organic ingestion rate (OIR) was determined by comparing the organic matter that remained after ten days of grazing with the material that was initially present on the ungrazed plates (control). Final values of organic matter of the control plates (at day 10) were used to correct OIR due to uncontrolled causes, such as loss of materials through physical effects of aeration, or addition due to mucus (Navarro and Chaparro, 2002).

The absorption efficiency (AE) was determined by the gravimetric method (Conover, 1966). For this, we determined the organic fraction of representative samples of the food supplied (i.e. biofilm contained in the glass plates) and of the faeces produced. The faeces produced by each gastropod were collected throughout the experiment and pooled every ten days for analysis. Samples of food and faeces were filtered through pre-ashed, pre-weighed, 25-mm glass fiber filters, rinsed with isotonic ammonium formate to remove the salts, dried to a constant weight at 100 °C, weighed, combusted at 450 °C for 3 h, and weighed again to estimate the organic and inorganic fraction contained in the food and faeces. The absorption rate (AR) was calculated as the product of the absorption efficiency and the organic food intake (Bayne et al., 1985).

Mucus production can represent an additional metabolic expense due to locomotion activity in gastropods (Navarro and Torrijos, 1995). To estimate the mucus production of *N. deaurata* exposed to 1, 4, 8, 11 and 14 °C an additional 60 day incubated group of limpets were held for two days, one limpet per clean, food free, glass plate. A short period of two days was selected to avoid any effects of prolonged periods of starvation. After this, all the mucus present on the glass plate (*n* = 6) and walls of the aquaria was scraped, filtered through 47 mm Whatman GF/C fiberglass filters (0.45 μm pore size) and dried at 100 °C for 24 h to estimate the dry weight. The filters were subsequently burned for 3 h at 450 °C to determine the organic content of the mucus produced in each experimental treatment. Values for mucus production were expressed as mg d^{-1} and transformed to energy equivalents (1 mg dry mucus corresponds to 6.90 joules (Gonzalez et al., 1990)). Scope for growth was corrected by discounting the mucus produced under each experimental condition.

To estimate the oxygen uptake (MO_2), individuals of *N. deaurata* were placed in glass chambers (140 mL) and immersed in a temperature-controlled water bath for each treatment (1, 4, 8, 11 and 14 °C). Oxygen uptake was measured using a Fiber Optic Oxygen Transmitter (FIBOX 4, PreSens) with pre-calibrated spots for the oxygen sensor (PreSens GmbH, Regensburg, Germany) adhered to the inner wall of the chambers. The oxygen concentration was measured at the beginning and end of the incubation time (2 h), which started 30 min after each limpet had been added to the chamber. Oxygen uptake values were expressed in mL day^{-1} after correcting the respirometer volume for the volume of the limpet. The measurements were made every ten days throughout the experimental period.

The scope for growth (SFG) gives a measure of the energy that is assimilated into organisms and is available for growth, and was calculated following Widdows et al. (1985) as follows.

$$SFG = C - R - F - M$$

Where C = energy consumed in food, R = respiratory costs (oxygen consumption), M = energy transferred to mucus and waste production through F = faeces. Energy lost as ammonia excretion was not measured in this study as it is considered a negligible energy loss (Bayne et al., 1985; Fuentes-Santos et al., 2018; Navarro et al., 2020).

Accordingly, oxygen uptake and absorption rates were converted to energy equivalents: 1 mL of O_2 corresponds to 19.9 J (Elliott and Davison, 1975) and 1 mg of organic food material corresponds to 21 J (McLusky, 1989); 1 mg dry mucus corresponds to 6.90 J (Gonzalez et al., 1990).

2.3. Acute experiments: activity

Subtidal and intertidal *N. deaurata* were collected as detailed above and transported to the Marine Research Centre Laredo of the Magellan University, where they were kept in flow through seawater at ambient temperature and salinity for at least 24 h to recover (see sample sizes in Table 1), but to ensure that their physiology under summer conditions, “field fresh”. For assessments of the thermal reaction norms of activity (temperature limits for duration tenacity and feeding) individuals were then transported in insulated cool boxes to the laboratory of the Center FONDAP-IDEAL where they were transferred to temperature-controlled tanks which were set at ambient temperature of 8 °C. The water in these tanks was heated or cooled to trial temperature by thermocirculators at a rate of 0.2 ± 0.1 °C h^{-1} (to ensure comparability with Morley et al., 2012). Animals were maintained at the experimental temperature for 24 h (Table 1), to allow their physiology to fully adjust, before the start of trials of duration tenacity or rasping rate. As a control for any impact from laboratory incubation under constant thermal temperatures, a further batch of subtidal *N. deaurata* were incubated at 8.5 °C (±0.1 °C) for two months before individuals were ramped to the experimental temperature as described above.

2.4. Thermal reaction norm of duration tenacity

Tenacity, the ability of limpets to clamp down onto the rock and avoid being dislodged by either waves or predators, varies between species and has traditionally been measured as the maximum force that can be resisted (Branch and Marsh, 1978). Measuring tenacity as the time limpets can clamp down onto the floor of the tank, and resist a force applied to dislodge them, allows the capacity for exhaustive muscle exercise to be measured as an assay of thermal tolerance (Morley et al., 2011). Preliminary experiments trialed different weights, which allowed the identification of a suitable force, 304 g for *N. deaurata*, such that most duration tenacity measurements at ambient temperature ranged between 5 and 30 min. This range was chosen so that the same muscle exercise physiology, exercise to exhaustion, was being tested in each species. A fine soft stainless-steel cradle (Leader wire, Bass Pro Shops) was hooked underneath the shell edge, with contact at 4 points around the shell (Grenon and Walker, 1981), before temperatures were changed at a rate of 0.2 ± 0.1 °C h^{-1} as detailed above. To standardise measurements, limpet shells were tapped three times to stimulate a clamping response (Grenon and Walker, 1981), before the weight was attached. 20 kg mono filament fishing wire was hooked to the stainless-steel cradle or cotton loop and passed over two 18KN pulleys (Petzl, France) supported by a retort stand frame. 20 s after the limpet shell was tapped, the weight was hooked to the line and gently lowered until the full force was supported directly above the centre of each limpet. The subsequent time taken for the limpet to be pulled from the substratum was recorded. The thermal reaction norm of duration tenacity of field fresh subtidal and field fresh intertidal *N. deaurata,* as well as subtidal *N. deaurata,* incubated for two months at 8.5 °C were measured (Table 1), with each limpet being used once, for a single measurement.

2.5. Thermal reaction norms for feeding

For feeding trials temperature control was completed in clear Perspex tanks, which allowed feeding to be filmed through the side of the tank (Morley et al., 2014). Individuals were placed on one of the glass plates used to feed limpets in the energy budget studies, which was propped against the wall of the tank. Three sequences of 6–10 radula rasps, with a Microsoft LifeCam Studio HD web camera, were recorded directly onto a computer hard drive using VideoVelocity software from Candy Labs. Each radula rasp starts with the opening of the mouth, followed by a forward stroke of the radula and then closure of the mouth.

Trials at each temperature were run for a maximum of 8 h. This was a compromise to allow enough time for sufficient numbers of individuals to feed (Table 1) while minimising any effect of the difference in exposure time of limpets measured at the beginning and end of this 8 h period to experimental temperatures. After feeding was recorded, the length of each limpet was measured and the limpet was removed (i.e. each limpet was only used once). The duration of each radula rasp was analysed from the time stamped videos and converted into the number of rasps per second.

2.6. Projections

Current (1985 to 2014) and projected future (2070 to 2099) sea surface temperature (SST) datasets were downloaded from the NOAA portal https://www.psl.noaa.gov/ipcc/cmip6/. Datasets were chosen for the 3 warmest months (summer - January-March) and 3 coldest months (winter - July-September). For the projected future datasets, the Shared Socioeconomic Pathway scenario 5-8.5 was selected, using the ensemble spread of the future average of all models.

The distribution of *N. deaurata* (González-Wevar et al., 2017) was mapped onto coastline datasets for the Southern hemisphere, south of 45°S. The summer range in SST was extracted and used to calculate the range of currently experienced summer temperatures. This temperature range was then mapped onto locations predicted in the future summer SST dataset, assuming the species will track the projected change in habitat temperature. The physiological upper temperature limits of *N. deaurata*, both the optimum temperature and the temperature of 50% of maximum were then plotted onto current and future projected sea surface 3 months summer temperatures. The same mapping was completed for the *N. concinna* distribution (error corrected from GBIF, 2021) and physiological limits estimates reported in several papers (Morley et al., 2012, 2014; Navarro et al., 2020).

All distribution calculations and figures were carried out using Esri ArcGIS v10.6 mapping software. Coastline data in the figure is from the Scientific Committee for Antarctic Research Antarctic Digital Databased, accessed November 2020.

2.7. Statistical analysis

The response of scope for growth, metabolic rate and absorption rate to temperature were analysed with repeated measures ANCOVA with individual as a random effect (Minitab 19), to account for the repeated measures on individuals through the duration of the experiment. Temperature, time and the interaction between time and temperature were included as fixed factors. Oxygen consumption rate was natural logarithm transformed to normalize residuals. Visual data inspection of the rasping rate data indicated a Gaussian distribution. Modelling the response with a second order polynomial produced a fit with normally distributed residuals and homogeneous variance across temperatures. Qgam 90% smooth additive quantile regression models were fitted to the duration tenacity data using the R-package qgam (Fasiolo et al., 2020) to allow the temperature at which the 90% upper quantile was a) maximal and b) the temperature at which tenacity was 50% of this quantile, to be calculated.

3. Results

N. deaurata mortality was low at 1, 4 and 8 °C but higher than 50% (of individuals included in each treatment) at temperatures above 8 °C (i.e. 11 and 14 °C; Fig. 1). All limpets died at 14 °C, and thus we do not present results from this treatment. Moreover, high mortality at 11 °C means that the biological responses measured in the small number of survivors must be interpreted with caution.

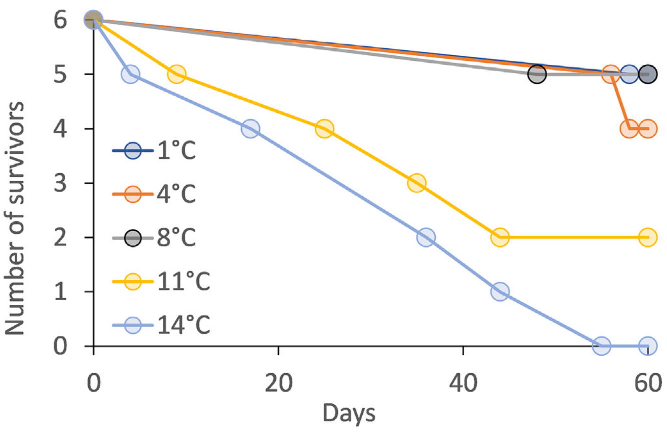

Fig. 1. Survival of *N. deaurata* during the chronic (scope for growth) experiment, excluding those in which mucus production was measured. Data points represent the day when mortality occurred, with an additional point at the end of the experiment, 60 days, representing the number of survivors at the end of the experiment.

N. deaurata mucus production did not vary with temperature, $F_{(1,4)} = 0.39$, $P = 0.58$, and was a small component of the scope for growth, on average 7% (Supplementary Table 1).

At 4 °C, the scope for growth in the subtidal limpet, *N. deaurata*, was positive through the two-month experiment (Fig. 2A, Table 2). At 1, 8 and 11 °C there was a significant reduction in the scope for growth through the duration of the experiment (Fig. 2A, Table 2). This is despite absorption rate being initially higher at 4, 8 and 11 °C than at 1 °C, and was caused by the rate of energy acquisition (here estimated through the absorption rate) reducing markedly though the duration of the experiment at 8 and 11 °C (Fig. 2B, Table 2). This reduction in energy balance at 8 and 11 °C was exacerbated by the increase in both metabolic costs (Fig. 2C, Table 2) and feeding activity (rasping rate; Fig. 3D, Table 2) at temperatures above 4 °C. The rasping rate, increased with temperature up to a maximum inflexion point of 12.4 °C, indicating that energy invested into feeding activity increased to temperatures well above those that were lethal in the chronic experiment.

The temperature of the maximum duration tenacity of *N. deaurata* was very similar, ranging from -1.4 to -0.2 °C, in the three trials (Fig. 3A-C). The temperature for 50% duration tenacity for these groups, which confirms a population-level temperature limit, ranging from 3.4 and 5.0 °C (Fig. 3A-C).

Projections based on the current and future summer SST envelopes (Fig. 4 b, d) predict a range contraction towards Cape Horn, with a shift in northern distribution limit from 50 to 52°S (Fig. 4 e, f). However, most of the measured physiological temperatures, upper limits and optima, for *N. deaurata* were below the minimum winter shallow seawater temperature of 5.9 °C currently experienced in Patagonia (Fig. 5). Indeed, there are no months in which average temperatures correspond to its physiological optima within its current geographic distribution, despite experiments being completed in summer (Fig. 4i, j). Only temperatures corresponding to 50% of the measured physiological performance of adults occur within their present geographic range, and only at the southern edge of its current range. These findings suggest the thermal physiology of this species of limpet is suboptimal within its current range. The physiological limits of *N. deaurata* from Chile overlap those of *N. concinna* from Antarctica (Fig. 5), rather than matching their currently experienced SST range.

Based on warming projections the range of *N. concinna* will likely shift further south, leading to extinction in the shallows at the sub-Antarctic island of South Georgia (54°S) and sub-optimal temperatures within most of its remaining current range. We predict that *N. concinna* will have the physiological capacity to expand its southern range limit from 69 to 78°S (Fig. 4 g, h). We also predict that the geographical extent of habitats providing the physiological optima of *N. concinna* will contract from 63° to 67°S (Fig. 4 k, l).

4. Discussion

The upper thermal limits for *N. deaurata* highlight important departures from macrophysiological expectations that physiological systems will be adapted to their experienced environmental conditions (Sunday et al., 2012; Gaston et al., 2009). The physiological limits measured for *N. deaurata* were mis-matched to its currently experienced environment, suggesting that currently experienced summer maximum temperatures (9-10 °C for the 3 summer months in the Straits of Magellan) are close to the limit for this species. Combined with high mortality at temperatures above 8 °C, our experiments strongly suggest this species has limited capacity to cope with predicted future summer temperatures. *N. deaurata* can, however, survive at temperatures as low as 1 °C, which is 4 °C below the average minimum sea surface temperatures they experience in the winter, even at the southern edge of their range at Cape Horn.

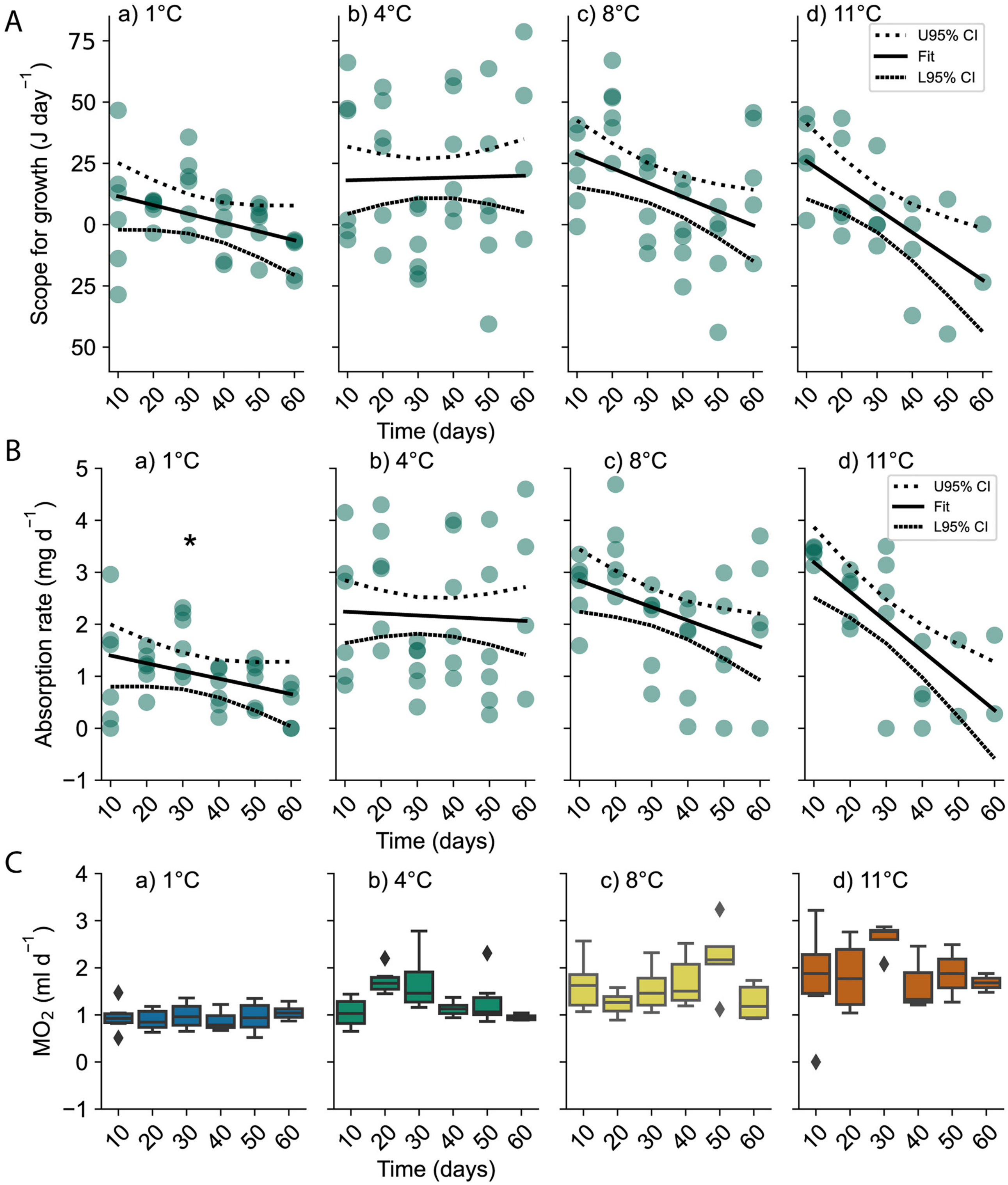

Fig. 2. Physiological temperature limits for the subtidal population of the limpet, *N. deaurata* during energy budget (chronic) experiments A) Scope for growth, B) Absorption rate and C) Oxygen consumption.The asterix (panel B) indicates that the absorption rate at 1 °C was significantly lower than at the higher temperatures. Metabolic rate was significantly lower at 1 °C than at 11 °C (Table 2). Boxes display median and interquartile ranges, the whiskers show the range of the data with diamonds indicating outliers.

This may indicate capacity to survive cold spells, and characterizing the ocean temperature at short time scales may reveal whether these limpets are exposed to colder then average temperatures. Even so, the temperature at which maximum energy was available for growth and reproduction (4 °C) and the optimal temperatures for duration tenacity (3.4 to 5.0 °C) suggests the optimum temperature for *N. deaurata* is also below the minimum sea surface temperatures they experience in the field. Species that have evolved during glacial paleoclimates have lower thermal windows than those with a warmer ancestry (Bennett et al., 2021). *N. deaurata* is an example from cold temperate southern hemisphere latitudes whose physiology matches with expectations of a species that has

Table 2
General Linear Model outputs for scope for growth, absorption rate and natural logarithm of metabolic rate. Analysis of covariance for rasping rate.

Source	DF	Adj SS	Adj MS	F-Value	*P*-Value
Scope for growth					
Time	1	7727	7726.8	15.05	0.000
Individuals	5	5173	1034.7	2.01	0.082
Temperature (°C)	3	2573	857.5	1.67	0.177
Time*Temperature (°C)	3	4502	1500.7	2.92	0.037
Error	113	58,026	513.5		
Total	125	78,326			
Absorption rate					
Time	1	21.88	21.88	21.76	0.000
Individuals	5	8.313	1.663	1.65	0.152
Temperature (°C)	3	17.86	5.955	5.92	0.001
Time*Temperature (°C)	3	11.47	3.824	3.80	0.012
Error	113	113.6	1.006		
Total	125	180.7			
Metabolic rate					
Time	1	0.0122	0.0122	0.13	0.716
Individuals	5	1.706	0.3411	3.72	0.004
Temperature (°C)	3	2.322	0.7741	8.44	0.000
Time*Temperature (°C)	3	0.1781	0.0594	0.65	0.586
Error	111	10.18	0.0917		
Total	123	20.43			
Rasping rate					
Regression	2	1.108	0.5539	52.62	0.000
Temperature^2	1	0.1499	0.1498	14.24	0.000
Temperature	1	0.3869	0.3869	36.75	0.000
Error	80	0.8420	0.0105		
Lack-of-Fit	2	0.0114	0.0057	0.53	0.588
Pure Error	78	0.8307	0.0106		
Total	82				

retained a cold climate legacy (Bennett et al., 2021). The recent glacial history of South America (Zachos et al., 2001) may have prevented *N. deaurata* adapting to the comparatively recent warming in the shallows.

Air temperatures, recorded at the weather station at Punta Arenas (Presidente Carlos Ibáñez del Campo) International airport have a wider range, with an average maximum of 14 °C in January, dropping to an average minimum of -1 °C in July. Thus the intertidal in this region experiences a typically wider range of temperatures than the subtidal, as has been noted elsewhere (Helmuth et al., 2016). Yet intertidal versus subtidal differences in individual thermal optima for duration tenacity were not observed here, indicating that the thermal window for duration tenacity has little scope for adjustment and is relatively well conserved in this species. The speed of evolution of both upper and lower thermal limits is phylogenetically constrained in ectotherms, particularly that of upper thermal limits (Bennett et al., 2021). Yet here we provide an example of a constraint on adjustment of the lower limit. This may be because the depth distribution of *N. deaurata* extends into the low intertidal where extreme low air temperatures experienced during low tide emersion in winter could exert the major evolutionary control over thermal physiology of this species (Bennett et al., 2021).

During glaciations nacellids could have either survived in ice free glacial refugia (Fernández Iriarte et al., 2020), or, as is thought to be the case with many Southern Ocean species, they could have evolved eurybathy, resulting in their capacity to survive over a wide depth range (Brey et al., 1996; Barnes and Kulinsky, 2010). However, there is no evidence of eurybathy in nacellid limpets, which, as grazers on primary production, are ecologically constrained to photic zones, and therefore likely to have survived in refugia (Fernández Iriarte et al., 2020). This is consistent with the thermal physiology measured in *N. deaurata* whose prospects within its current shallow water distribution in southern South America are, therefore, poor.

Our findings reinforce the impact of the physiological mismatch to conditions within the current distribution of *N. deaurata* with markedly different predictions of future distributions derived from physiological limits than those based on SST. Climate envelopes models (CEM) are commonly coupled with projections of future climate change to predict future species distributions (e.g. Griffiths et al., 2017). However, the accuracy of the predictions vary with the type of CEM employed and can be improved through mechanistic models that include species physiological performance (Hijmans and Graham, 2006). While current and future SST envelopes alone do not predict the redistribution of *N. deaurata* into the Southern Ocean (Fig. 4e, f), the physiological optimum temperature range for *N. deaurata* already occurs over much of the coastline of Antarctica, from 60 to 78°S (Fig. 4i). With summer temperatures of 3 °C already experienced during some summers in the shallows of the northern Antarctic Peninsula (Cárdenas et al., 2018), warming projections indicate that much of the western Antarctic Peninsula, as far south as 68°S, will become physiologically sub-optimal for *N. deaurata* by 2100 (Fig. 4j).

Much of the coastline around Antarctica is currently covered in ice. However, if ice retreats with the collapse of ice shelves and shrinkage of glaciers, as has happened on the Antarctic Peninsula (Cook et al., 2016), additional rocky shores will likely become available for colonisation. In fact, optimum temperatures for *N. deaurata* are predicted as far south as 78°S by 2100 suggesting a future range expansion is possible. Vulnerability assessments for polar regions are increasingly considering the potential for range expansion. Indeed, non-native marine invertebrates are periodically reported in the Southern Ocean, most recently on non-native kelp rafts in Deception Island South Shetland Islands (Avila et al., 2020), highlighting potential vectors for redistribution of species, which are predicted to increase in frequency (McCarthy et al., 2019; Cárdenas et al., 2020). A recent colonisation event, settlement of the mussel, *Mytilus* cf. *platensis*, was recorded on the Antarctic Peninsula (Cárdenas et al., 2020). It is yet to be confirmed if this species will become established but this is almost certainly a forerunner of future redistributions into a warming Southern Ocean (McCarthy et al., 2019) with cold-adapted species, such as the nacellid limpet clade from Patagonia being identified here as a likely candidate species to redistribute into the Antarctic. If *N. deaurata* can take advantage of increased opportunities to cross into the Southern Ocean (McCarthy et al., 2019; Hughes et al., 2020) and establish on the Antarctic coastline, these new populations will be direct competitors over much of the current range of *N. concinna* (Fig. 3 i, k). As climate continues to warm the physiological comparisons presented here suggest that *N. deaurata* could have a physiological advantage over much of the western Antarctic Peninsula. While there is no direct evidence that the range of N. deaurata has already retreated southwards, recent phylogenetic studies have reduced the northern range limit of this species on both the east (de Aranzamendi et al., 2009) and west (González-Wevar et al., 2019) coast of South America. Monitoring of limpet populations at their range edges, will be important as a means to test if these predictions from this study are realized in the field. Similar studies of closely related species on either side of other marine climate discontinuities (e.g. Hayden and Dolan, 1976 for the Americas) are required to increase our understanding of the mechanisms underlying these mismatches.

Current winter Southern Ocean temperatures along the Antarctic coastline (−2 to −1 °C; Fig. 4a), along with the low light and low food availability, are likely to limit growth of *N. deaurata* in this highly seasonal environment. Currently, growth of *N. concinna* is limited by food availability in the winter (i.e., reduced algal grazing, Fraser et al., 2002) and most growth occurs in the summer.

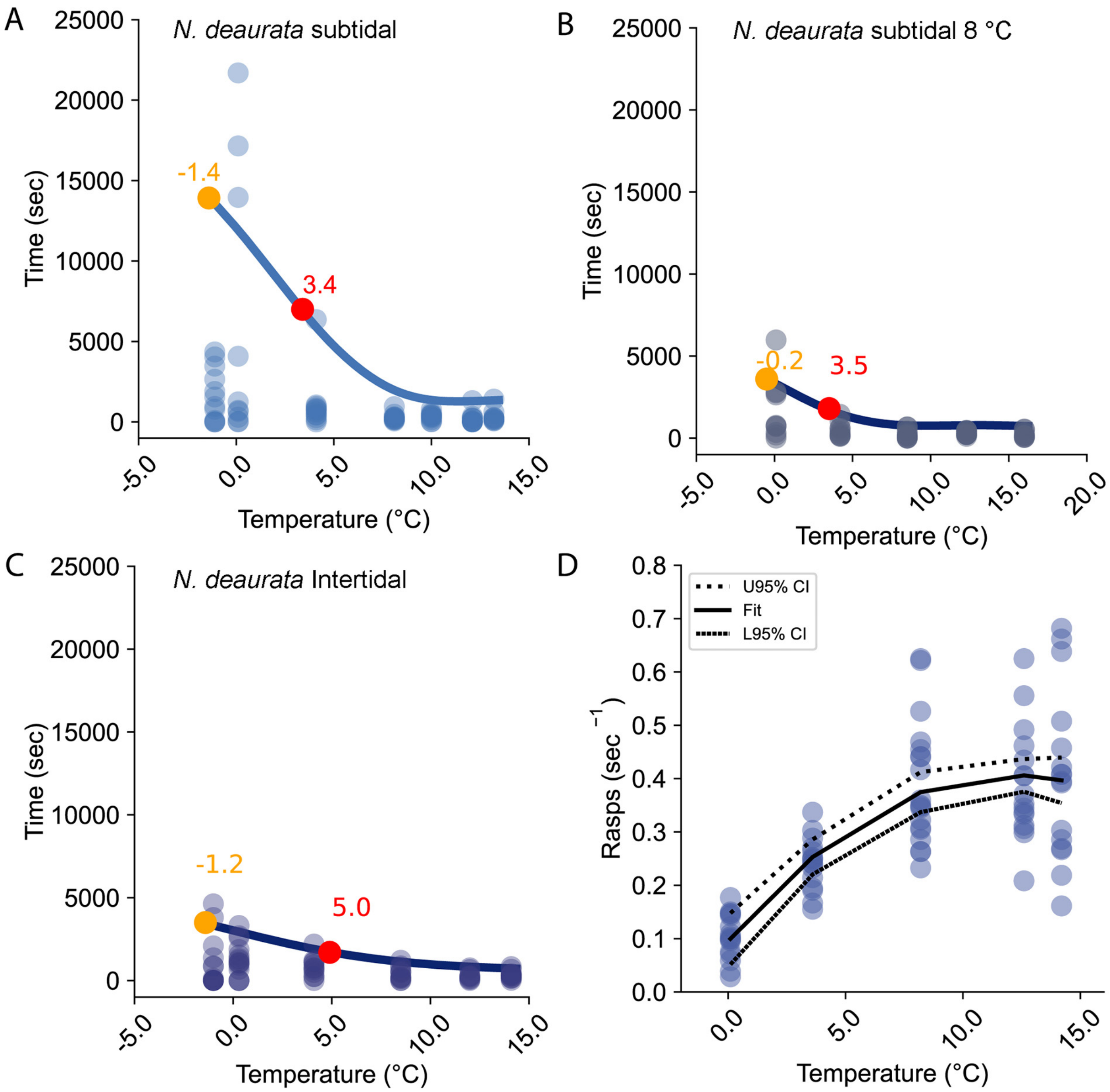

Fig. 3. Thermal responses of duration tenacity of A) field fresh subtidal, B) subtidal incubated at 8 °C for 2 months and C) field fresh intertidal, *N. deaurata*. D) Thermal response of *N. deaurata* radula rasping rate. A-C) The qgam smooth additive 90% quantile regression model fits are plotted. The temperature of maximum (yellow) and 50% tenacity (red) are marked. D) the increase in feeding rate with temperature. Rasps $sec^{-1} = 0.095 - 0.052\ T + 0.0021\ T^2$, where T = temperature (°C) (Table 2), D) qgam smooth additive 90% quantile regression model fit. The temperature of maximum (yellow) and 50% tenacity (red) are labelled.

Increasing summer temperatures over much of *N. concinna's* current range will preferentially favour the growth of N. *deaurata* over *N. concinna* during the crucial summer feeding period.

The abundance of nacellids in Patagonia and the duration of their planktonic larvae (Peck et al., 2016) both suggest that the nacellid family will likely colonize the Antarctic, such as by hitching a ride in ship ballast water or by post-larvae rafting on floating material (McCarthy et al., 2019; Hughes et al., 2020). The majority of the individuals, of both *N. deaurata* and *N. concinna*, are found in surface waters, between 0 and 20 m deep (Picken, 1980; Edgar and Stuart-Smith, 2016; González-Wevar et al., 2019) and they would be direct ecological competitors. The arrival and establishment of new species within Antarctic assemblages will likely alter biological interactions, with little known about the potential effects on communities and the population size of one of the key common shallow water macro-invertebrates, the Antarctic limpet. Further studies on the thermal sensitivity of reproduction, early life history stages, resilience to iceberg disturbance and freezing conditions are required to determine the likelihood of new colonists becoming self-sustaining populations. Clearly other factors than temperature will change with climate and likely affect the distribution of nacellid limpets (see Morley et al., 2020 for summary of Southern Ocean changes). For example, reduced salinity has a strong negative effect on *N. concinna*, and salinity may interact with temperature in constraining the physiological capacity of this species (Navarro et al., 2020).

These detailed physiological comparisons between two nacellid limpets highlight a clear departure from macrophysiological principles (Gaston et al., 2009), with evidence of a cold climate legacy to thermal physiology in this clade (Bennett et al., 2021). Phylogenetic information is commonly included within macrophysiological analyses, to account for evolutionary relatedness and the non-independence of species due to shared body plans (Garland et al., 2005). However, closely related taxa that span sharp climate transitions are potentially important

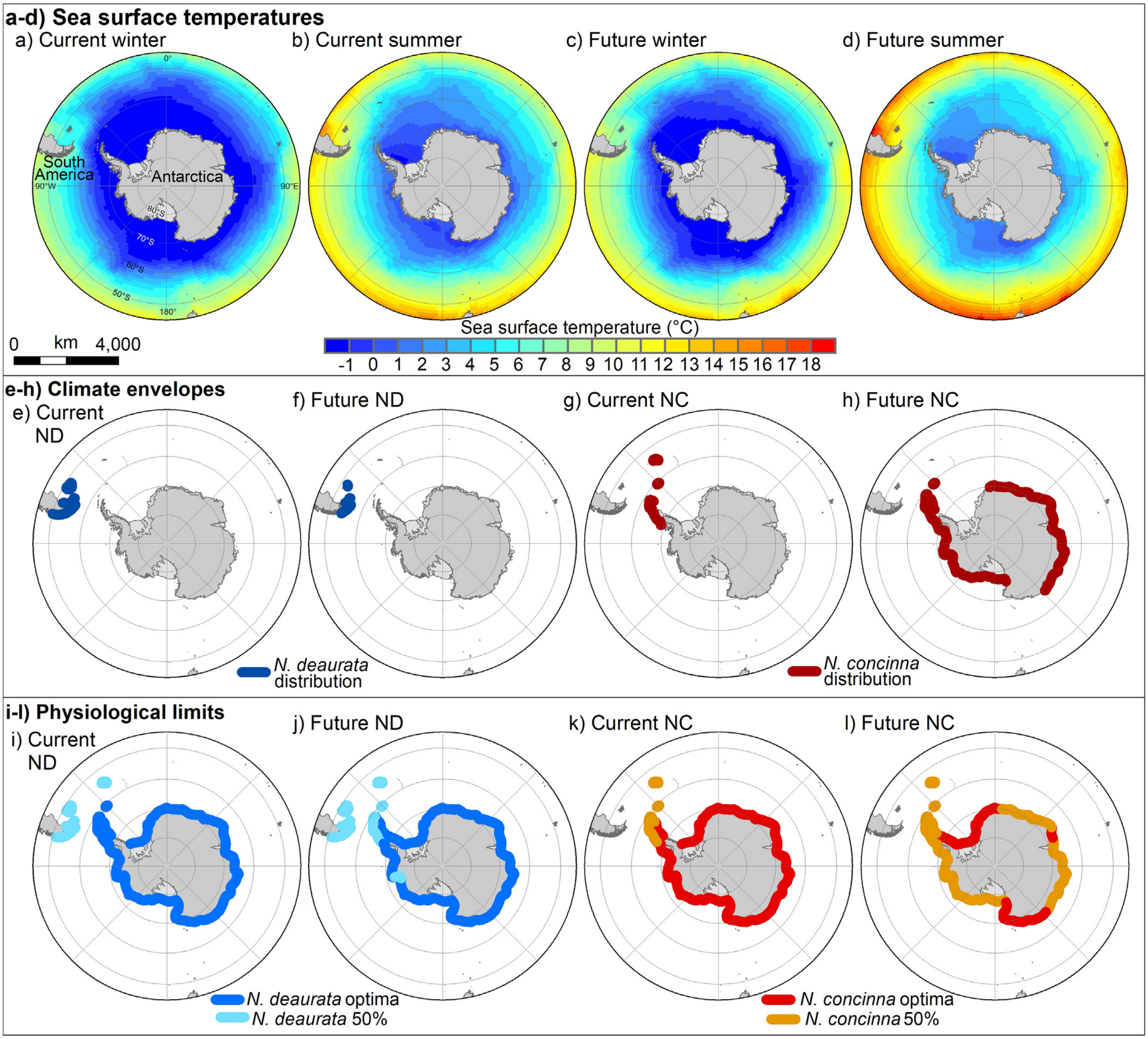

Fig. 4. Current (1985 to 2014) and future projected (2070 to 2099) winter (a, c) and summer (b, d) sea surface temperatures (SST). The current distributions of both the Patagonian (*N. deaurata* – ND) and Antarctic (*N. concinna* – NC) limpets (e, g) (15) and the predicted redistribution of both species if they maintain the same thermal niche (f, h), based on projected future summer SST. The geographical extent of measured optimal and 50% physiological limits for *N. deaurata* (i, j) and *N. concinna* (*k*, *l*), mapped onto current and future summer SST. Coastline downloaded from the SCAR Antarctic Digital Database, accessed November 2020.

models for investigating departures from expectations, as evidenced by this study. Such evolutionary constraints on physiology likely account for much of the unexplained variation in large scale assessments of species vulnerability to warming (e.g. Bennett et al., 2021). The combination of phylogeny, physiology and ecological studies will improve the accuracy of predicted range shifts and inform risk assessments relating to future changes in biodiversity.

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2021.150943.

CRediT authorship contribution statement

Simon A. Morley: Conceptualization, Methodology, Formal analysis, Investigation, Writing – original draft, Data curation. **Jorge M. Navarro:** Conceptualization, Methodology, Writing – review & editing, Funding acquisition, Project administration, Funding acquisition. **Alejandro Ortíz:** Methodology, Investigation, Writing – review & editing. **Camille Détrée:** Investigation, Writing – review & editing. **Laura Gerish:** Formal analysis, Visualization. **Claudio González-Wevar:** Writing – review & editing. **Amanda E. Bates:** Formal analysis, Writing – review & editing, Visualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

SAM was funded by Natural Environment Research Council core funding to the British Antarctic Survey's 'Biodiversity, Evolution and

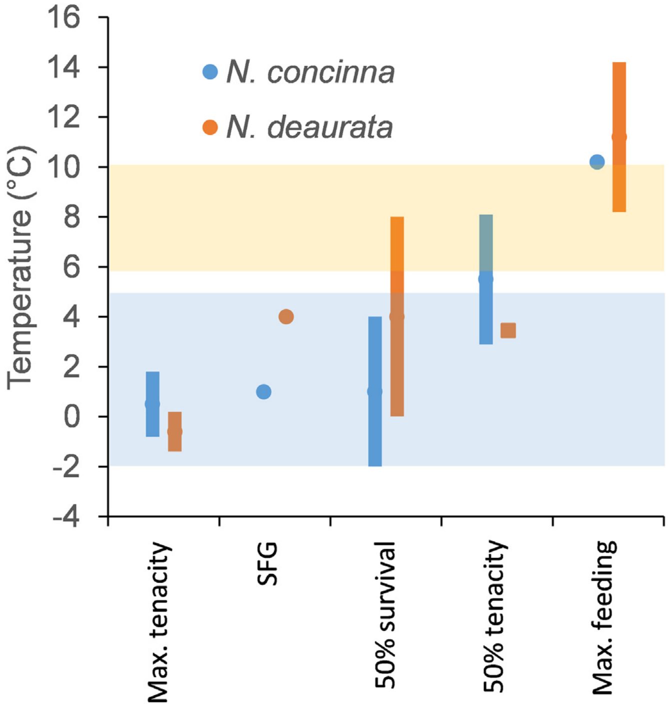

Fig. 5. Comparison of thermal physiological metrics for subtidal Antarctic *N. concinna* and subtidal Chilean *N. deaurata*. Means represent single measures and ranges represent the extremes of multiple measurements of thermal tolerance. Boxes indicate their current annual SST range, blue for *N. concinna* and orange for *N. deaurata*. Data for *N. concinna*: 50% survival and optimum scope for growth (Navarro et al., 2020), duration tenacity (Morley et al., 2012) and rasping rate (Morley et al., 2014).

Adaptation' Team and a Bursary from the Center FONDAP IDEAL 15150003. JMN, AO, and CD were funded by FONDAP-IDEAL 15150003, ANID Chile. We thank Fatemeh Tavafi for expert graphical support.

Data availability statement

The *N. deaurata* data is available at: Morley, S. A., Navarro, J. M., Ortiz, A., Detree, C., Gerrish, L., Gonzalez-Wevar, C., & Bates, A. E. (2021). Thermal physiology of the Patagonian limpet Nacella deaurata (Version 1.0) [Data set]. UK Polar Data Centre, Natural Environment Research Council, UK Research & Innovation. doi:https://doi.org/10.5285/C093EA38-A23D-4669-B88D-462BB49769D2. The *N. concinna* data used for comparison is published in Morley et al., 2012, 2014 and Navarro et al., 2020.

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