ON THE PHYSIOLOGICAL RESPONSES OF FALKLANDS INVERTEBRATES TO OCEAN WARMING: A PRELIMINARY REPORT

PREPARED BY J VAN DER GRIENT, S MORLEY

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VERSION	AUTHOR	DATE
1	Jesse van der Grient	6/3/2024
1	Simon Morley	11/3/2024
1	Al Baylis	11/3/2024
2	Jesse van der Grient	12/3/2024

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For more information, please contact The South Atlantic Environmental Research Institute (SAERI) at: info@saeri.ac.fk or visit www.south-atlantic-research.org

Stanley Cottage North
Ross Road
Stanley
FIQQ 1ZZ
Falkland Islands
+500 27374

Falklands House
14 Broadway
London
SW1H 0BH
United Kingdom
+44 (0)203 745 1731

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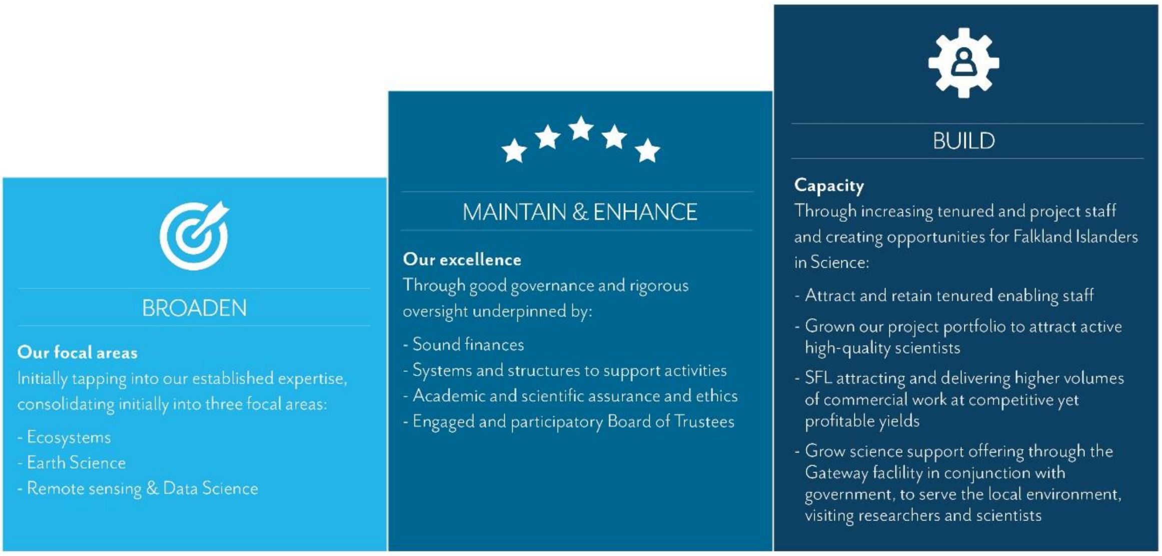

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1. SUMMARY

This preliminary report presents the methodology used in two physiological experiments conducted at Falklands Fish Farming Ltd, in the Falkland Islands. The experiments were carried out to provide an indication of vulnerability and resilience for key inshore animals to ocean warming. The Falkland Islands inshore area may warm in response to increased air temperatures, and increased frequency and intensity of marine heatwaves. The inshore biological community has links to offshore communities via ontogenetic migration, meaning that effects can be spread further. The first experiment details a rate of warming experiment, which used benthic, pelagic, and kelp-associated invertebrates and showed differences in tolerance to marine heatwaves and long-term warming between species and habitats. The second experiment investigated developmental effects of ocean warming for Patagonian squid egg masses, using egg masses from both the autumn and the spring spawning cohorts. The two cohorts differ in their responses to warming, likely reflecting adaptation to their seasonal environmental conditions.

2. INTRODUCTION

The Falkland Islands, an archipelago located on the eastern part of the Patagonian Shelf in the Southwest Atlantic Ocean, is a cold temperate environment. Ontogenetic migrations link inshore environments strongly to offshore areas (van der Grient et al., 2023). The extensive kelp forests around the Falklands coast provides habitat and food for various species, including invertebrates that are important prey for higher trophic-level species. In addition, several species, including those of commercial interest, may use the coastal environment during early parts of their life, while being in offshore areas during the adult life stage (Bayley et al., 2021; van der Grient et al., 2023). For example, Patagonian squid (*Doryteuthis gahi*) use the kelp forest as their spawning ground, but occur in deeper offshore areas as adults (Arkhipkin et al., 2000).

The Falkland Current is a northward flowing current that branches from the Antarctic Circumpolar Current. It brings cold water to the coastal environment around the Islands. The Current is relatively stable in temperature, and has remained cold over the last few decades compared to other areas on the Patagonian Shelf which are warming (Franco et al., 2022). However, while the Current can keep much of the marine environment cold, inshore environments could potentially warm via increased air temperatures and the increased frequency and intensity of marine heatwaves (MHW) (Oliver et al., 2018; Sen Gupta et al., 2020, 2020; Xu et al., 2022).

Changes in water temperature have the potential to affect the inshore animal communities. Biological rates, from biochemical, metabolic and activity rates, are affected by temperature (Brown et al., 2004). These physiological effects of temperatures on the biological rates vary between species, and ultimately mean that the physiological tolerances to ocean warming differ between species (Chown et al., 2009; Mora and Moya, 2006; Peck et al., 2009; Terblanche et al., 2007). The responses to both short-term warming via MHW and long-term warming related to climate change varies between species, and may depend on factors such as mobility, feeding guild, life stage, and habitat.

Here, we report on two experiments conducted using animals that use the Falklands inshore habitat. The experiments are a first of its kind for the Falkland Islands and provide the first data to understand vulnerability to ocean warming for inshore animals. The first experiment represents a rate of warming experiment, which is a dynamic assay where temperatures are raised at a constant rate until the organism collapses, indicating the critical thermal temperature (CT_{max}) (Morley et al., 2014; Peck et al., 2009; Terblanche et al., 2007). Using both fast and slow rates of warming treatments can provide an indication of how tolerant individuals are to MHW and long-term warming, and thus indicate which species are vulnerable and which are more resilient to ocean warming.

The second experiment investigated the change in respiration rate with increased temperature in Patagonian squid egg masses. Respiration rates provide an indication of energy use, as faster respiration is a proxy for higher energy usage. Faster respiration rates during embryonic development means the embryos require more energy as their development progresses. Cephalopods are known to be sensitive to temperature changes, and many factors related to their breeding behaviour are temperature dependent, including number of spawning peaks, recruitment pulses, spawning time, and growth rate (Forsythe, 2004; Moreno et al., 2005; Pecl and Jackson, 2008; Winter and Arkhipkin, 2015). The Patagonian squid has two major spawning peaks within a year, known as the autumn spawning cohort (ASC) and spring spawning cohort (SSC). Generally, these cohorts will experience different temperature conditions as the eggs develop, with the ASC egg masses experiencing the cold winter temperatures, and the SSC egg masses experiencing the warmer spring temperatures. It is no surprise, then, that there are differences in the development time between these two cohorts (table 1). The ASC hatches in early spring, while the SSC hatches in late spring/early summer, when it can develop a lot quicker because of the warmer temperatures (Arkhipkin and Middleton, 2003). Under MHW and/or long-term warming, ocean temperatures can change in any season. This experiment asked whether the response to ocean warming differed between the two cohorts, or whether one cohort may be more sensitive to ocean warming than the other. For example, the SSC may be closer to its thermal optimum, and if so, it will show a stronger negative response to warming than the ASC.

Table 1: Seasonal dynamics of the two spawning cohorts of the Patagonian squid in the Falkland Islands waters. Shading indicates presence in kelp forests. ASC = Autumn spawning cohort; SSC = spring spawning cohort

	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC
ASC	migration	feeding grounds			spawning		egg development		hatching		maturation	migration
SSC	hatching	maturation		migration			feeding grounds			spawning		hatching

3. METHODS

Both types of experiments were conducted at the Falklands Fish Farm (Ltd), owned by Fortuna, located in Moody Brook, East Falkland Islands, which is the only aquacultural facility in the Falklands with flow-through seawater facilities (figure 1). Note that the Falklands have no temperature-controlled facilities for these experiments. During the experiments, daily temperature checks were carried out, and these showed that ambient temperatures in control tanks could vary several degrees, especially during experiments that covered weeks. However, no adverse effects were observed in the control tanks.

Animals for both experiments were collected from the kelp forest or near the kelp forests by SCUBA divers (10-20 m depth), by snorkellers (<2 m depth), or using scoop nets or dredges (lobster krill only). Species collected for the first experiment (rate of warming) included the leaden whelk

(*Pareuthria plumbea*), pink pencil urchin (*Austrocidaris canaliculata*), scythe-edged serolis (*Acanthoserolis schythei*), kelp limpet (*Nacella mytilina*), kelp isopod (*Cassidinopsis emarginata*), kelp bivalve (*Gaimardia trapesina*), and lobster krill (*Grimothea gregaria*; two size classes). These individuals were collected in spring and summer 2022 and are resident (non-migratory) species. Species collected for the second experiment (respiration experiment) included Patagonian squid, for which egg masses from both cohorts were collected in 2023.

Organisms were kept in tanks of 900 litres and experimental tanks were heated by either 2KW PRO-Line titanium heaters (rate of warming experiment) or 650W D-D titanium heater (respiration experiment), controlled by 0.1°C precision digital thermostats. Animals were either kept in the main tank or were placed in smaller containers in the larger tank to avoid predation. The squid egg masses were placed in floating mesh containers with more opportunity for water exchange. See table 2 for the number of individuals used in each experimental treatment.

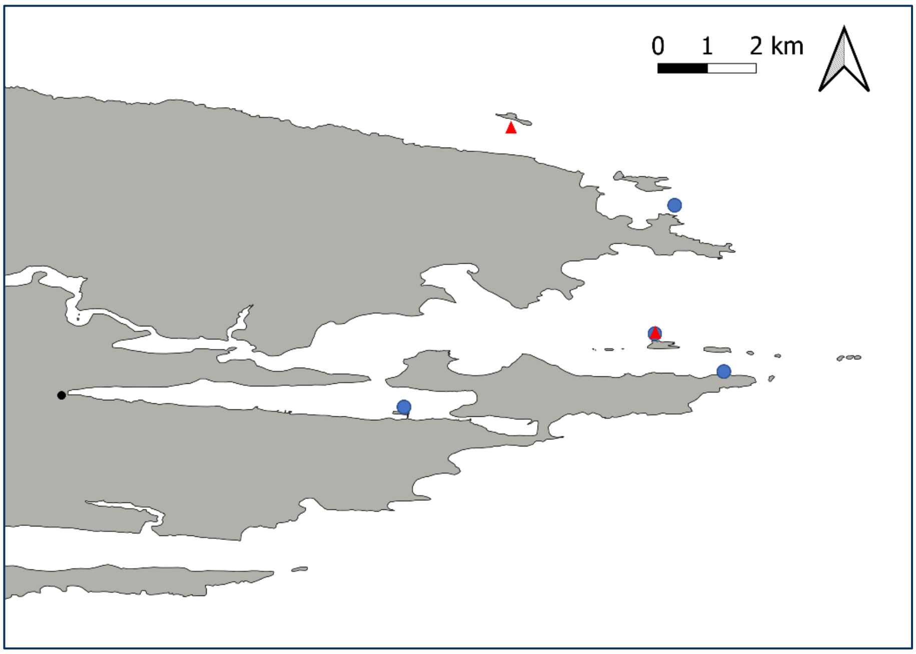

Figure 1. Sample locations for the different experiments (blue circles: rate of warming; red triangles: squid respiration), and Falklands Fish Farming aquacultural facility (black circle), Port William and Berkeley Sound, East Falkland.

During the first experiment, temperatures in the tanks were raised at 1°C hour^{-1}, 1°C day^{-1}, and 1°C week^{-1}. CT_{max} was determined for each individual either via tactile stimuli (*P. plumbea*, *A. schythei*, and *G. gregaria*), or visual observation (*A. canaliculata*, *P. plumbea*, *G. gregaria*, and *A. schythei*), with the lack of response indicating that CT_{max} had been reached. CT_{max} was assessed for each individual either every hour (1°C hour^{-1}), twice a day (1 °C day $^{-1}$) or every day (1 °C week^{-1}). Temperatures were not raised above 30°C. During the second experiment, temperatures were raised by 1°C day^{-1} for three days, followed by two habituation days and then a measurement day, after which the cycle was repeated, until the egg masses finished hatching. Hatching occurred for all eggs tested, regardless of treatment. Measurement involved enclosing the squid egg masses in a closed respiration chamber, which was assessed at regular time intervals for the change in dissolved oxygen concentration in the chamber, until the chamber contained roughly 70% oxygen concentration. The repeated measurements were used to calculate the respiration rate (μmol O_2 h^{-1} g^{-1}) for each egg mass. The time intervals used were dependent on the egg mass size, chamber size, and stage of development, which egg masses close to hatching or hatching respiring much quicker and thus requiring shorter measurement intervals to allow for the calculation of the respiration rate.

Table 2. List of the species included in the experiments, with the number of individuals/egg masses used in each experimental treatment.

Species	Scientific name	Rate/Cohort	N
Small lobster krill	*Grimothea gregaria*	°/hour	15
		°/day	12
		°/week	9
Large lobster krill	*Grimothea gregaria*	°/hour	8
		°/day	8
		°/week	7
Scythe-edge serolis	*Acanthoserolis schythei*	°/hour	7
		°/day	7
		°/week	7
Pink pencil urchin	*Austrocidaris canaliculata*	°/hour	10
		°/day	10
		°/week	7
Kelp limpet	*Nacella mytilina*	°/hour	8
		°/day	8
		°/week	8
Leaden whelk	*Pareuthria plumbea*	°/hour	9
		°/day	8
		°/week	7
Kelp bivalve	*Gaimardia trapesina*	°/hour	13
		°/day	9
		°/week	7
Kelp isopod	*Cassidinopsis emarginata*	°/hour	7
		°/day	5
		°/week	11
Patagonian squid	*Doryteuthis gahi*	ASC	12
		SSC	9

4. RESULTS

Preliminary results are presented here. Statistical analysis is ongoing, and findings will be prepared for submissions to peer-reviewed scientific journals.

Experiment 1

Invertebrates differed in their tolerance to ocean warming for all treatment tested (table 3). Note that the serolid isopod data for the 1°C hour^{-1} is absent as the water was not warmed above 30°C (heaters were limited to 30°C), and the serolid isopods had not reached their CT_{max} yet. Generally, species had higher CT_{max} in the 1°C hour^{-1} compared to the other two experiments, and higher CT_{max} for 1°C day^{-1} compared to 1°C week^{-1}, except for large lobster krill, which showed roughly similar CT_{max} values for each treatment. Serolid isopods had the highest CT_{max} values in the 1°C hour^{-1} treatment (above 30°C), followed by the leaden whelk, while large lobster krill had the lowest CT_{max} values in this treatment. Kelp limpets showed the largest range in CT_{max}, while large lobster krill and leaden whelk showed the smallest range in CT_{max} values in this treatment (5, and 1°C, respectively). Serolid isopods had the highest CT_{max} values in the 1°C day^{-1} treatment, while kelp limpets had the lowest. Pencil urchins showed the largest range in CT_{max} values, while large lobster krill showed the smallest range in this treatment (5.5, and 0.5°C, respectively). Large lobster krill had the highest CT_{max} values in the 1°C week^{-1} experiment, while kelp isopods had the lowest. Both kelp isopods and serolid isopods showed the largest range in CT_{max} values in this experiment (12, and 0°C, respectively).

Table 3. Summary information for each species tested in each of the three rates of warming treatments. Values are in °C. Min = minimum; max = maximum. Empty cells indicate no estimates were obtained here as individuals did not collapse before or at 30°C.

	Hour			Day			Week		
Species	Min	Median	Max	Min	Median	Max	Min	Median	Max
Small lobster krill	25	26	27.5	18	21	22.5	14	16	25
Large lobster krill	23	23	24	22.5	23	23	24	24	24
Pencil urchin	25.5	26	27.5	18	19	23.5	19	20	21
Leaden whelk	29	30	30	21	23	24.5	20	20	21
Kelp bivalve	26.5	28.5	29.5	17.5	19.5	20.5	13	14	15
Kelp isopod	23	24	25	18.5	19.5	19.5	13	13	25
Kelp limpet	25	29	30	16	18	20	13	15.5	20
Serolid isopod				23.5	28.5	28.5	13	19	25

Experiment 2

Squid respiration rate increased with temperature in both ASC and SSC cohorts, and for both treatments (table 4). As there is no temperature-control facility in the Falklands, and daily temperatures varied across the treatment period, and the control tanks also varied slightly in temperature. However, while respiration rates increased with temperature in control tanks, it did so more strongly with time, reflecting the general increase in respiration rate as the squid embryos develop into paralarvae. Generally, respiration rates increased linearly with temperature for the control treatments in both cohorts, and for the treated SSC squid egg mass, but it increased exponentially with temperature in the ASC squid egg masses. This indicates that there are differences in plasticity between the two cohorts, likely reflecting adaptations to seasonal conditions. The variability and trends in the treated squid egg masses for both cohorts indicated that some warming will not result in an increased energy use on average, although it is not known under this experimental design whether this will affect the paralarvae in size or weight, meaning that post-hatching effects could still play a role in terms of transferring ocean warming impacts to the wider food web.

Table 4. Average respiration rates of Patagonian squid egg masses for both cohorts across the two treatments.

Cohort	Date	Treatment	Temperature (°C)	Respiration rate (μmol O_2 $hour^{-1}$ g^{-1})	SD
ASC	01/08/2023	Treated	5.5	0.05	0.04
		Control	6.8	0.08	0.07
	08/08/2023	Treated	5.1	0.08	0.08
		Control	5.1	0.05	0.05
	14/08/2023	Treated	8.6	0.13	0.06
		Control	6.7	0.07	0.03
	20/08/2023	Treated	11.2	0.19	0.05
		Control	6.3	0.12	0.04
	26/08/2023	Treated	14.2	0.18	0.15
		Control	5.1	0.14	0.04
	01/09/2023	Treated	17.3	0.37	0.12
		Control	8.2	0.20	0.07
	07/09/2023	Treated	19.9	0.74	0.10
		Control	6.4	0.22	0.10
	13/09/2023	Control	8.0	0.20	0.07
	19/09/2023	Control	5.1	0.21	0.09
	25/09/2023	Control	7.7	0.25	0.06
	01/10/2023	Control	9.2	0.26	0.06
	07/10/2023	Control	8.1	0.33	0.07
	14/10/2023	Control	8.6	0.37	0.07
	19/10/2023	Control	12.0	0.30	0.03
SSC	26/11/2023	Treated	12.6	0.10	0.05
		Control	12.6	0.13	0.10
	02/12/2023	Treated	14.6	0.25	0.10
		Control	9.3	0.23	0.22
	08/12/2023	Treated	17.6	0.19	0.09
		Control	9.7	0.17	0.08
	14/12/2023	Treated	20.3	0.53	0.33
		Control	10.9	0.38	0.08
	20/12/2023	Treated	23.6	0.35	NA
		Control	14.2	0.44	0.15
	26/12/2023	Control	11.8	0.37	NA
	01/01/2024	Control	11.0	0.34	NA

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SOUTH ATLANTIC
ENVIRONMENTAL
RESEARCH INSTITUTE

www.south-atlantic-research.org
@SAERI_FI

FALKLAND ISLANDS OFFICE
Stanley Cottage North, Stanley, Falkland Islands. FIQQ 1ZZ
Tel: +500 27374 Email: info@saeri.ac.fk

UK REGISTERED OFFICE
Falkland House, 14 Broadway, Westminster, London, United Kingdom, SW1H 0BH
Tel. +44 (0)203 745 1731