

Changes in metabolic rate of spiny lobster under predation risk

Felipe A. Briceño^{1,*}, Elias T. Polymeropoulos¹, Quinn P. Fitzgibbon¹,
Jeffrey M. Dambacher², Gretta T. Pecl¹

¹Institute for Marine and Antarctic Studies (IMAS), University of Tasmania, Hobart, Tasmania 7001, Australia

²CSIRO, GPO Box 1538, Hobart, Tasmania 7001, Australia

ABSTRACT: Animals exposed to high levels of predation risk may exhibit a variety of changes in life history, behaviour, physiology and morphology that can affect survival. Under predation threat, prey individuals may increase their aerobic metabolism to allocate energy toward escaping behaviours (e.g. 'fight or flight'), although the associated energetic cost of such behaviour remains largely unknown. Lobsters display different anti-predatory responses, such as sheltering and/or escaping, but the underlying energetic cost of such responses has not been examined. Here, we tested the aerobic metabolic response of southern rock lobsters *Jasus edwardsii* in the presence of predator (Maori octopus *Octopus maorum*) olfactory cues (kairomones) using open-flow respirometry. We examined the routine metabolic rate of lobsters in response to predator kairomones during the active phase of their diurnal cycle (at night) to investigate the physiological anti-predator response when lobsters are most vulnerable. Our findings revealed that lobsters strongly reduced their routine metabolism for 3 h by 31.4 % when exposed to kairomones in comparison to controls. Our findings suggest that under laboratory conditions, lobsters exposed to predation risk during the night reduce their activity to avoid predators, i.e. the anti-predator mechanism is to be immobile or inactive rather than showing a fight-or-flight response. Lobster immobility may be an energetically advantageous anti-predator response in the short term; however, prolonged or regular predator exposure could have significant consequences on foraging time and foraging area, with an overall impact on lobster performance, particularly in environments with high predator presence such as fishing grounds.

KEY WORDS: Predation risk · Fight-or-flight · Aerobic metabolism · Kairomones · *Jasus edwardsii* · Octopus

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INTRODUCTION

Predation can play a key role in the ecological and evolutionary dynamics of populations, as well as in the structure and dynamics of food webs, communities and ecosystems (Murdoch et al. 2003). Early population ecology theory has generally conceived predation as a functional response (e.g. predator searching for and consuming prey) based on the dynamics of the relative density of the prey population, assuming prey as individuals to be unresponsive entities (e.g. Murdoch & Oaten 1975). Over the

last decades, however, a large body of evidence has suggested that prey is anything but unresponsive (Sih 1985, Lima & Dill 1990, Preisser et al. 2005). Predation risk, or the non-consumptive effects (NCEs), that a predator might exert on its prey, can strongly alter key prey traits such as behaviour, morphology, life history and physiology, exerting selective pressures with evolutionary implications (Lima & Dill 1990, Werner & Peacor 2003, Hawlena & Schmitz 2010, Sheriff & Thaler 2014). These NCEs can have severe, even fatal, impacts on prey (Preisser et al. 2005), affecting prey demography (Zanette et al.

*Corresponding author: fbricenoj@gmail.com

2014), community structure and ecosystem processes (Hawlena & Schmitz 2010, Trussell & Schmitz 2012).

Predation risk can alter organismal physiological nutrient balances by inducing energetically costly stress responses involving hormonal, cellular and metabolic processes (Hawlena & Schmitz 2010). The general paradigm for predation stress responses (reviewed by Hawlena & Schmitz 2010) involves increased levels of glucocorticosteroids (hormonal) and heat shock proteins (cellular) resulting in increased cardiorespiratory activity and aerobic metabolic rate (Slos & Stoks 2008). The increase in aerobic metabolism is associated with the 'fight-or-flight' response (e.g. Slos & Stoks 2008) as a consequence of a redirection of energy to locomotory structures to allow an enhanced ability to escape predators (Hawlena & Schmitz 2010). These stress responses can have substantial consequences for prey at different time scales, from short-term impacts on acute survival, to long-term responses such as inhibition of development and reproduction, slower growth rate, as well as reduced body condition and assimilation efficiency (conversion of food into body tissue) (Hawlena & Schmitz 2010). While our current knowledge of prey stress responses under predation risk mostly comes from terrestrial and freshwater predator–prey systems, very little is known about the physiological response of prey under predation risk in the marine realm (Trussell et al. 2006, Matassa & Trussell 2014).

In activating physiological mechanisms associated with anti-predator responses, prey must first evaluate the level of risk and the benefit of defence (Kats & Dill 1998, Cooke et al. 2003). 'Sensing' for predator risk reduces uncertainty in prey decision-making (Sih 1992), and many animals assess chemical cues from the environment (Kats & Dill 1998) to detect and evade predators (Ferrari et al. 2010). Aquatic crustaceans may rely strongly on water-borne chemicals for assessing predation risk, as is the case for spiny lobsters, which can avoid potential predators by detecting chemical cues from key predators such as octopus (e.g. Berger & Butler 2001, Buscaino et al. 2011, Gristina et al. 2011) or alarm cues from injured or killed conspecifics (Shabani et al. 2008, Briones-Fourzán 2009, Hazlett 2011).

The risk allocation hypothesis suggests that prey adaptively allocate their foraging efforts and therefore their exposure to predation across high-risk and low-risk situations (Lima & Bednekoff 1999). Additionally, the spatial component in such decision-making by prey (e.g. food or shelter) can also involve the selection of areas for foraging (e.g. broad-scale habitat vs. patchy habitat) (Sih 1992). For example, feeding

rates are higher in open habitats compared with patchy areas where refuges are more abundant, although they represent highly dangerous areas with increased predation risk (Sih 1992). In lobsters, sheltering behaviour appears to be an evolutionary trait, with predation risk as one of the most important factors altering shelter occupancy (e.g. Weiss et al. 2008).

Predators can directly interact with fisheries, generating mortality by consuming organisms from the fishing gear during capture, known as 'depredation' (Uhlmann & Broadhurst 2015). Trap- or pot-based fishing activities for lobsters enhance their predation risk because these activities can reduce the lobsters' capacity to escape predators, and the act of fishing can also attract key predators such as octopus. The southern rock lobster *Jasus edwardsii* is highly exposed to predation risk by the Maori octopus *Octopus maorum* on fishing grounds in southern Australia (Brock & Ward 2004, Hunter et al. 2005, Harrington et al. 2006, Briceño et al. 2015, 2016) and New Zealand (Ritchie 1972). Octopus hunting strategy is more effective when lobsters are in confined spaces (e.g. natural shelters) (Bouwma & Herrnkind 2009) and consequently is very successful on individuals confined in fishing traps (Brock & Ward 2004). Additionally, octopus also consume the bait within lobster traps in some fisheries (e.g. South Australia, Brock et al. 2003; South Africa, Groeneveld et al. 2006), demonstrating the habituation of octopus to the lobster fishery. It is presently unclear how octopus abundance and predation activity on the fishing grounds can modify key lobster life history traits such as growth, feeding and reproduction.

High-predation-risk environments can generate chronic stress responses to predation risk, resulting in reduced assimilation efficiency (e.g. Trussell et al. 2006), decreases in production (growth and reproduction) and altered body nutrient content (Hawlena & Schmitz 2010). Examining the energetic cost of responses to predation risk (e.g. Cooke et al. 2003) is therefore a fundamental step in evaluating the stress physiology of lobsters under predation risk. Moreover, quantifying the energetic costs associated with predation will allow a better understanding of how changes in aerobic metabolism affect prey at an individual level (Cooke et al. 2003), and how such changes may be propagated at population level (Zanette et al. 2014).

Spiny lobsters are generally nocturnal foragers, remaining inside their shelter during the day and foraging outside the shelter at night, resulting in a basic circadian pattern in most lobster species (MacDiarmid et al. 1991, Weiss et al. 2008). However, circa-

dian patterns can be modulated by different intrinsic (e.g. mating behaviour and molting cycle, Childress & Jury 2006) and extrinsic factors (e.g. intense sunlight and moon phase, Childress & Jury 2006), with predation risk being one of the most important selective forces in lobster shelter occupancy (Weiss et al. 2008). In some spiny lobsters, elevated predation risk is able to drive diurnal foraging behaviour, shelter choice, and gregariousness (see Loflen & Hovel 2010, Withy-Allen & Hovel 2013, Berriman et al. 2015). Previous research has shown a strong circadian rhythm in lobster metabolic rates which correlates with activity, indicating a strong relationship between behaviour (e.g. movement) and energy expenditure (Crear & Forteach 2000). Understanding of the physiological responses of prey individuals under predation risk requires consideration of the effect of circadian rhythm on metabolic rates, as anti-predator responses can largely differ between day and night in crustaceans (see Sakamoto et al. 2006). Studies on aquatic physiological ecology have played an important role in linking individual-based energetic traits (e.g. metabolic rates) with predator-prey traits (e.g. escaping behaviour), demonstrating how lab-based experimental physiology can assist in addressing ecological questions with implications for fishery and conservation management (Cooke et al. 2013, 2014, Hollins et al. 2018).

In this study, we hypothesized that lobsters under predation risk increase their metabolic rates according to the general stress paradigm (Hawlana & Schmitz 2010). First, we examined how lobster routine metabolic rate (RMR) changes throughout the circadian cycle. This experiment was considered as a baseline to define a suitable period to add kairomones from octopus, taking into account when lobster aerobic metabolism would be highest. We then recreated scenarios of predation risk during the night (high activity, nocturnal scenario) in which lobster RMR was examined under presence and absence of octopus odour or kairomones. The current study represents the first attempt to define aerobic metabolic changes associated with anti-predator responses at individual levels in lobsters.

MATERIALS AND METHODS

Animal collection

A total of 25 inter-moult adult *Jasus edwardsii* were collected in a scientific reserve with an area of approximately 1 km² at Crayfish Point near Hobart in

Tasmania, Australia (42° 57.2' S, 147° 21.2' E). Lobsters were collected with lobster traps in February 2014, and individuals of both sexes measuring up to 110 mm of carapace length (minimal legal size for fishing) were used. In addition, Maori octopus individuals (3–6 kg; n = 3) were collected as by-catch from the same trapping survey. Lobsters and octopus were maintained at the aquaculture facilities of the Institute for Marine Antarctic Studies, University of Tasmania, Hobart, Australia. Lobsters were separated by sex into 2 rectangular tanks (1900 l, 2.22 × 2.05 × 0.93 m) and provided with hollow concrete building blocks (15 tank⁻¹) as shelters. Lobsters were fed with live mussels *Mytilus galloprovincialis* 3 times wk⁻¹ to satiation. Octopus were individually placed in 800 l circular tanks with artificial shelters. Tanks were covered with black mesh to avoid escaping behaviour, and octopus were fed with prawns (*Fenneropenaeus merguensis*) daily to satiation. Lobsters and octopus were kept at ambient temperature (16.5 ± 1°C) and salinity at 35 ± 1‰ with a natural light cycle over 2 wk before starting the experiments. Octopus collection, maintenance and handling were conducted under the University of Tasmania Animal Ethics Committee, permit approval no. A0013584.

Respirometry

The rate of oxygen consumption was measured using an intermittent open-flow respirometry system as described in detail by Jensen et al. (2013a). Two 3.55 l respirometric chambers (radius: 48 mm; length: 480 mm) were immersed in a 455 l tank ('bath') to ensure temperature stability. Each chamber contained an oyster mesh (5 mm mesh size) fitted to the lower section to provide a tractional surface as suggested for crustacean respirometry (Dall 1986). Dissolved oxygen was recorded every 10 s using a luminescent dissolved oxygen optode (Hach LDP, HQ40d, Hach). Two submersible aquarium pumps (Quietone 1200) were connected to each chamber. One pump was used to mix the water inside the chamber and to deliver water past the oxygen optode at a rate of 1.0 exchange min⁻¹ (3.55 l min⁻¹) (closing cycle). The other pump was intermittently exchanging water between the inside of the chamber and the outside of the chamber at a rate of 1.0 exchange min⁻¹ (flushing cycle). A flushing cycle was performed every 10 min using a digital timer (DRT-1, Sentinel). This resulted in measurements of oxygen consumption every 10 min (i.e. 6 measurements h⁻¹) that were averaged to pro-

vide hourly means for analysis. Respirometry chambers were carefully rinsed with fresh water after each trial and sterilized with chlorine after every second trial. During oxygen consumption measurements, oxygen levels never fell below 90% saturation to avoid inducing a hypoxic stress response by the lobsters (Jensen et al. 2013a). Background oxygen consumption was measured in empty chambers after each trial for 2 to 4 h as described by Jensen et al. (2013a). Lobsters were fasted for 72 h before any measurement to generate a similar post-prandial state among individuals (Jensen et al. 2013a). All respirometry trials were undertaken with 2 lobsters that were individually and randomly placed into 1 of the 2 respirometric chambers, with an acclimation period of ~6 h. Data from this period were not included in the analyses.

Circadian pattern in lobster RMR

Changes in RMRs throughout the circadian pattern of lobster activity were measured in inter-moult adults of both sexes ($n = 16$; 514–732 g) under a natural light cycle from 12:12 to 10:14 h of light:dark during March–April (2014). We define the diurnal phase as the time between 06:00 and 18:00 h (twilight), and the nocturnal phase as between 18:00 and 06:00 h (dawn). The circadian pattern of lobster RMR was examined for 24 h, with trials starting approximately at 12 h (noon), with each trial examining 2 lobsters only used once. Trials were undertaken at 16°C ($\pm 1^{\circ}\text{C}$).

RMR was differentiated between night and day as 'RMRn' and 'RMRd', respectively. Additionally, the standard metabolic rate (SMR) was calculated as the mean of the lowest 10% of measured values following Fitzgibbon et al. (2014a).

Lobster routine metabolism under nocturnal predation risk scenarios

The effect of predation risk on lobster routine metabolism during the night was examined using predator odour as a kairomone (inter-species chemical cues). This experiment was

undertaken using exclusively males ($n = 10$; 461–769 g) between June and July 2014. The exclusion of females was due to disparity of the moulting cycle between the sexes (Ziegler et al. 2004), which is accompanied by profound physiological changes (Fitzgibbon et al. 2014b).

Water temperature was maintained at the same temperature as in the circadian pattern experiment ($16 \pm 1^{\circ}\text{C}$) using a titanium heater (2000 W, 8.3 A). Three male octopus (4–6 kg each) were randomly used for the trials; the same individual was not used in consecutive trials. In addition, a red light was used to observe lobsters over the nocturnal periods. These light conditions did not alter the circadian rhythm in other lobster species (e.g. *Panulirus argus*, Weiss et al. 2006), such as has been reported for *in situ* behavioural observations of *J. edwardsii* (Mills et al. 2005).

Experimental system

We used an experimental set-up that consisted of 3 main units (Fig. 1): the conditioning tank (unit A), the

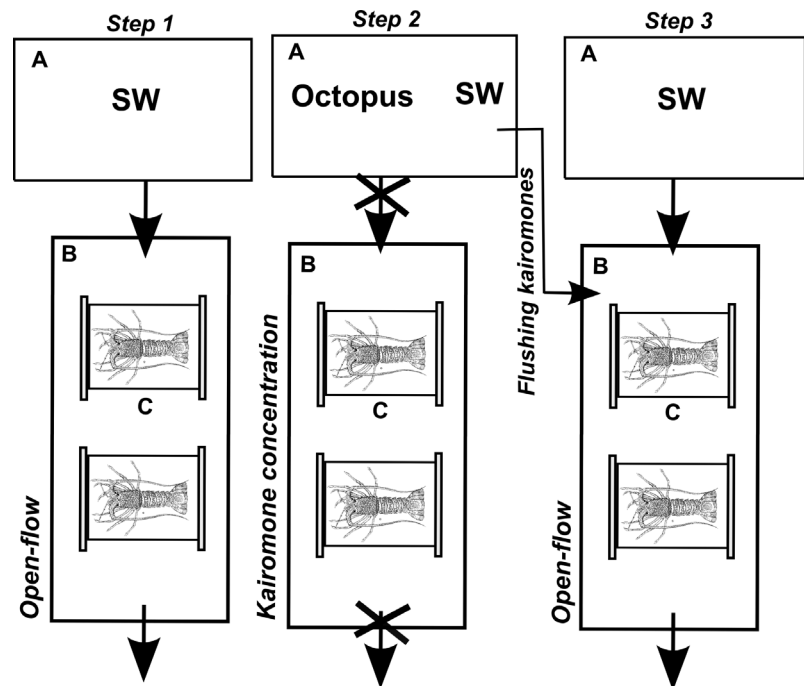


Fig. 1. Protocol to depict nocturnal predation risk scenarios used in *Jasus edwardsii* adult respirometry. The experimental set-up consisted of 3 units: the conditioning tank (A), the treatment tank or 'bath' (B) and the respirometric chambers (C). Units A and B were connected by open-flow circulation of seawater (SW) indicated with black arrows. The protocol was as follows: (Step 1) Two lobsters were acclimated for 6 h in unit C with an open-flow circulation. (Step 2) An octopus was held in unit A for 1 h and the open-flow was stopped over this period. (Step 3) The octopus was removed and kairomones were flushed into unit B

treatment tank (unit B) and the respirometric chambers (unit C). Units B and C were described in the respirometry subsection above. Unit A was a circular tank (180 l) used to prepare octopus kairomones. This tank was supplied with mechanically filtered water from an open-flow water system (50 micron cartridge). Unit A was placed approximately 60 cm above unit B, and both units were connected with a PVC tube (50 mm diameter). The water outlet from B was directly discarded, allowing an open-water circulation from A to B. In addition, water from the bath was incorporated into the respirometric chambers during the flushing cycles previously described in the respirometry section.

To depict the predation risk scenarios under night conditions, we developed the following protocol (Fig. 1):

Step (1) Lobster acclimation. Two lobsters were individually placed into each respirometry chamber from approximately 12:00 until 18:00 h (6 h).

Step (2) Kairomone concentration. The concentration of kairomones was achieved by holding an octopus in the conditioning tank for 1 h without water exchange. A 1 h concentration period was used to standardize the accumulation of octopus kairomones without resulting in a deterioration of such cues as recently demonstrated (e.g. <1 h, Chivers et al. 2013). Additionally, the concentration period was suitable to minimize octopus excretion that also may have altered our results, as predator faeces can also act as kairomones (Ferrari et al. 2010). To ensure the lack of predator faeces, octopus were deprived of food for 2 d prior to experimentation. Furthermore, water condition (i.e. temperature and dissolved oxygen) was monitored in the conditioning tank, where the dissolved oxygen was kept at saturation level (>90%) using an air stone. After 1 h, the octopus was gently removed from unit A and placed back in the maintenance tank.

Step (3) Kairomone exposure. The water from unit A containing the kairomones was directly flushed into the bath during the last 2–3 min of the flushing cycle of the respirometer, recreating an acute kairomone exposure. After flushing, the conditioning tank was immediately thoroughly rinsed with fresh water. The open-flow water system was then recon-

nected, allowing the new seawater to flow from unit A to unit B but with no octopus in it.

By using this protocol, we assumed that (1) lobsters were acutely exposed to octopus kairomones and (2) such exposure was gradually weakened as cues were diluted over the time after reconnecting the open-flow water circulation (Step 3). Considering the water exchange in the bath, it was estimated that kairomones remained within this unit for <3 h.

Lobster RMRs were examined during 48 h trials over 2 nights (nights 1 and 2, Fig. 2). Each night, we applied 1 of the 2 predation risk scenarios: the scenario under predation risk (treatment) or the scenario without predation risk (control), with the order of these scenarios randomised among consecutive trials. The protocol for the control experiments was the same as previously described for the predation risk treatment but with the absence of kairomones. Each octopus was used more than once, although not in consecutive trials. Lobsters were used only once.

Under the presence of kairomones, RMRn after kairomone exposure (KE) was differentiated as 'RMRnrisk'. RMRnrisk was recorded until the end of the nocturnal period of respirometry (06:00 h), resulting in a period of 6 h after KE.

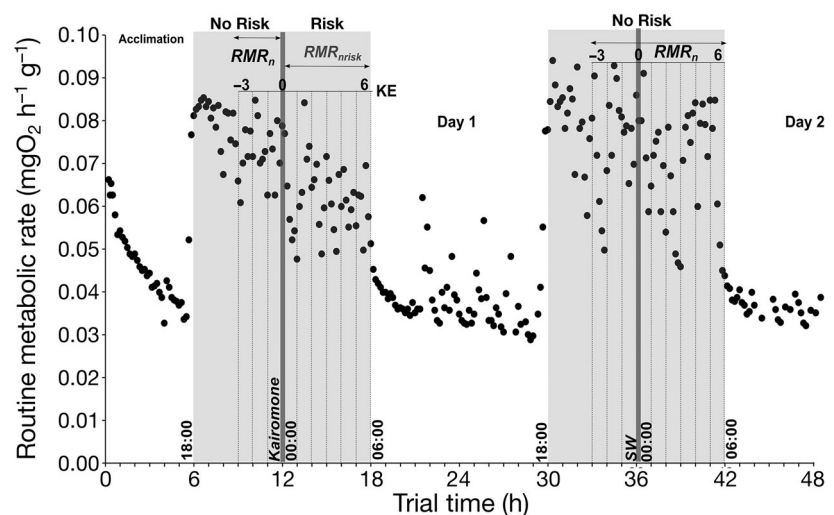


Fig. 2. Example of a respirometry trial for *Jasus edwardsii* adults (700 g; 17°C) for 48 h to describe the nocturnal predation risk scenario. Lobsters were acclimated for 6 h in the respirometric chambers. Nighttime is specified by light grey boxes (18:00–06:00 h). Each dot represents 1 measurement of metabolic rate ($\text{mg O}_2 \text{ h}^{-1} \text{ g}^{-1}$) taken every 10 min. Routine metabolic rate (RMR) was calculated as hourly mean resulting from 6 measurements h^{-1} . Nocturnal RMR (RMRn) was examined over 2 consecutive nights (Nights 1 and 2) where 1 of the 2 treatments (absence/presence of kairomones) was applied (approximately at midnight). In this example, lobster was exposed to octopus cues on the first night and the resulting rates after kairomone exposure (KE) (vertical solid lines) are specified as 'RMRnrisk' in the second night, the same protocol was applied but only including seawater (SW) with the resulting rate used as control and referred to as RMRn

Data analysis

Metabolic rates and background respiration were determined by linear regressions of the rate of decline in dissolved oxygen concentration for every 10 min over the closing cycle. Individual animal measurements were averaged to present hourly means in order to account for temporal variation in oxygen consumption rates resulting from spontaneous activity, which is a well-known component of animal routine metabolism.

Temporal changes in routine metabolism were analysed using generalized linear mixed models (GLMMs), which could account for the lack of independence in repeated oxygen measurements (Zuur et al. 2009). Normality of residuals was assessed by visual inspection (histogram of model residuals), and homogeneity of variance was tested by Bartlett's test for normal distribution of data (Sokal & Rohlf 1995). The circadian pattern of RMR was examined by a GLMM including the period (day/night) as a fixed effect and individuals as a random effect. Differences in RMR between predation risk scenarios were examined by including predation risk scenarios (absence/presence of kairomones) and time (e.g. hours after KE) as an interaction term (predation risk \times time), as well as the order of treatments among nights as fixed effects and individual as a random effect. Additionally, the significance of factors was further examined by 1-way ANOVA with significant differences identified by Tukey's HSD tests for post hoc multiple comparisons. The significance value used was 0.05. All analyses were performed in R (v.3.4.4), using packages 'lme4' for the GLMMs and 'ls means' for Tukey's HSD tests.

RESULTS

Circadian pattern in lobster routine metabolism

Mean nocturnal RMR was $0.062 \text{ mg O}_2 \text{ h}^{-1} \text{ g}^{-1}$, significantly higher than mean diurnal RMR ($0.040 \text{ mg O}_2 \text{ h}^{-1} \text{ g}^{-1}$) ($F_{1,299} = 233.226$, $p < 0.001$), indicating a profound circadian pattern in lobster aerobic metabolism (Fig. 3). Lobsters typically increased RMRd by 50 %

between 14:00 and 18:00 h (twilight), and then remained at an average RMRn of $0.062 \text{ mg O}_2 \text{ h}^{-1} \text{ g}^{-1}$ until 06:00 h (dawn). Additionally, RMRd rapidly decreased between 06:00 and 07:00 h, which was quite consistent among individuals, with a mean RMRd of $0.038 \text{ mg O}_2 \text{ h}^{-1} \text{ g}^{-1}$. The SMR was $0.03 \text{ mg O}_2 \text{ h}^{-1} \text{ g}^{-1}$. Overall, RMRd and RMRn were 1.3 and 2.1 times higher than SMR, respectively.

Routine metabolism under nocturnal predation risk

Analysis of RMRn before KE showed no variability among individuals ($F_{1,14} = 0.0576$, $p = 0.818$). Lobsters exposed to octopus kairomones strongly reduced their RMRnrisk for 3 h by up to 31.42% ($0.02 \text{ mg O}_2 \text{ h}^{-1} \text{ g}^{-1}$) (Fig. 4), resulting in significant differences among predation risk scenarios ($F_{1,113} = 13.16$, $p < 0.001$) as well as for the interaction term (predation risk \times time) ($F_{1,113} = 7.423$, $p < 0.01$). This response differed significantly between ex-

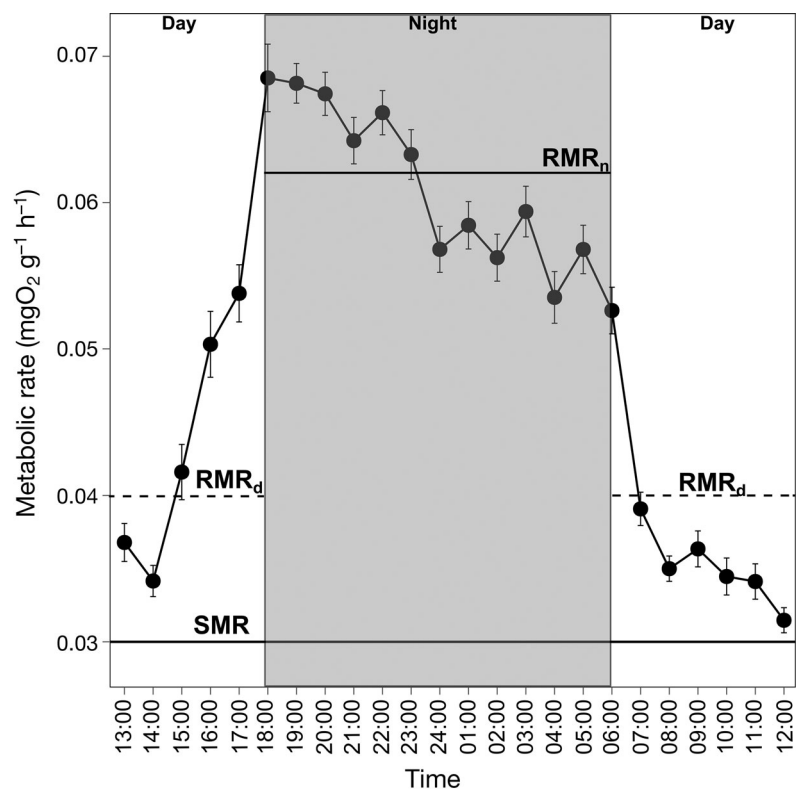


Fig. 3. Circadian pattern in mean \pm SE routine metabolic rate (RMR) in adult *Jasus edwardsii* ($n = 16$, 514–732 g, 17°C). The grey box represents the nocturnal period between 18:00 and 06:00 h. Mean values of RMR during nighttime (RMRn = $0.062 \text{ mg O}_2 \text{ h}^{-1} \text{ g}^{-1}$) and daytime (RMRd = $0.040 \text{ mg O}_2 \text{ h}^{-1} \text{ g}^{-1}$) are specified by the upper (solid) and dashed lines, respectively. Mean value of standard metabolic rate (SMR = $0.03 \text{ mg O}_2 \text{ h}^{-1} \text{ g}^{-1}$) is shown as the lower solid line

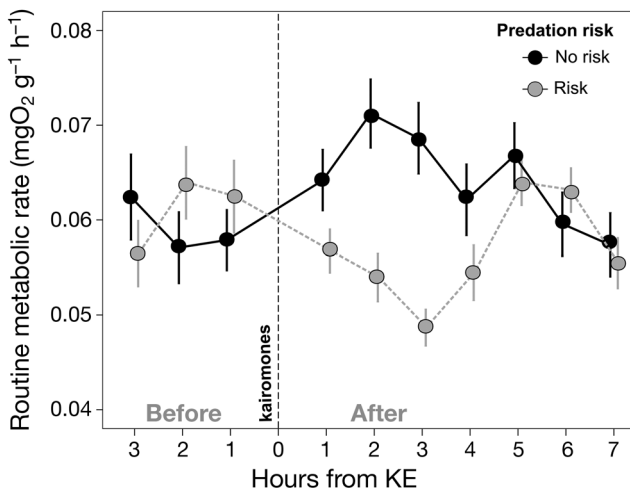


Fig. 4. Mean \pm SE routine metabolic rate of *Jasus edwardsii* adults under nocturnal predation risk scenarios ($n = 10$; 461–769 g). The vertical dashed line specifies the time when kairomones (octopus odour) were added (approximately at midnight). KE: kairomone exposure

posed and control lobsters at 2 (Tukey's HSD, $t = 3.148$, $p < 0.05$) and 3 (Tukey's HSD, $t = 3.634$, $p < 0.01$) hours after KE. Furthermore, the reduction in routine metabolism at 3 h after KE also resulted in lower variability among individuals (coefficient of variation = 31%) compared to controls (38.2%). Between 3 and 5 h after being exposed, animals rapidly increased their RMR, reaching similar values to pre-treatment conditions. Independently of the treatment, RMRn was strongly reduced from 5 h onwards, demonstrating the effect of time ($F = 3.89$, $df = 51$, $p < 0.05$), which was close to dawn (06:00 h). Considering the pattern in RMR observed in threatened animals, 2 periods were identified: (1) RMR decrease over the first 3 h, and (2) subsequent RMR recovery with a duration of 2 h.

DISCUSSION

In this study, we examined the effect of predator kairomones on the routine metabolism of adult *Jasus edwardsii* as a proxy of the energetic cost experienced by lobsters under predation risk. We report (1) the presence of a circadian pattern in lobster RMRs, resulting in increasing oxygen consumption of lobsters during nighttime and (2) how temporal changes in metabolic rates can be altered during the night under simulated predation risk scenarios. Our findings demonstrate that lobsters did not increase their RMRs under predation

risk as we expected in our initial hypothesis, based on the general stress response (Hawlena & Schmitz 2010). Instead, lobsters reduced their routine metabolism by approximately 31% for up to 3 h under the nocturnal KE. Individual activity within a respirometric chamber is metabolically expressed as routine metabolism, hence animals that move more in the chambers consume more oxygen as largely documented in crustacean respiratory physiology (Crear & Forteach 2000, Kemp et al. 2009, Toscano & Monaco 2015). The decreasing RMR observed after KE would suggest that lobsters reduce activity as an anti-predator mechanism (e.g. immobility), appearing as an alternative hypothesis to the general stress response. We further discuss the energetic and ecological implications of immobility as an avoidance predator mechanism in this lobster species, contributing new insights into physiological mechanisms underlying decision-making in prey under predation risk in aquatic organisms.

Circadian pattern in lobster routine metabolism

Changes in light cycle play a crucial role in the regulation of activity in lobsters demonstrating a circadian rhythm in activity (Childress & Herrnkind 1994, Weiss et al. 2008). In this study, the RMRn increased by approximately 50% compared with the RMRd, which is similar to that reported in other lobsters (*Panulirus cygnus*, Crear & Forteach 2001). Major changes in RMR were observed during twilight (18:00 h) and dawn (06:00 h), as previously reported in *J. edwardsii* (Crear & Forteach 2000), as well as in other lobsters (*P. homarus*, Kemp et al. 2009; *P. cygnus*, Crear & Forteach 2001). Such changes in lobster activity throughout the light cycle have been also reported in field (e.g. MacDiarmid et al. 1991) and laboratory (Williams & Dean 1989) studies in *J. edwardsii*. The circadian rhythm of RMR is suggested to match changes in activity by lobsters within the respirometer (Crear & Forteach 2000, 2001, Kemp et al. 2009). Previous studies in *J. edwardsii* have reported a strong correlation between activity and metabolic rate by continuous observations from a respirometer with video cameras (Crear & Forteach 2000). Although we did not perform systematic observations of lobster activity within the respirometer, random observations during trials confirmed that lobsters became more active during the night and inactive during the day.

Routine metabolism under a nocturnal predation risk scenario

Nocturnal routine metabolism of lobsters was reduced by up to 31.42% 3 h after KE in comparison with controls, with RMR_{risk} returning to control levels 5 h after KE. Our findings do not match the general premise of increased respiration rates as the first physiological response of prey under predation risk. Instead, we found that threatened lobsters reduced their RMR_n. Similar decreases in aerobic metabolism under predation risk have been reported in arachnids (e.g. Okuyama 2015), fish (Holopainen et al. 1997, Cooke et al. 2003) and tadpoles (Steiner & Van Buskirk 2009). Reductions in metabolism and cardiovascular activity are suggested to mitigate the risk of predation, reducing the need to invest in costly anti-predator responses such as escaping behaviours (e.g. fight-or-flight response) (Hawlena & Schmitz 2010).

'Immobility-or-flight' response in lobsters?

Predation risk can be minimized in lobsters by 2 major strategies (Herrnkind et al. 2001, Buscaino et al. 2011): (1) predator-avoidance mechanisms (e.g. sheltering, immobility and nocturnal activity); and (2) anti-predator mechanisms (e.g. escape, aggregation, cooperative defence and weaponry). Such mechanisms, in addition, can operate sequentially, as recently reported in some rock lobsters (*Palinurus elephas*, Buscaino et al. 2011). For example, a lobster might remain immobile to avoid detection by a predator; however, once detected it may use the ultimate avoidance behaviour of tail-flipping to move away from the predator and towards safer areas (Mills et al. 2008, Buscaino et al. 2011). Integrating such information with our results, we have demonstrated that the reduction in lobster routine metabolism under predation risk confirms the immobility response as a predator avoidance mechanism in this species. This can be further supported by studies using octopus as a predator model on decapods in which inactivity is the most common strategy to avoid an encounter with octopus (see Table A1 in the Appendix).

Changes in prey activity induced by the presence of a predator's odour are well-known across taxa (Kats & Dill 1998), and reduction in prey activity also appears to be associated with the presence of visual predators like octopus (Hanlon & Messenger 1998). However, recent advances in our understanding of the octopus olfactory system (e.g. *Octopus vulgaris*,

Polese et al. 2015) suggest that chemical signalling can be another source of sensory input that could work in combination with visual cues or alone to provide ecological information, especially in light-limited habitats (Nilsson et al. 2012). The role of olfaction in octopus seems to be strongly associated with reproduction (Polese et al. 2015), although previous studies on octopus (Boyle 1983) and cuttlefish (Boal & Golden 1999) have demonstrated that individuals exposed to food odour increase movement (e.g. arousal) and ventilation rates. The olfactory capacity of octopus for prey searching indicates a potential alternative hypothesis to explain the immobility response by lobsters. If *O. maorum* is able to detect kairomones from *J. edwardsii* as a target prey, lobster immobility may rise as a strategy to reduce lobster kairomone or metabolite emission in order to remain 'chemically quiet'. Lobsters are hard-shelled animals that store urine and faeces, allowing them to be 'chemically quiet' when necessary (e.g. reproduction, Atema 1995). For example, urine signals can be used during lobster dominance (e.g. *Panulirus argus*, Shabani et al. 2009) and courtship, as chemical cues in the urine are involved with memory (Atema 1995) and individuals can avoid agonistic behaviour by hiding their reproductive status by chemical quiescence (e.g. Díaz & Thiel 2004).

Previous information on chemical ecology among conspecifics should be taken into account for designing experiments to examine lobster physiological responses under predation risk. In this study, each respirometry trial was undertaken with 2 lobster individuals that were visually and chemically exposed to the same experimental conditions. *J. edwardsii* is a gregarious species during sub-adult and adult stages (Butler et al. 1999), so signals between individuals are biologically/ecologically relevant. The physiological response by lobsters to predator exposure in the wild is also likely to include intraspecific cues. Hence, future investigations including the number of conspecifics on lobster physiology are desirable as examined in fish respirometry (Herskin 1999).

So far there is little information about the energetic cost associated with either predator avoidance or anti-predator mechanisms in lobsters. Escape response such as tail-flipping is a high-cost energetic behaviour in crustaceans, as large muscle fibres that facilitate tail-flipping are involved (England & Baldwin 1983, Jimenez et al. 2008). The dependency on anaerobic metabolism results in an oxygen debt which must be aerobically recovered (Jimenez et al. 2008, Jensen et al. 2013b). We suggest that the low-

ering of metabolic rates from the immobility response may operate as an energetic strategy rather than investing in a costly escape behaviour such as tail flipping (e.g. 'flight') (Hawlena & Schmitz 2010). Such a strategy can be further examined using studies investigating the excess post-exercise oxygen consumption (EPOC) as a proxy of energetic cost and recovery in lobsters (e.g. *Sagmariasus verreauxi*, Jensen et al. 2013b). Lobsters required around $8.36 \text{ mg O}_2 \text{ h}^{-1} \text{ g}^{-1}$ and more than 10 h for recovery following tail-flipping until exhaustion, representing around 1.2 times the standard metabolism needed during such recovery a period (Jensen et al. 2013b). Using these values, we further explored our findings by comparing the daily energetic cost needed for standard (e.g. resting) and routine metabolism (e.g. activity) in the presence/absence of predation risk, as well as EPOC from Jensen et al. (2013b) (using the caloric equivalent $1 \text{ mg O}_2 \text{ g}^{-1} = 14.3 \text{ J mg}^{-1}$; Lucas 1993) (Fig. 5).

According to our energy estimations, a single escaping event until exhaustion would be 17.5% above the energy required for nocturnal activity assuming a period of 12 h. In contrast, the immobility response may represent a 'saving' strategy compared with tail-flipping, although it would imply around 50% of the nocturnal period under inactivity. The activation of both anti-predator strategies (immobility or flight) may depend on the type of cues (e.g. chemical and visual) and on kairomone concentrations, as previously suggested across taxa (Lima & Steury 2005), with a greater perceived risk likely resulting in a flight response. Although in this study kairomones were not quantified to recreate the predation risk scenarios, under the experimental conditions tested here, *J. edwardsii* did not perform tail-flipping as an anti-predator response. Whilst we compared both defence mechanisms from an energetic point of view, such strategies are possibly equally effective in reducing the lethal effect of predators, and are likely used in combination. Studies have described behavioural responses of lobster–octopus interaction in an experimental arena, describing the sequence as 'freezing' — weaponing — tail-flipping (see Buscaino et al. 2011), which certainly validates the hypothesis of immobility as a primary defensive mechanism before displaying costly escaping behaviours in *J. edwardsii*. It is worth mentioning that tail-flipping can also impose other challenges for lobsters, as the process can move the organism to a completely unknown environment and increase the exposure in the water column to predators who are reactive to movement-based prey.

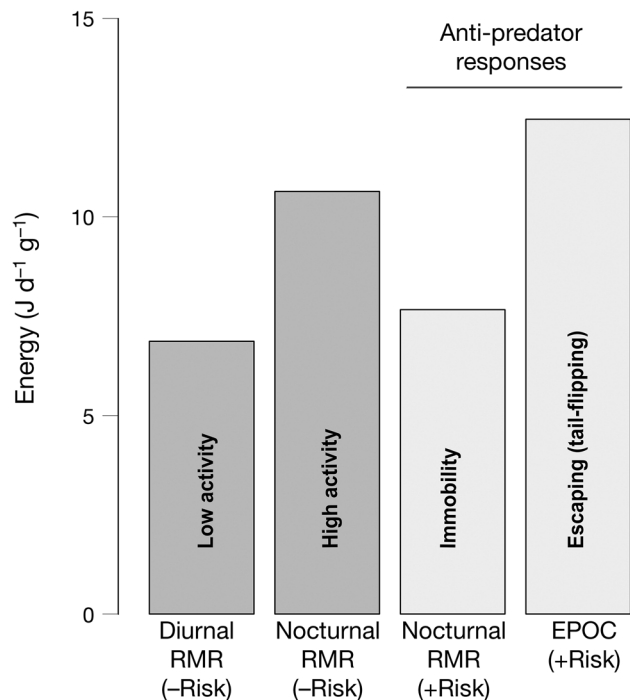


Fig. 5. Daily energy requirements for lobster activity using routine metabolic rate (RMR) at 2 levels from circadian pattern (dark grey bars): low activity (diurnal RMR) and high activity (nocturnal RMR) without predation risk (-Risk) which are compared with 2 anti-predator responses (light grey bars): immobility from the lowering in nocturnal RMR under predation risk (+Risk) here reported as escaping or tail-flipping from Jensen et al. (2013b). Diurnal and nocturnal RMR were calculated assuming a 12:12 h day:night period. RMR under risk was calculated as 31.4% of nocturnal RMR (-Risk), assumed to be constant over the nocturnal period (12 h). The escaping response, in addition, was calculated using the excess-post exercise oxygen consumption (EPOC) from Jensen et al. (2013b), representing the energy required for a single escaping event performing tail-flipping until exhaustion (see Jensen et al. 2013b)

Linking lab-based physiological information with behavioural traits such as prey defence mechanisms can lead to context-dependent responses which must be considered for future studies. For example, the confined space (i.e. the respirometry chamber) in which lobsters were exposed to predator cues could have limited the display of defensive mechanisms known in lobsters (e.g. tail-flipping or walking). Recent studies have suggested the relevance of examining methodological and functional relationships (Careau et al. 2008) between behavioural and physiological responses in an ecological context (e.g. predation risk with chemical cues) (e.g. Toscano & Monaco 2015). In the study by Toscano & Monaco (2015), crabs exposed to predator cues within respirometry chambers became more active than crabs

exposed in a mesocosm under the same predation risk. The authors attributed such behavioural differences to the lack of refuge habitat in the respirometry chambers, likely leading to enhanced attempts to hide or escape. Although respirometry chambers used here may act as a sheltered space for threatened lobsters, it is unclear whether the same avoidance response (immobility) may occur in an open experimental set-up (e.g. arena). Future studies examining physiological (e.g. metabolic rates) responses in a predator–prey context should examine such methodological relationships (e.g. Toscano & Monaco 2015). However, this may itself create additional practical challenges, as accurate oxygen consumption measurements strongly rely on the restrictive methodological aspects of respirometry (e.g. animal size:chamber volume proportionality, Clark et al. 2013).

Cue concentration is an important extrinsic factor that can modulate prey anti-predator responses in aquatic systems (Ferrari et al. 2010). Prey likely use kairomone concentration to adjust the intensity of their anti-predator response in a threat-sensitive manner (Helfman 1989) to optimize fitness in the trade-off between predator avoidance responses (e.g. sheltering) and fitness-related activities (e.g. foraging) (Ferrari et al. 2010). In this study, the predation risk scenario was recreated by exposing lobsters to a single and highly concentrated octopus cue during the flushing phases of respirometry for 1 h. Additionally, it is expected that other extrinsic factors, such as habitat type, water motion and chemistry (Ferrari et al. 2010), could also play important roles in lobster chemical ecology, and should be considered in future investigations. Aggregative behaviour, size distribution of conspecifics and the availability of size-structured shelters are factors that can vary predation risk in lobsters (e.g. Berger & Butler 2001), and their inclusion in experimental designs would be desirable to achieve a more realistic background to examine lobster physiological traits under predation risks.

Ecological implications

Low-cost energetic strategies such as immobility may be used more regularly in individuals from regions with high predation pressure, which are less likely to waste energy in flight responses, preserving energy to cope with more extreme stress events (e.g. attack) given the abundance of predators as reported in freshwater fishes (Brown et al. 2005, Gravel et al. 2011). Predation risk for lobsters may be elevated in

fishing areas, given high abundance of predators like octopus as has been demonstrated in southeastern Australia (Briceño et al. 2015, 2016). As octopus can be attracted by lobster traps (e.g. baiting, Brock et al. 2003, Phillips et al. 2012), lobster fishing may increase consumptive and non-consumptive effects towards foraging lobsters. Further to direct KE emission from the abundance of octopus in the fishing grounds, octopus depredation within lobster traps might also increase the emission of alarm cues from injured or freshly killed conspecifics, further reducing lobster activity (Shabani et al. 2008, Hazlett 2011). A reduction in activity or increase in sheltering behaviour would be expected in threatened lobster individuals, negatively affecting both growth and fitness as demonstrated in other marine organisms (Trussell et al. 2006, Matassa & Trussell 2014). Increasing sheltering behaviours during the night may result in negative effects on lobster growth as foraging rates would be reduced.

Studies have demonstrated that size selectivity by a fishery (e.g. targeting larger individuals) can significantly modify life history and reproduction traits in fish stocks, resulting in individuals maturing earlier and at smaller sizes (Heino et al. 2015). The heritable component of fishery effects on fish stocks is known as ‘fisheries-induced evolution’ (see Heino et al. 2015), which has been recently examined from a physiological point of view (see Hollins et al. 2018). In South Australia, octopus depredation occurs mainly on large male lobsters (size- and sex-dependent mortality), mirroring lobster catchability in this fishery (Briceño et al. 2015). It is unclear whether octopus depredation can also lead to an impact on lobster populations by exacerbating the consumption of large individuals which are also targeted by the lobster fishery. Likewise, reproductive females can also be targeted by octopus depredation throughout the fishing season (Briceño et al. 2015), potentially impacting shifts in lobster population traits. This deserves further attention of future studies examining lobster physiological and behavioural responses under predation, as only males were used in this study.

Spiny lobsters moving to new areas, and therefore experiencing a change in habitat, is a well-known response to predation risk (Childress & Jury 2006). If *J. edwardsii* move to new habitats under predation risk, the type of refuge and level of food availability can be crucial for survival, especially at early life history stages, as juveniles are more dependent on habitat conditions (Herrnkind et al. 1997). A reduction in sheltering areas can modify physiological traits in

prey individuals, as the lack of shelter can increase maintenance requirements in aquatic organisms (Millidine et al. 2006, Toscano & Monaco 2015). Such physiological alterations may be more elevated in habitats where both lobsters and octopus can compete for shelter (e.g. *P. argus*, Berger & Butler 2001), although in some rock lobster species (e.g. *P. interuptus*), it is possible to find individuals sharing shelter space with octopus during daytime. This may lead to profound alterations in lobster physiology associated with the re-allocation of resources from growth and reproduction to survival, resulting in altered demographic traits as demonstrated in other taxa (Zanette et al. 2014) and which should be examined by future studies on *J. edwardsii*.

Contrasting lobster life history, reproductive, behavioural and physiological traits with different levels of predation risk by octopus could be addressed by future research to examine the effect of fishing in shaping this predator–prey interaction. In doing so, future examinations should also evaluate behavioural and physiological responses by lobsters under a mortality threat in more complex trophic habitats such as marine protected areas, as lobster are able to modify important behavioural defensive traits (e.g. shelter dwelling and gregariousness) in comparison with fishing areas (see Loflen & Hovel, 2010).

New disciplines integrating eco-physiological traits of aquatic organisms into management and conservation decision-making are quickly emerging (i.e. conservation physiology, Cooke et al. 2013), and outcomes from the current study may serve as a baseline for future studies on eco-physiological traits and predator–prey interactions.

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APPENDIX

Table A1. Behavioural studies using octopus–crustacean interactions as predator–prey models, indicating field (F) or laboratory (L) investigations

Prey	Cue type	Prey response	Reference
Shore crab <i>Gaetice depressu</i>	Chemical	Reduction of activity	Sakamoto et al. (2006) (L)
European spiny lobster <i>Palinurus elephas</i>	Visual, chemical and tactile	Avoidance	Gristina et al. (2011) (L)
European spiny lobster <i>Palinurus elephas</i>	Visual, chemical and tactile	Avoidance	Buscaino et al. (2011) (L)
Caribbean spiny lobster <i>Panulirus argus</i>	Chemical	Avoidance	Berger & Butler (2001) (F); Horner et al. (2006) (L); Butler & Lear (2009) (F)
Caribbean spiny lobster <i>Panulirus argus</i>	Visual and chemical	Shelter occupancy	Weiss et al. (2008) (F)
Hermit crabs <i>Dardanus venosus</i> and <i>Pagurus pollicaris</i>	Chemical	Avoidance	Ross & Boletzky (1979) (L), Brooks 1991 (L)

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