

Artificial light at night does not alter heart rate or locomotor behaviour in Caribbean spiny lobster (*Panulirus argus*): insights into light pollution and physiological disturbance using biologgers

S. Clay Steell^{1,*}, Steven J. Cooke¹ and Erika J. Eliason²

¹Fish Ecology and Conservation Physiology Laboratory, Department of Biology, Carleton University, 1125 Colonel By Dr., Ottawa, ON K1S 5B6, Canada

²Department of Ecology, Evolution and Marine Biology, University of California, Santa Barbara, CA 93106, USA

*Corresponding author: Fish Ecology and Conservation Physiology Laboratory, Department of Biology, Carleton University, 1125 Colonel By Dr., Ottawa, ON K1S 5B6, Canada. Email: steell@ualberta.ca

Light pollution is a rapidly growing threat to biodiversity, with many unknown or poorly understood effects on species and ecosystems spanning terrestrial and aquatic environments. Relative to other taxa, the effects of artificial light at night on aquatic invertebrates are poorly understood, despite the abundance and integral significance of invertebrates to marine and freshwater ecosystems. We affixed heart rate and acceleration biologgers to adult Caribbean spiny lobster (*Panulirus argus*), an ecologically, culturally and economically significant species in the western Atlantic ocean, to test the effect of artificial light at night on this species' physiology and behaviour relative to appropriate controls. The experiment was conducted in a simulated reef mesocosm in The Bahamas with incandescent lighting used to illuminate it at 1 lux, approximating light levels offshore of urban areas. In the conditions tested here, artificial light at night was found to have no effect on heart rate or locomotor activity in *P. argus*. We observed a dissociation between activity and heart rate at both short-term and long-term temporal scales. Lobsters were more active at night and nocturnal activity was higher in trials closer to new moon; however, heart rate did not vary with diel or lunar cycle. There was less than 8% difference between daytime and night time average heart rate despite the average percentage of time spent active almost tripling in nights versus days, to 19.5% from 7.2%, respectively. Our findings suggest *P. argus* may have some resilience to low levels of light pollution, which warrants further research on aspects of this species' life history, performance and fitness in the face of this potential anthropogenic disturbance.

Key words: heart rate, accelerometer, biologging, spiny lobster, light pollution, stress

Editor: Craig Franklin

Received 8 April 2020; Revised 12 August 2020; Editorial Decision 22 September 2020; Accepted 5 October 2020

Cite as: Steell SC, Cooke SJ, Eliason EJ (2020) Artificial light at night does not alter heart rate or locomotor behaviour in Caribbean spiny lobster (*Panulirus argus*): insights into light pollution and physiological disturbance using biologgers. *Conserv Physiol* 8(1): coaa097; doi:10.1093/conphys/coaa097.

Introduction

Light pollution is a rapidly growing threat to terrestrial and aquatic biodiversity worldwide (Gaston *et al.*, 2013; Koen *et al.*, 2018). A growing body of research has elaborated the ways in which unnatural light at night impacts organisms and ecosystems, which include disruptions of sensory perception, diel cycle and ecological interactions (Hölker *et al.*, 2010; Davies *et al.*, 2016). Such disruptions are underpinned by physiological processes, the study of which can inform how organisms respond to light pollution, particularly when its effects are not visible to the naked eye (Navara and Nelson, 2007; Gaston *et al.*, 2013). Most research on the subject has focused on terrestrial systems; however, light pollution threatens marine and freshwater organisms and is less well understood in these aquatic environments (Davies *et al.*, 2016). Davies *et al.* (2014) estimated that 22% of coastal areas on Earth (excluding Antarctica) experience some degree of light pollution, which Kyba *et al.* (2017b) estimated is growing by 2.2% in area and brightness annually as coastal areas worldwide continue to rapidly urbanize (Neumann *et al.*, 2015).

Diverse biomarkers are used to assess how animals respond to extrinsic stimuli, including those of anthropogenic origin such as light pollution, which collectively contribute to allostatic load (McEwen and Wingfield, 2010). In the context of wild organisms, there is particular interest in understanding how anthropogenic disturbances influence performance, fitness and population-level ecological processes (Wikelski and Cooke, 2006; Dantzer *et al.*, 2014). Light pollution has been found to disrupt hormone cycles or induce stress in several species of fish (inferred largely from glucocorticoids), such as European perch (*Perca fluviatilis*) (Brüning *et al.*, 2015; Brüning *et al.*, 2018), bonefish (*Albula vulpes*) (Szekeres *et al.*, 2017), Atlantic salmon (*Salmo salar*) (Migaud *et al.*, 2007) and baunco (*Girella laevis*) (Pulgar *et al.*, 2019), along with altering aquatic animal behaviour (Gaston *et al.*, 2015; Thums *et al.*, 2016; Fischer *et al.*, 2020) and ecosystem structure (Perkin *et al.*, 2011; Underwood *et al.*, 2017). Few studies have investigated the effect of light pollution on aquatic invertebrates, despite their abundance and integral significance in aquatic ecosystems. Moderate levels of artificial light at night (i.e. 4–15 lux) have been found to suppress activity and alter behaviour in four species of North American crayfish (Jackson and Moore, 2019; Fischer *et al.*, 2020), and the Japanese spiny lobster (*Panulirus japonicus*) has been reported to suppress activity at extremely low levels of artificial light at night (1.8×10^{-4} lux) (Nagata and Koike, 1997). We are aware of only one study to date that has measured hormones in an aquatic invertebrate subjected to artificial light at night in an attempt to understand if it contributed to allostatic load (Jackson and Moore, 2019), which found that it did not affect levels of haemolymph serotonin in two species of North American crayfish, despite disrupting their behaviour and activity levels. While hormone levels can reflect an animal's status over a given period of time prior to sampling, other endpoints can be used to assess

stress responses more continuously and at higher resolution, such as heart rate (f_H) and locomotor activity. Moreover, so-called 'stress hormones' (i.e. glucocorticoids) are increasingly recognized as having diverse roles in organism function (MacDougall-Shackleton *et al.*, 2019).

Heart rate has been used as a measure of physiological status and allostatic load in a range of animal taxa, including the decapod crustaceans. Decapods have the most complex circulatory system among crustaceans, similar to that of basal vertebrates, and changes in f_H have been found to be a reliable indicator of physiological state in numerous decapod species (McGaw and Reiber, 2015). As in fish and other vertebrates, f_H often increases with exposure to stress; however, decapods may also undergo bradycardia (slowing of f_H) or ascardia (temporary cessation of f_H) when exposed to a physiological challenge depending on its rapidity, duration and severity (Brown *et al.*, 2004; McLean and Todgham, 2015). The measurement of f_H in decapods has historically been confined to tethered or constrained animals; however, McGaw *et al.* (2018) developed a novel methodology for measuring f_H in free-moving decapods using f_H biologgers. In addition, advances in acceleration biollogger technology (i.e. accelerometers) have made it possible to remotely measure activity in small, free-moving animals (Brown *et al.*, 2013; Cooke *et al.*, 2016), activity being a primary determinant of f_H in decapods as well as a measure of behavioural response to a stimulus (Bertelsen, 2013; Goldstein *et al.*, 2015; Gutzler *et al.*, 2015; Jury *et al.*, 2018).

In this study, we used heart rate biologgers along with tri-axial accelerometers to explore the physiological and behavioural response of Caribbean spiny lobster (*Panulirus argus*) to light pollution. *Panulirus argus* forms one of the most culturally and economically significant fisheries in the western Atlantic Ocean, employing over 60 000 people and generating more than \$1 billion in revenue annually (Winterbottom *et al.*, 2012; FAO, 2018; CLME+, 2019). In The Bahamas, where *P. argus* is known as crawfish, the fishery is the largest and most valuable in the country (Smith and Zeller, 2013; Sherman *et al.*, 2018) and the Bahamian fishery is the largest in the species' range (CLME+, 2019). While the Bahamian fishery was certified by the Marine Stewardship Council in 2018 (Gascoigne *et al.*, 2018), *P. argus* has had a 'data deficient' IUCN Red List status over its entire range since its last assessment in 2009 (Butler *et al.*, 2013) and its fisheries are likely overfished in many places (CRFM, 2011; Winterbottom *et al.*, 2012; WECAFC, 2018; CLME+, 2019). *Panulirus argus* is also an ecologically significant species, influencing community structure through predation, underpinning trophic linkages from chemosynthetic primary production and forming an important part of its predators' diets (Smith and Herrkind, 1992; Higgs *et al.*, 2016; Gnanalingam and Butler IV, 2018). As a nocturnal generalist with a light-mediated circadian cycle of activity that forages in shallow nearshore areas, *P. argus* may be increasingly subjected to light pollution as coastal and offshore development near their

habitat continues, and its heavily-exploited status may make this species particularly sensitive to emerging anthropogenic disturbances. To our knowledge, the effect of light pollution on any aspect of this species' biology or ecology has not been investigated to date. As it has the potential to disrupt diel endocrine cycles that mediate physiological processes (Castanon-Cervantes *et al.*, 1999; McGaw and Reiber, 2015; Jackson and Moore, 2019), we hypothesized that artificial light at night would (1) increase f_H in *P. argus*, indicating that it is contributing to allostatic load, and (2) decrease its nocturnal activity as has been found in *P. japonicus* and other decapods, indicating a behavioural alteration (Nagata and Koike, 1997; Jackson and Moore, 2019; Fischer *et al.*, 2020).

Methods

Animal collection and husbandry

Lobsters ($n = 36$, mean body mass 499.7 ± 97 g, all data are reported as means $\pm$ SEM) were collected with SCUBA from patch reefs and forereefs between 3 and 15 m deep near Cape Eleuthera, The Bahamas ($24^\circ 50' 31$ N, $76^\circ 20' 40$ W) between 31 December 2017 and 3 February 2018, using a curved pole to coax them out of reef crevices and into a hand net. Lobsters were held in outdoor circular 750-L tanks that were aerated and continuously supplied with fresh seawater (5 L min^{-1}) at ambient temperature (mean = $23.4 \pm 0.24^\circ\text{C}$) at the Cape Eleuthera Institute, which was less than 5 km from capture sites. Lobsters were held in laboratory conditions for a minimum of 3 days and held for a maximum of 14 days before experimentation. Lobsters were fed a combination of squid, mackerel and tilapia *ad libitum* during holding and were fasted for 48 hours before experimentation to ensure they were in a post-absorptive state and that f_H measurements were not confounded by elevated postprandial metabolism. While the duration of elevated postprandial metabolism is not known for *P. argus*, it can remain elevated for several days in other decapods at similar temperatures (Whiteley *et al.*, 2001; Perera *et al.*, 2007; McGaw and Reiber, 2015), and the duration of this experiment was shorter than the typical onset of starvation-associated declines in heart rate and metabolism in decapods (Ansell, 1973; Depledge, 1985). With the exception of one lobster that moulted during the third light treatment trial of this experiment (see below), all lobsters were in an intermoult period.

Surgical and instrumentation protocol

The method used for affixing heart rate biologgers in this study was adapted from that in McGaw *et al.* (2018) (see online supplementary materials for a video). Briefly, lobsters were held by an assistant in a shallow tray of aerated seawater so that their gills were irrigated during the procedure, which took 11 minutes to complete on average. The best position to hold them was found to be with one hand arched over the head and the other hand firmly holding the tail so that it stayed curved, in which the lobster was unable to flex

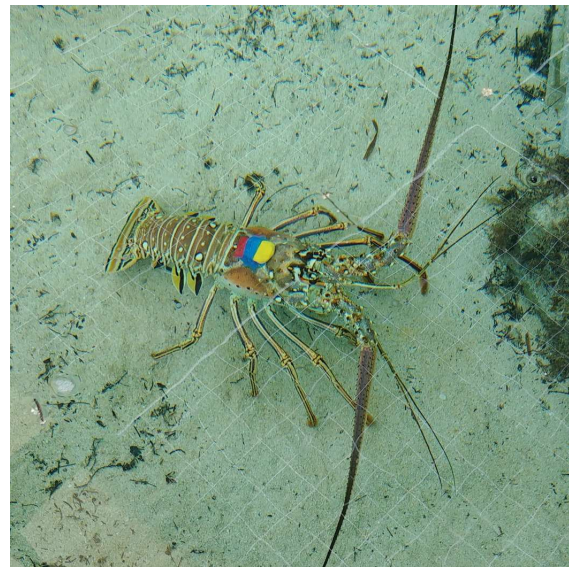


Figure 1: A lobster instrumented with a tri-axial accelerometer, affixed above a sheet of periphery wax covering the heart rate biollogger.

its tail and attempt escape. An oval-shaped section of the carapace was removed by shaving the edges of the area directly above the heart, which is clearly delimited in decapod crustaceans (McGaw *et al.*, 2018), with a handheld rotary tool (Dremel® 7300-N/8 MiniMite, Mt. Prospect, USA) fitted with an abrading burr attachment. This carapace section was then carefully removed with forceps, exposing a thin layer of dermis above the heart. Surgident® periphery wax (Heraeus Kulzer, South Bend, USA) was formed into a ring and scored along its bottom edge with a teasing needle tool before applying cyanoacrylate glue and affixing it to the carapace surrounding the exposed section. Leadless heart rate and temperature loggers (DST micro-HRT, Star Oddi, Gardabaer, Iceland; 25.4×8.3 mm; 3.3 g in air) were placed on the dermis above the heart, with the two measurement electrodes in full contact with the tissue and the end with the grounding electrode facing posteriorly. The ring of periphery wax was then sculpted to hold the logger in place, and a flattened sheet of periphery wax was placed over it and merged with the ring to fully cover the logger and exposed dermis. A tri-axial accelerometer (Human Activity Monitor model X-16, Gulf Coast Data Concepts, Waveland, MS; $55.9 \times 39.4 \times 15.2$ mm; 20 g in air) sealed with Plasti Dip® (Plasti Dip Intl, Blaine, USA) was secured above this flattened sheet with cyanoacrylate glue and a band of periphery wax (Fig. 1).

Experimental setup and protocol

This study took place in a simulated shallow reef mesocosm at the Cape Eleuthera Institute. The mesocosm was constructed with a 3.7-m-diameter, 1.8-m-deep circular tank furnished with a sand bottom and cinderblock shelters collected from

a nearshore rubble dump, as these environmental simulacra have been found to minimize the confounding effects of laboratory conditions on f_H measurement in other decapod crustacean species (Florey and Kriebel, 1974; Aagaard *et al.*, 1995; McGaw and Nancollas, 2018; McGaw *et al.*, 2018), and this species is commonly found in shallow patch reefs of a similar area and depth at high densities (Bertelsen 2013, Gutzler *et al.* 2015). The mesocosm was aerated and supplied with fresh seawater at approximately 1 l min^{-1} , with the water drained and refilled between trials.

Heart rate loggers and tri-axial accelerometers were used to measure lobsters' f_H and activity, respectively. Accelerometers were used in order to measure activity in total darkness, as opposed to other means of measuring activity such as video, as activity is one of the primary determinants of f_H in decapod crustaceans (McGaw and Reiber, 2015). Heart rate loggers were set to record f_H over a 5 second period (125 Hz) every 10 minutes and save electrocardiogram (ECG) data once an hour for validation purposes, with start time delayed by either 24 or 48 hours depending on measurement trial (see below) to save memory and battery. Accelerometers were set at 25 Hz and activated immediately following instrumentation.

The experiment was carried out over 4 successive trials, each lasting 4 days and 4 nights. Each trial started immediately following instrumentation, with 8–10 lobsters placed in the mesocosm. A Surgery Recovery Trial was first conducted ($n=8$) from 13 January to 17 January 2018 to ensure f_H and activity had stabilized by the third day following surgery and instrumentation, when we intended to start using the data in analysis. In this trial, the heart rate loggers' start time was delayed by 24 hours. Three successive light treatment trials were then conducted, with Trial 1 from 20 January to 24 January 2018 ($n=9$), Trial 2 from 24 January to 28 January 2018 ($n=10$) and Trial 3 from 6 February to 10 February 2018 ($n=9$) in which the fourth night was unnaturally lit to compare it to the third night, which was naturally dark (Fig. 2). The heart rate loggers' start time was delayed by 48 hours in these three trials, and the fourth night was indirectly illuminated with a 60-watt incandescent light bulb positioned so that the illuminance at the surface of the mesocosm was 1 lux, measured with a handheld lux meter (Dr Meter®, Hisgadget Inc., Union City, CA, USA), turned on at 17:20, half an hour before sunset. An incandescent bulb was chosen as it approximates the spectra of high-pressure sodium lamps, the most common street lighting worldwide, and 1 lux was chosen as it approximates the 'sky-glow' found near urbanized coastal areas (Perkin *et al.*, 2014; Brüning *et al.*, 2015; Dąbrowski *et al.*, 2015). Natural night time illuminance was at or below the 0.1 lux lower detection limit of the lux meter, consistent with ground and satellite observations of light pollution and moonlight illuminance for the area (Falchi *et al.*, 2016; Kyba *et al.*, 2017a). Lunar cycle ranged between third quarter and new moon during the Surgery Recovery Trial, ranged between first quarter and full moon during Trials 1 and 2 and ranged between full moon

and third quarter during Trial 3. Average temperatures for the Surgery Recovery Trial, Trial 1, Trial 2 and Trial 3 were $23.1 \pm 0.1^\circ\text{C}$, $23.6 \pm 0.1^\circ\text{C}$, $21.9 \pm 0.1^\circ\text{C}$ and $25.3 \pm 0.1^\circ\text{C}$, respectively, with the difference between minimum and maximum temperature less than 2.7°C in all trials.

Following experimentation, the accelerometers and heart rate loggers were removed and a new sheet of periphery wax was used to cover the exposed tissue. Lobsters were allowed to recover in the wet laboratory and fed *ad libitum* for 48 hours before being released on reefs near where they were caught. McGaw *et al.* (2018) observed moulting in animals held in tanks following this procedure, after which the excised area of the shell regrew normally, suggesting released lobsters could soon recover. Such a recovery of the excised shell area was observed in the lobster that moulted during Trial 3. All work was carried out under the Cape Eleuthera Institute's research permit from The Bahamas Department of Marine Resources.

Data preparation

DST micro-HRT heart rate loggers automatically calculate a Quality Index (QI) for each measurement ranging from 0 (best) to 3 (worst) based on the ability of its algorithm to estimate f_H from an ECG recording. The loggers and this algorithm were designed for use in small mammals, and these f_H estimates and corresponding QI have not been validated in decapod crustaceans. To do so, ECG recordings were analysed manually using the Pattern Finder software (v. 1.11.0, Star Oddi, Gardabaer, Iceland). Three ECG recordings were randomly selected from each QI in each lobster in the Surgery Recovery Trial and compared to the loggers' corresponding f_H estimates. Only f_H estimates with QI=0 were found to be accurate, with an average accuracy of 98.3%, as opposed to the average accuracies of 75.9%, 76.7% and 63% of estimates with QI=1, QI=2 and QI=3, respectively. Heart rate was therefore filtered to only include measurements of QI=0. This resulted in temporal data gaps in some lobsters, for which f_H was measured manually using Pattern Finder from the ECG recordings saved hourly. As such, temporal gaps in f_H data were never longer than 1 hour. Lobsters that had only one measurement per hour for more than 6 consecutive hours were excluded from analysis, resulting in the exclusion of 12 lobsters out of the 36 total.

Accelerometer data were converted into overall dynamic body acceleration (ODBA) in g units by summing the absolute difference between dynamic acceleration and static acceleration in each of its three axes, with static acceleration derived from a 6 second running mean per the methodology of Shepard *et al.* (2008). Behaviour in a given moment was categorized with a 1 second running mean of ODBA, based on 2.5 hours of video recorded of an instrumented lobster's movements, from three categories with non-overlapping ODBA thresholds: sitting (ODBA, $\leq 0.05 \text{ g}$), walking (ODBA, >0.05 and $\leq 1.5 \text{ g}$) or bursting (ODBA, >1.5) (i.e. when lobsters rapidly swim backwards by flapping their tail).

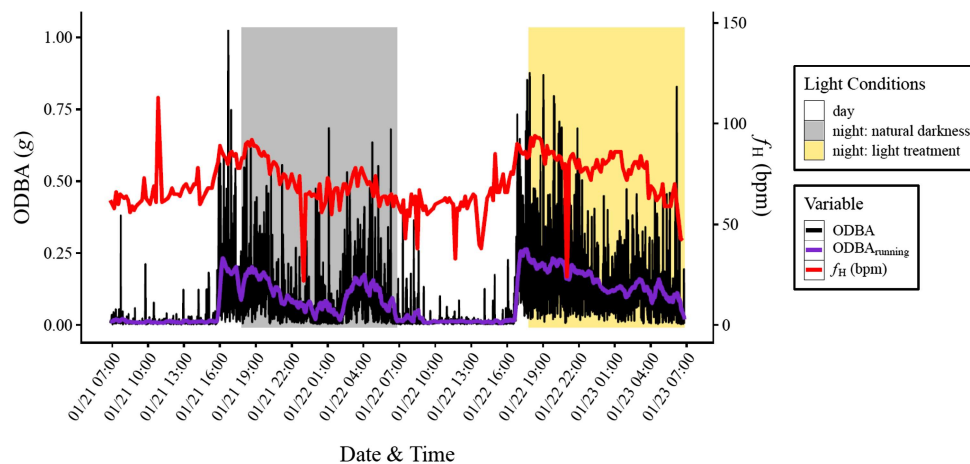


Figure 2: Examples of heart rate (f_H), activity (overall dynamic body acceleration, or ODBA) and a running mean of activity ($ODBA_{\text{running}}$) recorded in a lobster in Trial 2 (Jan 2018). Day and night were distinguished with sunrise and sunset times at 6:50 and 17:50, respectively, with the fourth night following instrumentation indirectly lit by an incandescent bulb for an illuminance of 1 lux at the mesocosm surface. ODBA was derived by summing the absolute difference between dynamic acceleration and static acceleration in each of the three axes recorded by the accelerometers, with static acceleration derived from a 6 second running mean. $ODBA_{\text{running}}$ was derived as a 25-minute running mean of ODBA.

Statistical analysis

Heart rate was averaged by day and night ($f_{H\text{-diel}}$) for analysis, with day and night distinguished by sunrise and sunset times at 6:50 and 17:50, respectively, which minimized discrepancies in sunrise and sunset times across the trials to less than 15 minutes. Daily or nightly average heart rate ($f_{H\text{-diel}}$) was analysed in ANCOVA models separately between the Surgery Recovery Trial ($n=6$) and the light treatment trials ($n=14$). These sample sizes were due to the 12 lobsters excluded for temporal gaps in $f_{H\text{-diel}}$ and another 6 lobsters excluded for accelerometer failures. In the model for the Surgery Recovery Trial, the effect of sequential days and nights (day 2, night 2, day 3, night 3, day 4 and night 4) was tested on $f_{H\text{-diel}}$, with daily or nightly average ODBA and body mass as covariates. In the model for the light treatment trials, the effects of sequential days and nights (day 3, night 3 with natural darkness, day 4 and night 4 with the light treatment) and trial (Trial 1, Trial 2 and Trial 3) were tested on $f_{H\text{-diel}}$, with daily or nightly average ODBA and body mass as covariates. Sex could not be analysed in these models as it was unevenly distributed between trials, but there was no consistent difference between the sexes across trials and only a 1.1% difference in $f_{H\text{-diel}}$ between them overall. Daily or nightly average heart rate ($f_{H\text{-diel}}$) was log-10 transformed in the Surgery Recovery Trial model to meet assumptions.

Activity was analysed in ANOVA models separately between the Surgery Recovery Trial and the light treatment trials, with the percentage of time lobsters spent walking averaged by day and night (A_{diel}) for analysis. Lobsters were found not to engage in bursting behaviour outside of the first few hours following instrumentation, so A_{diel} represented the total proportion of time lobsters were active in the times

examined. Body mass was not included as a covariate in these models as it did not meet the assumption of linearity with the dependent variable, and as above sex was not included as it was unevenly distributed between trials. In the model for the Surgery Recovery Trial, the effect of sequential days and nights was tested on A_{diel} . In the model for the light treatment trials, the effect of sequential days and nights and the effect of trial were tested on A_{diel} . As these models did not test f_H , they could include lobsters that were excluded from the f_H models above, so the sample sizes for the Surgery Recovery Trial model and light treatment trial model were 8 and 22, respectively. A_{diel} was log-10 transformed in both models to meet assumptions.

To assess whether f_H and activity over certain times of night were affected by the light treatment in ways that could be masked by averaging them in $f_{H\text{-diel}}$ and A_{diel} , respectively, f_H and ODBA were visualized by hourly increments in each trial (Fig. 3). Lobsters displayed a spike in activity around their nightly emergence, starting shortly before sunset and lasting 1–2 hours, in which ODBA was 15%–30% higher than activity over the rest of the night. The models above were therefore repeated on the average of f_H and the percentage of time lobsters spent walking between 17:20 and 19:20, denoted as $f_{H\text{-dusk}}$ and A_{dusk} , respectively, to compare f_H and activity during nightly emergence between night 3 dusk (natural darkness) and night 4 dusk (natural dusk in the Surgery Recovery Trial; unnaturally lit in the light treatment trials). 17:20 was chosen as the start of this temporal window as it was when the light was turned on half an hour before sunset in night 4 of the light treatment trials, with 19:20 chosen as its end because the spike in activity typically lasted 2 hours or less. In order to test the effect of activity on f_H at this 2-hour resolution, ODBA had to be averaged by

a rolling mean leading up to a given f_H measurement, as f_H can remain elevated for several hours following bouts of activity in decapods (Rose *et al.*, 1998; Chabot and Webb, 2008; McGaw and Reiber, 2015). To determine the temporal relationship between activity and f_H , a cross-correlation function was applied to the last 48 hours of ODBA and f_H measurements from individuals in the Surgery Recovery Trial, using the 'ccf' function in the R 'stats' package (version 3.4.4, R Foundation for Statistical Computing, Vienna, Austria). This cross-correlation function tests whether two time series correlate at temporal lags and whether these correlations are significant. The last 48 hours was chosen as the signal length as it was the only temporal window analysed where all lobsters had at least some significant correlations (e.g. compared to the last 24 hours or the third or fourth night following instrumentation, in which some lobsters had no significant correlations). It was found that, on average among significant correlations, f_H led ODBA at 25 ± 2.9 minutes, so a 25-minute running mean was applied to ODBA to use in the f_{H-dusk} and A_{dusk} models, henceforth referred to as $ODBA_{running}$. f_{H-dusk} was analysed in ANCOVA models separately between the Surgery Recovery Trial ($n=6$) and the light treatment trials ($n=14$), with the effect of night 3 dusk versus night 4 dusk tested on f_{H-diel} , the average of $ODBA_{running}$ over dusk and body mass included as covariates, and trial included as a variable in the model for the light treatment trials. A_{dusk} was analysed in ANOVA models separately between the Surgery Recovery Trial ($n=8$) and the light treatment trials ($n=22$). The effect of night 3 dusk versus night 4 dusk was tested on A_{dusk} , with trial included as a variable in the model for the light treatment trials. Body mass was not included as a covariate in the A_{dusk} models as it did not meet the assumption of linearity with the dependent variable. A_{dusk} was log-10 transformed in both models to meet assumptions.

Interactions were tested in all models by including interaction terms, and if an interaction occurred models were separated to analyse the difference between night 3 (natural darkness) and night 4 (light treatment) separately from the difference between day 3 and day 4. The effect of sequential days and nights and the effect of trial on both f_{H-diel} and A_{diel} interacted significantly ($P=0.04$ for both), so separate ANCOVA models were run for each comparing night 3 to night 4 and day 3 to day 4. Post hoc Tukey HSD analyses were run for each model to determine which factor levels were driving significant differences. All statistical tests were performed in R (R version 3.4.4, RStudio Inc., Boston, MA, USA).

Results

Surgery recovery trial

In the Surgery Recovery Trial, f_{H-diel} and A_{diel} had stabilized by the third day following instrumentation (Fig. 4A, 4B). Post hoc testing found no significant difference in f_{H-diel} between day 3, night 3, day 4 and night 4. Daily or nightly average ODBA did not significantly affect f_{H-diel} , and f_{H-diel}

significantly declined with body mass ($P < 0.001$; see below for scaling exponents and coefficients). Mean f_{H-diel} between the third day and fourth night following instrumentation was 78.1 bpm in the surgery recovery trial.

The percentage of time lobsters spent walking (A_{diel}) significantly differed over time ($P < 0.001$), however unlike f_{H-diel} , post hoc testing found no significant difference in A_{diel} between day 2, day 3 or day 4, or between night 2, night 3 or night 4. According to post hoc testing, A_{diel} approached being significantly higher in night 3 than day 3 ($P = 0.06$) and was significantly higher in night 4 than day 4 ($P = 0.04$). On average, lobsters in the Surgery Recovery Trial spent 23.4% of the night walking, compared to 8.4% of the day walking (Fig. 4B).

Significant correlations between f_H and ODBA were relatively weak, between $r = 0.12$ and $r = 0.14$. According to the cross-correlation function run on f_H and ODBA in the last 48 hours of the Surgery Recovery Trial, f_H correlated with ODBA at a 25 ± 2.9 minute lag, on average among significant correlations; however, this lag ranged from 14 to 35 minutes across individuals.

The results from the models for f_{H-dusk} and A_{dusk} were consistent with those for f_{H-diel} and A_{diel} . There was no significant difference in f_{H-dusk} or A_{dusk} between night 3 dusk and night 4 dusk (Fig. 4C, 4D). The average of $ODBA_{running}$ over dusk had no effect on f_{H-dusk} .

Light treatment trials

Daily or nightly average heart rate (f_{H-diel}) did not significantly differ between night 4 (light treatment) and night 3 (natural darkness), and did not significantly differ between day 3 and day 4 (Fig. 5A). Over the course of the experiment, trial had no significant effect on f_{H-diel} in either model. Though not tested for significance due to model separation, there was less than an 8% difference in f_{H-diel} between nights and the preceding day in all trials, with no consistency in nights having higher or lower f_{H-diel} than days (Fig. 6). Daily or nightly average ODBA did not significantly affect f_{H-diel} in either model. Daily or nightly average heart rate (f_{H-diel}) significantly declined with body mass ($p = 0.002$) in the model comparing nights and approached significantly declining in the model comparing days ($p = 0.056$). The scaling exponent (b) and coefficient (a) between $\log_e$ -transformed body mass (kg) and $\log_e$ -transformed f_{H-diel} (bpm) from day 3 to night 4 in all trials was $b = -0.301$ and $a = 4.076$, respectively. Mean f_{H-diel} over Trial 1, Trial 2 and Trial 3 was 82.6, 84.7 and 88.3 bpm, respectively.

The average daily or nightly percentage of time lobster spent walking (A_{diel}) did not differ significantly between night 4 (light treatment) and night 3 (natural darkness) (Fig. 5B). Though not tested for significance due to model separation, lobsters were more active during nights than days, on average spending 19.5% of nights walking versus 7.2% of days

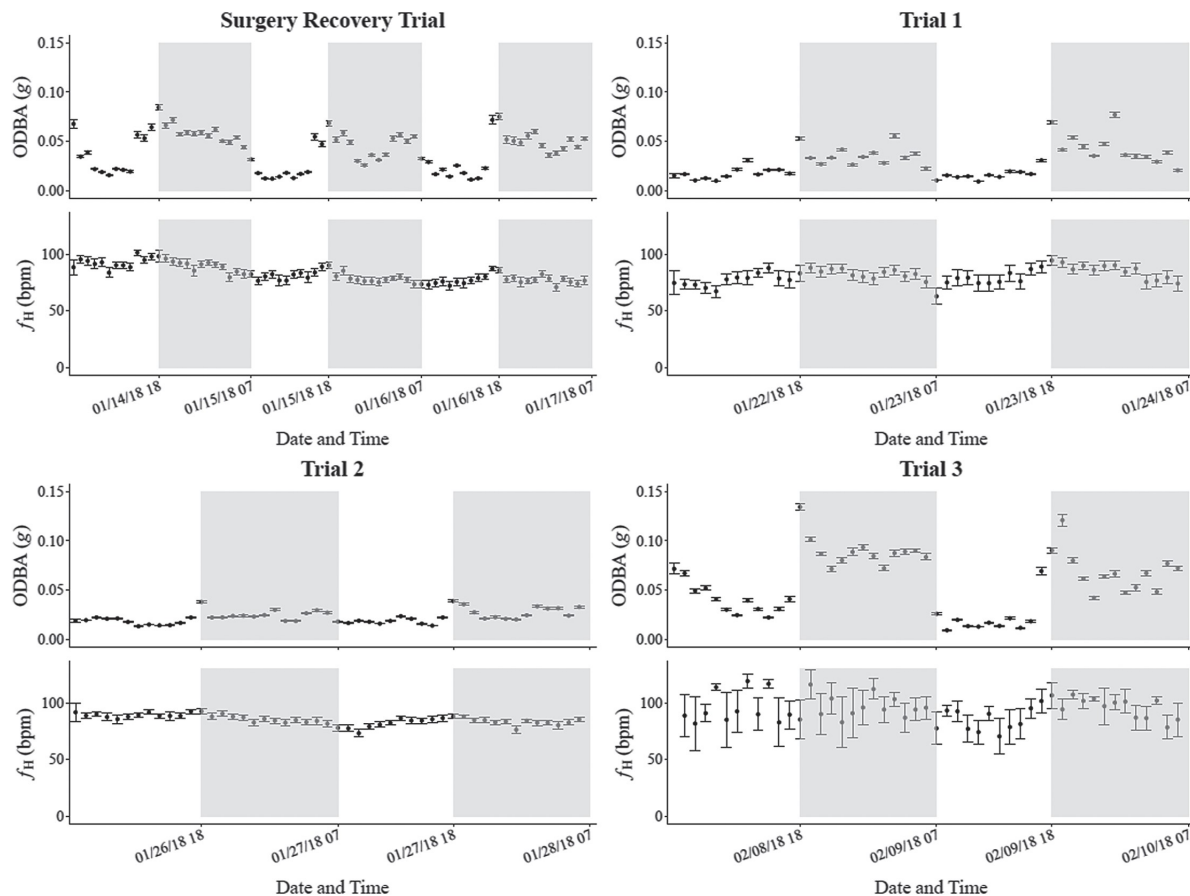


Figure 3: Heart rate (f_H) and activity (overall dynamic body acceleration, or ODBA) by hour in each of the four trials in this study. ODBA was derived by summing the absolute difference between dynamic acceleration and static acceleration in each of the three axes recorded by the accelerometers, with static acceleration derived from a 6-second running mean. Shaded areas represent night time, with sunrise and sunset times at 6:50 and 17:50, respectively.

walking. Over the course of the experiment, trial significantly affected activity in both days ($P=0.012$) and nights ($P<0.001$). In nights, according to post hoc testing, A_{diel} was significantly higher in Trial 3 than in Trial 1 ($P=0.002$) or Trial 2 ($P<0.001$) and was significantly lower in Trial 2 than Trial 1 ($P<0.001$). In days, according to post hoc testing, A_{diel} was significantly higher in Trial 3 than Trial 1 ($P=0.03$) or Trial 2 ($P=0.014$), whereas Trial 1 and Trial 2 did not significantly differ. On average, lobsters walked 12.6% of the time in the Trial 1, 8.7% of the time in Trial 2 and 23% of the time in Trial 3 (Fig. 6).

Results from the models for $f_{H\text{-dusk}}$ and A_{dusk} were consistent with those for $f_{H\text{-diel}}$ and A_{diel} . There was no significant difference in $f_{H\text{-dusk}}$ or A_{dusk} between night 4 dusk (artificial light) and night 3 dusk (natural light) (Fig. 5C, 5B). The average of $ODBA_{\text{running}}$ over dusk had no effect on $f_{H\text{-dusk}}$. Over the course of the experiment, trial had no significant effect on $f_{H\text{-dusk}}$, whereas A_{dusk} significantly differed between

trials ($p<0.001$) with the same pattern as A_{diel} . According to post hoc testing, A_{dusk} was significantly higher in Trial 3 than in Trial 1 ($p<0.001$) or Trial 2 ($p<0.001$), and was significantly lower in Trial 2 than Trial 1 ($p<0.001$). On average, lobsters spent 25.7% of dusk walking in Trial 1, 14.2% in Trial 2 and 55.3% in Trial 3.

Discussion

As unnatural light at night has been found to disrupt endocrine cycles and induce glucocorticoid-mediated stress responses in a suite of fish and terrestrial species (e.g. Gaston *et al.*, 2013; Brüning *et al.*, 2015; Szekeres *et al.*, 2017; Pulgar *et al.*, 2019), as well as alter behaviour in several species of decapod crustaceans (Nagata and Koike, 1997; Jackson and Moore, 2019; Fischer *et al.*, 2020), we hypothesized that *P. argus* would display a cardiac and behavioural response to its exposure. Contrary to our expectation, we found no change in f_H or activity between natural night time and night time

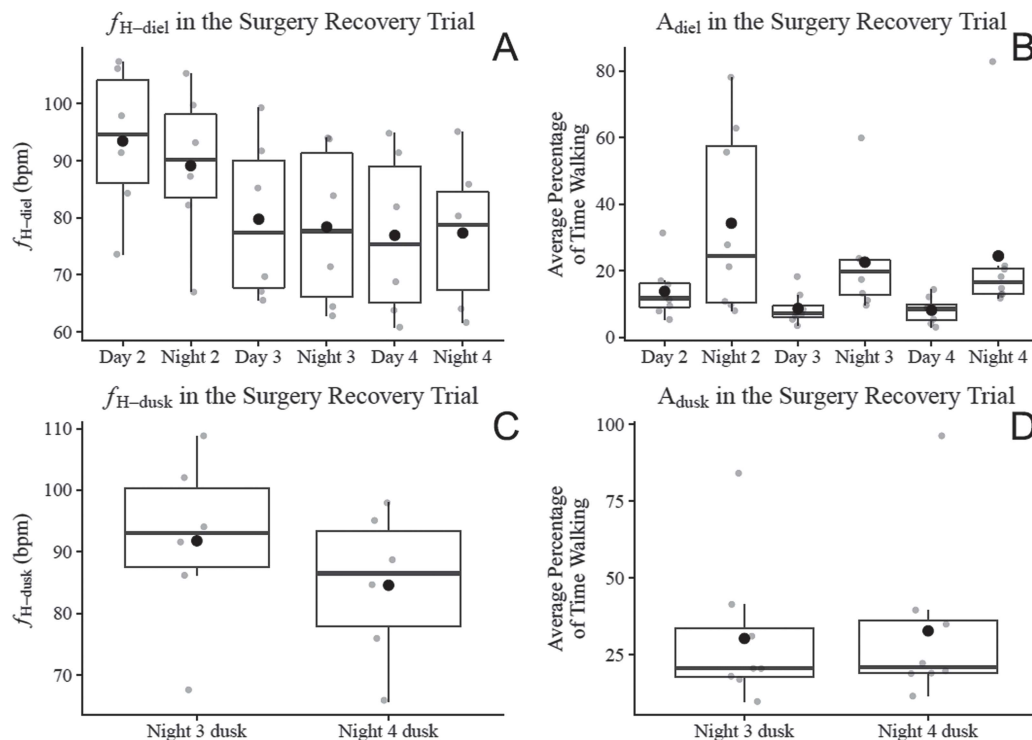


Figure 4: Daily and nightly average heart rate (f_{H-diel}) and the percentage of time lobsters spent walking (A_{diel}) over the surgery recover trial (A and B, respectively) and the average of f_H and the percentage of time lobsters spent walking between 17:20 and 19:20 (f_{H-dusk} and A_{dusk} , respectively) between night 3 dusk and night 4 dusk in the Surgery Recovery Trial (C and D, respectively). Filled black points represent means, and horizontal black bars represent medians. Day and night were distinguished with sunrise and sunset times at 6:50 and 17:50, respectively, with the fourth night following instrumentation indirectly lit by an incandescent bulb for an illuminance of 1 lux at the mesocosm surface. The percentage of time lobsters spent walking was determined through the calibration of a 2.5-hour video of an accelerometer-instrumented lobster, which determined that ODBA recordings between 0.05 and 1.5 g corresponded to walking. ODBA was derived by summing the absolute difference between dynamic acceleration and static acceleration in each of the three axes recorded by the accelerometers, with static acceleration derived from a 6-second running mean.

artificially lit at 1 lux to approximate light pollution near urban areas, nor between nightly emergence around sunset with and without this light treatment. The f_H and diel levels of activity we observed were in line with past measurements in this species (Maynard, 1960; McGaw *et al.*, 2018) and those reported for wild *P. argus* affixed with accelerometers in the Florida Keys (Gutzler *et al.*, 2015), respectively, indicating that our mesocosm conditions or experimental protocol did not confound the lobsters' regular physiology or phenology. To appropriately interpret these findings, we must consider the insights and limitations our observations provide into the relationships between f_H , cardiac output, physiological disturbance and behaviour in this species.

We observed a potential dissociation between f_H and cardiac output, necessitating a nuanced consideration of how our f_H measurements may reflect a stress response to artificial light at night. In our models for f_{H-diel} , we used daily or nightly average ODBA as a covariate to account for the effect of locomotor activity on f_H , and in our models for f_{H-dusk} , we

used a 25-minute running mean of ODBA ($ODBA_{running}$) as a covariate to account for the effect of recent locomotor activity on a narrower range of f_H readings. Contrary to precedence showing a positive relationship between f_H and activity in decapods due to the energetic demands imposed by locomotion (Rose *et al.*, 2001; Chabot and Webb, 2008; McGaw and Reiber, 2015), we observed a dissociation between these characteristics. Daily or nightly average ODBA did not significantly affect f_{H-diel} , $ODBA_{running}$ did not significantly affect f_{H-dusk} , and even the best correlations between ODBA and f_H identified by a cross-correlation function and used to derive the 25-minute running mean for $ODBA_{running}$ were relatively weak, between $r=0.12$ and $r=0.14$. As such, f_{H-diel} hardly differed between nights and days despite a marked increase in activity in nights versus days, nor between trials despite differences in nocturnal activity over lunar cycle (see below). It is possible that cardiac output does not increase following locomotor activity in *P. argus*, as such a dissociation has been reported in green crab (*Carcinus maenas*) and American lobster (*Homarus americanus*), in which f_H sometimes

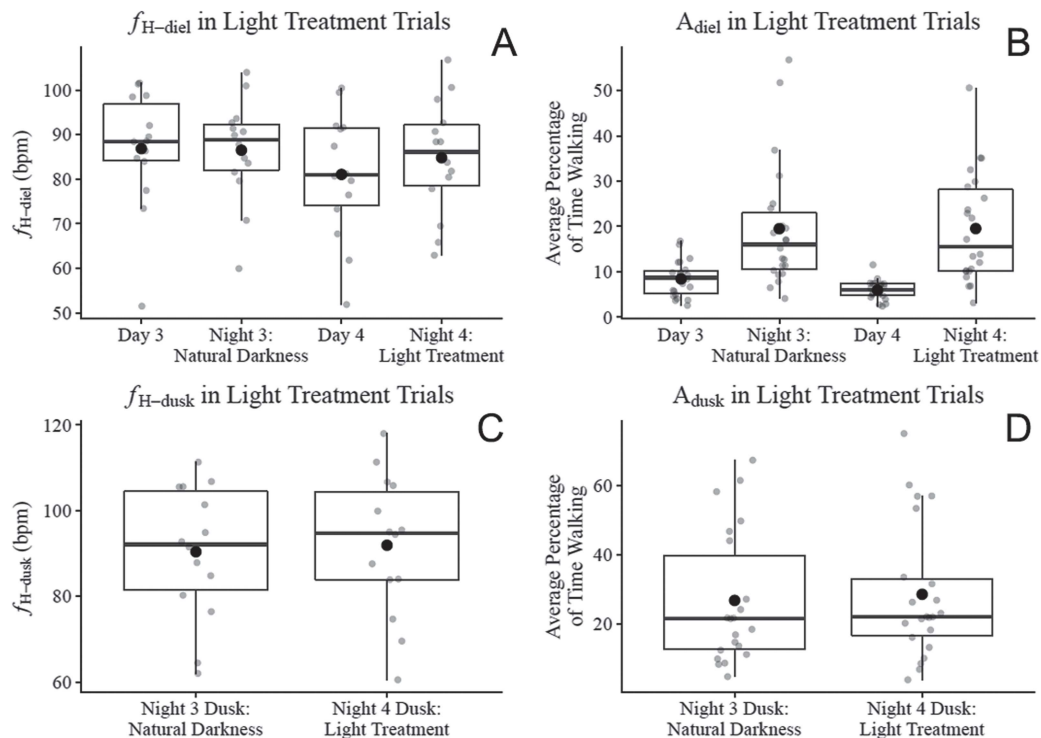


Figure 5: Daily and nightly average heart rate (f_{H-diel}) and the percentage of time lobsters spent walking (A_{diel}) over the light treatment trials (A and B, respectively) and the average of f_H and the percentage of time lobsters spent walking between 17:20 and 19:20 (f_{H-dusk} and A_{dusk} , respectively) between night 3 dusk and night 4 dusk in the light treatment trials (C and D, respectively). Filled black points represent means, and horizontal black bars represent medians. Day and night were distinguished with sunrise and sunset times at 6:50 and 17:50, respectively, with the fourth night following instrumentation indirectly lit by an incandescent bulb for an illuminance of 1 lux at the mesocosm surface. The percentage of time lobsters spent walking was determined through the calibration of a 2.5-hour video of an accelerometer-instrumented lobster, which determined that ODBA recordings between 0.05 and 1.5 g corresponded to walking. ODBA was derived by summing the absolute difference between dynamic acceleration and static acceleration in each of the three axes recorded by the accelerometers, with static acceleration derived from a 6-second running mean.

increased before the onset of locomotion (Aagaard *et al.*, 1995; O'Grady *et al.*, 2001). A more likely explanation for the dissociation we observed, however, is that cardiac stroke volume varied in response to locomotion rather than f_H , as f_H and stroke volume can vary independently in decapods to determine overall cardiac output (McMahon and Burnett 1990, McGaw *et al.*, 1994; McGaw and McMahon, 1996). While f_H has been found to be the primary determinant of cardiac output during locomotion in European lobster (*Homarus vulgaris*), blue crab (*Callinectes sapidus*) and *C. maenas* (Booth *et al.*, 1982; Hamilton, 1987; Hamilton and Houlihan, 1992), stroke volume has been found to be a greater determinant of cardiac output than f_H during locomotion in Dungeness crab (*Cancer magister*) (McMahon *et al.*, 1979; Wachter and McMahon, 1996). The relative significance of f_H versus stroke volume to cardiac output may also change with locomotor activity, as found in *H. americanus*, where stroke volume becomes a greater determinant of cardiac output than f_H only at higher walking speeds (Rose *et al.*, 2001). The heart rate biologgers we used cannot mea-

sure stroke volume so we can only speculate, but the sustained periods of locomotion we observed with little to no change in f_H suggest *P. argus* actively modulates stroke volume to compensate for the energetic demands and required cardiac output of movement and activity.

In the absence of locomotion, changes in the balance of neurohormones that mediate cardiac output generally act on f_H more than stroke volume in decapods (McGaw *et al.*, 1995; McGaw and Reiber, 2015). Artificial light at night can disrupt the circadian cycles of other neurohormones, such as melatonin or serotonin, which can have cascading impacts on these cardiac-mediating neurohormones (Castanon-Cervantes *et al.*, 1999; McGaw and Reiber, 2015; Jackson and Moore, 2019). A dissociation between f_H and a glucocorticoid-mediated stress response in this species is therefore unlikely, despite the dissociation we observed between f_H and locomotion, as such a response would likely be reflected in f_H before stroke volume. As we observed no effect of an artificial light treatment on f_H or activity, we may

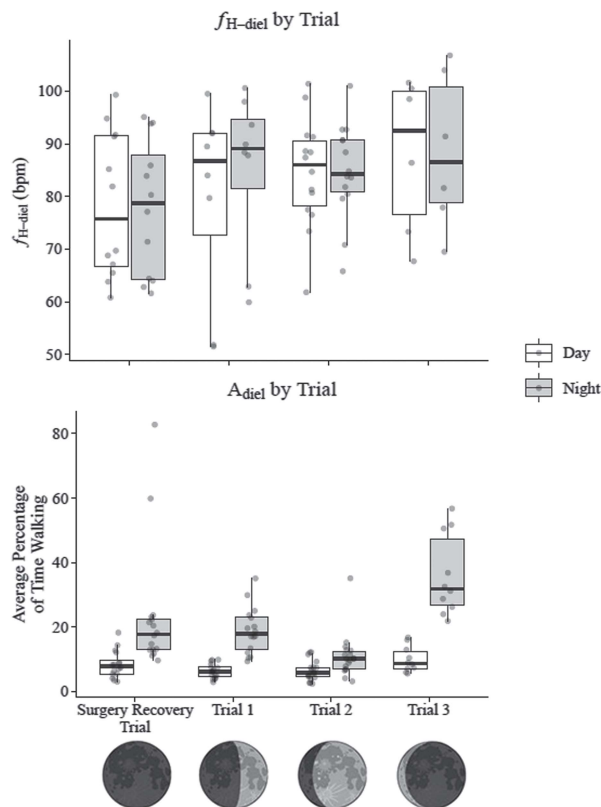


Figure 6: Daily and nightly average heart rate ($f_{H\text{-diel}}$) and the percentage of time lobsters spent walking (A_{diel}) by trial, with an illustration of lunar cycle phase depicted below the x-axis. Dates for the Surgery Recovery Trial, Trial 1, Trial 2 and Trial 3 were 13–17 January 2018, 20–24 January 2018, 24–28 January 2018 and 6–10 February 2018, respectively. Lunar cycle phase on the final night of the Surgery Recovery Trial, Trial 1, Trial 2 and Trial 3 was new moon, first quarter, waxing gibbous (3 days before full moon) and waning crescent (3 days after third quarter). Day and night were distinguished with sunrise and sunset times at 6:50 and 17:50, respectively. Data plotted for the Surgery Recovery Trial include only that from day 3 to night 4 in order to be consistent with Trials 1 to 3. The percentage of time lobsters spent walking was determined through the calibration of a 2.5-hour video of an accelerometer-instrumented lobster, which determined that ODBA recordings between 0.05 and 1.5 g corresponded to walking. ODBA was derived by summing the absolute difference between dynamic acceleration and static acceleration in each of the three axes recorded by the accelerometers, with static acceleration derived from a 6-second running mean.

assume that under the conditions tested here, artificial light at night does not represent a meaningful challenge to allostatic load or the circadian rhythm of f_H in *P. argus*. This is partly consistent with the findings of Jackson and Moore (2019), who found no effect of artificial light at night on haemolymph serotonin in two species of freshwater crayfish, rusty crayfish (*Faxonius rusticus*) and virile crayfish (*Faxonius virilis*). It is possible that our light treatment disrupted the lobsters'

endocrine balance at a magnitude small enough not to cause a change in f_H or behaviour; however, it is unlikely such a small change would have contributed meaningfully to allostatic load (Dantzer *et al.*, 2014; McEwen and Wingfield, 2010). Our findings that artificial light at night does not disrupt this species' regular activity levels or nightly emergence differ from past studies reporting suppression of activity in other decapods species exposed to artificial light at night, such as *P. japonicus*, another shallow-water panulirid that was sensitive to illuminance as low as 1.8×10^{-4} lux (Nagata and Koike, 1997). This suggests that behavioural responses to light pollution may be species-specific in decapods, with *P. argus* displaying a lower sensitivity than *P. japonicus* or the four freshwater crayfish species analysed by Jackson and Moore (2019) and Fischer *et al.* (2020), however further research on these species using lower-intensity light levels found near urban areas would be necessary to test such a hypothesis.

Altogether, our findings suggest *P. argus* may be physiologically resilient to artificial light at night, and may be less impacted by light pollution at a physiological and behavioural level compared to previously-analysed fish and terrestrial species (Gaston *et al.*, 2013; Brüning *et al.*, 2015; Szekeres *et al.*, 2017; Pulgar *et al.*, 2019). This would mean that light pollution effects do not manifest in sublethal impacts to performance or fitness in *P. argus*, as has been found for other anthropogenic disturbances in this species like fishery interactions (Vermeer, 1987; Parsons and Eggleston, 2005; Maxwell *et al.*, 2009), and that its fisheries may not be as threatened by light pollution as those for other species. Uncertainties remain in how light pollution fully impacts *P. argus* biology and ecology, however, such as how their predators and prey are affected and how this could impact trophic interactions (Higgs *et al.*, 2016; Underwood *et al.*, 2017), whether ecosystem processes in *P. argus* habitat are affected in ways that manifest in performance or fitness impacts (Navara and Nelson, 2007; Boudreau and Worm, 2012; Ayalon *et al.*, 2019), how the strongly lunar-mediated planktonic larval distribution and settlement of *P. argus* are affected (Eggleston *et al.*, 1998), or whether long-term exposure to artificial light at night manifests in a more chronic physiological response. Answering these questions would be necessary to understand the vulnerability of *P. argus* and the sustainability of its fisheries in the face of light pollution, however our findings offer some preliminary insight into its resiliency to this anthropogenic threat. This may be particularly relevant as marine protected areas (MPAs) are increasingly utilized to conserve marine species and promote sustainable fisheries, including MPAs proposed to facilitate *P. argus* conservation (Lipcius *et al.*, 2001; CRFM, 2011; Bertelsen, 2013; WECAFC, 2018), as light pollution is increasingly encroaching on MPAs globally and may impact their efficacy (Davies *et al.*, 2016).

An incidental observation in this study was that nocturnal activity in *P. argus* varied over the lunar cycle, with a marked suppression in Trial 2 just prior to full moon. While the increase in activity from Trial 2 (close to full moon) to Trial

3 (close to new moon) may have been augmented by a 3.4°C increase in average temperature, the decline in activity from Trial 1 (first quarter) to Trial 2 was accompanied by a more subtle cooling of 1.7°C. Temperature changes at such small magnitudes typically do not influence movement in other decapod species, suggesting these changes in activity could be due to lunar cycle (MacDiarmid *et al.*, 1991; González-Gurriarán and Freire, 1994; Hines *et al.*, 1995; González-Gurriarán *et al.*, 2002). Fishers have anecdotally reported higher catches of *P. argus* around new moon, however the few studies conducted on the topic have produced conflicting results. Lopezategui *et al.* (2011) found no correlation between lunar cycle and *P. argus* landings in Cuba, whereas Sutcliffe Jr (1956) reported higher landings during phases of low moonlight in Bermuda. Using acoustic telemetry, Bertelsen (2013) found that one-third of *P. argus* tagged on patch reefs in the Florida Keys were significantly more active during new moon and phases of low moonlight than during full moon, with a higher likelihood of entering fishers' traps. Why such a relationship between nocturnal activity and lunar cycle occurs and why it may only manifest in some individuals or some places is unclear. Lunar cycle has been found to regulate moulting in other decapods, with ornate rock lobster (*Panulirus ornatus*), blue crab (*C. sapidus*) and European green crab (*C. maenas*) moulting during or close to full moons (Ryer *et al.*, 1990; Skewes *et al.*, 1994; Zeng *et al.*, 1999). Moulting synchronization may lower the individual odds of predation, cannibalism, or interspecific competition for shelter during this vulnerable time, but we are only aware of evidence for *P. argus* synchronizing moults to photoperiod and temperature (Lipcius and Herrnkind, 1982, 1987; Quackenbush and Herrnkind, 1983), and not lunar cycle. While lower nocturnal activity would be expected during moulting synchronization, we did not observe any moults during Trial 2 (the closest trial to full moon) or in lobsters held for acclimation and release before, during, and after full moon. As such, *P. argus* may regulate moulting independently of lunar cycle, as found in southern rock lobster (*Jasus edwardsii*) (MacDiarmid *et al.*, 1991), and other factors may explain the suppression of activity we observed near full moon. Light from the full moon may make *P. argus* more vulnerable to predation, as for the crab *Neohelice granulata* (López and Rodríguez, 1998), or tides closer to the full moon may create stronger currents that deter activity. Regardless of the reasons, lunar periodicity in capture likelihood, trap encounter, or other measures of fishing mortality are not currently incorporated into *P. argus* management in The Bahamas or in other countries (Butler *et al.*, 2013; Gascoigne *et al.*, 2018; WECAFC, 2018; CLME+, 2019). Further research on this topic is warranted to determine drivers of *P. argus* lunar periodicity in movement and activity and whether this information can be used to better manage the species and its fisheries (Srisurichan *et al.*, 2005; Lopezategui *et al.*, 2011; Bertelsen, 2013).

In conclusion, we found evidence that artificial light at night does not alter heart rate or locomotor activity in *P. argus*, indicating that this species may be relatively resilient to

light pollution. We used incandescent light at 1 lux to approximate the typical illuminance and spectra of light pollution in urbanized nearshore areas (Perkin *et al.*, 2014; Brüning *et al.*, 2015); however, further research on different light spectra and intensities would be valuable to determine the impact of increasingly-used LED street lighting and high-intensity point sources of offshore light pollution like oil platforms or ship anchorages (Migaud *et al.*, 2007; Aubrecht *et al.*, 2010; Fischer *et al.*, 2020). By pairing two biologging devices equipped with heart rate and acceleration sensors, we determined the prospects and limitations of this approach for studying the physiology and behaviour of wild or free-moving decapod crustaceans. As we were limited to measuring f_H , further research is warranted to explore cardiac function in *P. argus*, and how f_H and stroke volume change in response to light pollution and other forms of anthropogenic disturbance. Such an approach would likely require using methods like pulsed Doppler, impedance conversion, or infrared transmission, however, which require varying degrees of animal constraint or tethering that can confound measurements of cardiac function (Aagaard *et al.*, 1995; McGaw and Nancollas, 2018; McGaw *et al.*, 2018). The heart rate biologgers we used therefore offer a compelling means of measuring f_H in free-moving or wild decapods, but may be limited in the insight they offer by their inability to measure stroke volume. Their applicability may vary with species, as some decapods exhibit a more predictable relationship between f_H and stroke volume than others (Hamilton, 1987; Hamilton and Houlihan, 1992; Rose *et al.*, 2001; McGaw and Reiber, 2015). Pre-existing information on this relationship exists for relatively few decapod species, meaning future use of these biologgers in other species must balance the limitations of using solely f_H measurements with the value of understanding their physiology in the face of anthropogenic disturbances. Another consideration is that these biologgers must be retrieved to download collected data, which may be challenging in highly mobile species like *P. argus*. While a similar study in the wild with *P. argus* would be valuable, our findings demonstrate that conditions in a mid-sized mesocosm did not confound this species' regular phenology or f_H (Maynard, 1960; Gutzler *et al.*, 2015; McGaw *et al.*, 2018). Despite these limitations, this technology shows promise for understanding the biology of decapod species threatened by anthropogenic disturbance in a scalable and relatively low-cost way (McGaw *et al.*, 2018).

Funding

This work was supported by the Natural Sciences and Engineering Research Council of Canada and the Canada Research Chairs Program [to S.J.C.] and by the University of California, Santa Barbara [to E.J.E.].

Acknowledgements

We extend many thanks to the staff, interns and visiting researchers at the Cape Eleuthera Institute for their assistance

in this study's field and mesocosm components, as well as the people of Eleuthera and The Bahamas for their hospitality.

References

- Aagaard A, Warman CG, Depledge MH, Naylor E (1995) Dissociation of heart rate and locomotor activity during the expression of rhythmic behaviour in the shore crab *Carcinus maenas*. *Mar Freshwater Behav Physiol* 26: 1–10.
- Ansell AD (1973) Changes in oxygen consumption, heart rate and ventilation accompanying starvation in the decapod crustacean *Cancer pagurus*. *Neth J Sea Res* 7: 455–475.
- Aubrecht C, Elvidge C, Ziskin D, Rodrigues P, Gil A (2010) Observing Stress of Artificial Night Lighting on Marine Ecosystems—a Remote Sensing Application Study. *ISPRS TC VII Symposium 100 Years ISPRS*. Institute of Photogrammetry and GeoInformation, Leibniz University, Hannover, Germany.
- Ayalon I, de Barros Marangoni LF, Benichou JL, Avisar D, Levy O (2019) Red Sea corals under artificial light pollution at night (ALAN) undergo oxidative stress and photosynthetic impairment. *Glob Change Biol* 25: 4194–4207.
- Bertelsen RD (2013) Characterizing daily movements, nomadic movements, and reproductive migrations of *Panulirus argus* around the Western Sambo Ecological Reserve (Florida, USA) using acoustic telemetry. *Fish Res* 144: 91–102.
- Booth CE, McMahon BR, Pinder AW (1982) Oxygen uptake and the potentiating effects of increased haemolymph lactate on oxygen transport during exercise in the blue crab, *Callinectes sapidus*. *J Comp Physiol* 148: 111–121.
- Boudreau SA, Worm B (2012) Ecological role of large benthic decapods in marine ecosystems: a review. *Mar Ecol Prog Ser* 469: 195–213.
- Brown RJ, Galloway TS, Lowe D, Browne MA, Dissanayake A, Jones MB, Depledge MH (2004) Differential sensitivity of three marine invertebrates to copper assessed using multiple biomarkers. *Aqua Toxicol* 66: 267–278.
- Brown DD, Kays R, Wikelski M, Wilson R, Klimley AP (2013) Observing the unwatchable through acceleration logging of animal behavior. *Anim Biotelemetry* 1: 20.
- Brüning A, Hölker F, Franke S, Preuer T, Kloas W (2015) Spotlight on fish: light pollution affects circadian rhythms of European perch but does not cause stress. *Sci Total Environ* 511: 516–522.
- Brüning A, Kloas W, Preuer T, Hölker F (2018) Influence of artificially induced light pollution on the hormone system of two common fish species, perch and roach, in a rural habitat. *Conserv Physiol* 6: coy016.
- Butler M, Cockcroft A, McDiarmid A, Wahle R (2013) *Panulirus Argus*, Caribbean Spiny Lobster. *The IUCN Red List of Threatened Species* 2011: eT169976A6697254 <https://www.iucnredlist.org/species/169976/6697254>.
- Castanon-Cervantes O, Battelle B, Fanjul-Moles ML (1999) Rhythmic changes in the serotonin content of the brain and eyestalk of crayfish during development. *J Exp Biol* 202: 2823–2830.
- Chabot CC, Webb LK (2008) Circadian rhythms of heart rate in freely moving and restrained American lobsters, *Homarus americanus*. *Mar Freshwater Behav Physiol* 41: 29–41.
- CLME+ (2019) Ecosystem approach to fisheries for the Caribbean spiny lobster *Panulirus argus*. *Combined Large Marine Ecosystems Plus Hub* <http://www.fao.org/fi/static-media/MeetingDocuments/WECAFC/WECAFC2019/17/Ref.35e.pdf>.
- Cooke SJ, Brownscombe JW, Raby GD, Broell F, Hinch SG, Clark TD, Semmens JM (2016) Remote bioenergetics measurements in wild fish: opportunities and challenges. *Comp Biochem Physiol Part A Mol Integ Physiol* 202: 23–37.
- CRFM (2011) Baseline review of the status and management of the Caribbean spiny lobster fisheries in the CARICOM region. *CRFM Technical & Advisory Document, No. 2011/5* http://www.crfm.int/~uwohxjxf/images/Baseline_Review_of_the_Status_and_Management_of_the_Spiny_Lobster_Formatted.pdf.
- Dąbrowski P, Cetner MD, Samborska IA, Kalaji MH (2015) Measuring light spectrum as a main indicator of artificial sources quality. *J Coast Life Med* 3: 400–406.
- Dantzer B, Fletcher QE, Boonstra R, Sheriff MJ (2014) Measures of physiological stress: a transparent or opaque window into the status, management and conservation of species? *Conserv Physiol* 2: cou023.
- Davies TW, Duffy JP, Bennie J, Gaston KJ (2014) The nature, extent, and ecological implications of marine light pollution. *Front Ecol Environ* 12: 347–355.
- Davies TW, Duffy JP, Bennie J, Gaston KJ (2016) Stemming the tide of light pollution encroaching into marine protected areas. *Conserv Lett* 9: 164–171.
- Depledge MH (1985) The influence of nutritional state on the circulatory and respiratory physiology of the shore crab, *Carcinus maenas*. *J Mar Biol Assoc U K* 65: 69–78.
- Eggleston DB, Lipcius RN, Marshall LS Jr, Ratchford SG (1998) Spatiotemporal variation in postlarval recruitment of the Caribbean spiny lobster in the Central Bahamas: lunar and seasonal periodicity, spatial coherence, and wind forcing. *Mar Ecol Prog Ser* 174: 33–49.
- Falchi F, Cinzano P, Duriscoe D, Kyba CC, Elvidge CD, Baugh K, Portnov BA, Rybnikova NA, Furgoni R (2016) The new world atlas of artificial night sky brightness. *Sci Adv* 2: e1600377.
- FAO (2018) Fishery and Aquaculture Country Profiles. Bahamas (2018). In *Country Profile Fact Sheets*. FAO Fisheries and Aquaculture Department, <http://www.fao.org/fishery/facp/BHS/en#CountrySector-Statistics>
- Fischer JR, Gangloff MM, Creed RP (2020) The behavioural responses of 2 Appalachian crayfish to cool and warm spectrum LED lights at night. *Freshwater Sci* 39: 000–000.

- Florey E, Kriebel ME (1974) The effects of temperature, anoxia and sensory stimulation on the heart rate of unrestrained crabs. *Comp Biochem Physiol Part A Physiol* 48: 285–300.
- Gascoigne J, Matthews T, Groeneveld J (2018) Marine stewardship council (MSC) public certification report: the Bahamas spiny lobster fishery. <https://fisheries.msc.org/en/fisheries/the-bahamas-spiny-lobster-fishery/@assessments>.
- Gaston KJ, Bennie J, Davies TW, Hopkins J (2013) The ecological impacts of night time light pollution: a mechanistic appraisal. *Biol Rev* 88: 912–927.
- Gaston KJ, Visser ME, Hölker F (2015) The biological impacts of artificial light at night: the research challenge. *Philos Trans R Soc* 370: 20140133.
- Gnanalingam G, Butler MJ IV (2018) Examining the relationship between size and feeding preferences in the Caribbean spiny lobster *Panulirus argus* (Latreille, 1804)(Decapoda: Achelata: Palinuridae). *J Crust Biol* 38: 245–249.
- González-Gurriarán E, Freire J (1994) Movement patterns and habitat utilization in the spider crab *Maja squinado* (Herbst) (Decapoda, Majidae) measured by ultrasonic telemetry. *J Exp Mar Biol Ecol* 184: 269–291.
- González-Gurriarán E, Freire J, Bernárdez C (2002) Migratory patterns of female spider crabs *Maja squinado* detected using electronic tags and telemetry. *J Crust Biol* 22: 91–97.
- Goldstein JS, Dubofsky EA, Spanier E (2015) Into a rhythm: Diel activity patterns and behaviour in Mediterranean slipper lobsters, *Scyllarides latus*. *ICES J Mar Sci* 72: i147–i154.
- Gutzler BC, Butler MJ IV, Behringer DC (2015) Casitas: a location-dependent ecological trap for juvenile Caribbean spiny lobsters, *Panulirus argus*. *ICES J Mar Sci* 72: i177–i184.
- Hamilton NM (1987) Respiratory and Circulatory Changes Accompanying Aquatic Treadmill Exercise of *Carcinus maenas* (L.) and *Homarus Vulgaris* (ME) (PhD Thesis). University of Aberdeen
- Hamilton NM, Houlihan DF (1992) Respiratory and circulatory adjustments during aquatic treadmill exercise in the European shore crab *Carcinus maenas*. *J Exp Biol* 162: 37–54.
- Higgs ND, Newton J, Attrill MJ (2016) Caribbean spiny lobster fishery is underpinned by trophic subsidies from chemosynthetic primary production. *Curr Biol* 26: 3393–3398.
- Hines AH, Wolcott TG, González-Gurriarán E, González-Escalante JL, Freire J (1995) Movement patterns and migrations in crabs: telemetry of juvenile and adult behaviour in *Callinectes sapidus* and *Maja squinado*. *J Mar Biol Assoc U K* 75: 27–42.
- Hölker F, Moss T, Griefahn B, Kloas W, Voigt CC, Henckel D, Hänel A, Kappeler PM, Völker S, Schwöpe A (2010) The dark side of light: a transdisciplinary research agenda for light pollution policy. *Ecol Soc* 15: 13–24.
- Jackson KM, Moore PA (2019) The intensity and spectrum of artificial light at night alters crayfish interactions. *Mar Freshwater Behav Physiol* 52: 131–150.
- Jury SH, Langley T, Gutzler BC, Goldstein JS, Watson WH (2018) Monitoring the behaviour of freely moving lobsters with accelerometers. *Bull Mar Sci* 94: 533–553.
- Koen EL, Minnaar C, Roever CL, Boyles JG (2018) Emerging threat of the 21st century lightscape to global biodiversity. *Glob Change Biol* 24: 2315–2324.
- Kyba C, Mohar A, Posch T (2017a) How bright is moonlight. *Astron Geophys* 58: 31–32.
- Kyba CC, Kuester T, De Miguel AS, Baugh K, Jechow A, Hölker F, Bennie J, Elvidge CD, Gaston KJ, Guanter L (2017b) Artificially lit surface of earth at night increasing in radiance and extent. *Sci Adv* 3: e1701528.
- Lipcius RN, Herrnkind WF (1982) Molt cycle alterations in behaviour, feeding and diel rhythms of a decapod crustacean, the spiny lobster *Panulirus argus*. *Mar Biol* 68: 241–252.
- Lipcius RN, Herrnkind WF (1987) Control and coordination of reproduction and moulting in the spiny lobster *Panulirus argus*. *Mar Biol* 96: 207.
- Lipcius RN, Stockhausen WT, Eggleston DB (2001) Marine reserves for Caribbean spiny lobster: empirical evaluation and theoretical metapopulation recruitment dynamics. *Mar Freshwater Res* 52: 1589–1598.
- López LS, Rodríguez EM (1998) Somatic growth in juveniles of the estuarine crab *Chasmagnathus granulata* Dana 1851 (Brachyura, Grapsidae), under laboratory conditions. *Invest Mar* 26: 127–135.
- Lopeztegui A, Baisre JA, Capetillo N (2011) Influence of lunar cycle on catches of spiny lobster *Panulirus argus* (Decapoda: Palinuridae) in the Gulf of Batabanó, Cuba. *Rev Biol Trop* 59: 207–216.
- MacDiarmid AB, Hickey B, Maller RA (1991) Daily movement patterns of the spiny lobster *Jasus edwardsii* (Hutton) on a shallow reef in northern New Zealand. *J Exp Mar Biol Ecol* 147: 185–205.
- MacDougall-Shackleton SA, Bonier F, Romero LM, Moore IT (2019) Glucocorticoids and “stress” are not synonymous. *Integ Organ Biol* 1: obz017.
- Maxwell KE, Matthews TR, Bertelsen RD, Derby CD (2009) Using age to evaluate reproduction in Caribbean spiny lobster, *Panulirus argus*, in the Florida keys and Dry Tortugas, United States. *N Z J Mar Freshwater Res* 43: 139–149.
- Maynard DM (1960) Heart rate and body size in the spiny lobster. *Physiol Zool* 33: 241–251.
- McEwen BS, Wingfield JC (2010) What’s in a name? Integrating homeostasis, allostasis and stress. *Horm Behav* 57: 105.
- McGaw JJ, Airriess CN, McMahon BR (1994) Patterns of haemolymph-flow variation in decapod crustaceans. *Mar Biol* 121: 53–60.

- McGaw IJ, McMahon BR (1996) Cardiovascular responses resulting from variation in external salinity in the Dungeness crab, *Cancer magister*. *Physiol Zool* 69: 1384–1401.
- McGaw IJ, Reiber CL (2015) Circulatory physiology. In *The Natural History of Crustaceans* 4, Oxford University Press, Oxford, UK, pp. 199–246
- McGaw IJ, Nancollas SJ (2018) Experimental setup influences the cardiovascular responses of decapod crustaceans to environmental change. *Can J Zool* 96: 1043–1052.
- McGaw IJ, Steell SC, Leeuwen TEV, Eliason EJ, Cooke SJ (2018) Application of miniature heart rate data loggers for use in large free-moving decapod crustaceans: method development and validation. *Physiol Biochem Zool* 91: 731–739.
- McGaw IJ, Wilkens JL, McMahon BR, Airriess CN (1995) Crustacean cardioexcitatory peptides may inhibit the heart in vivo. *J Exp Biol* 198: 2547–2550.
- McLean KM, Todgham AE (2015) Effect of food availability on the growth and thermal physiology of juvenile Dungeness crabs (*Metacarcinus magister*). *Conserv Physiol* 3.
- McMahon BR, McDonald DG, Wood CM (1979) Ventilation, oxygen uptake and haemolymph oxygen transport, following enforced exhausting activity in the Dungeness crab *Cancer magister*. *J Exp Biol* 80: 271–285.
- McMahon BR, Burnett LE (1990) The crustacean open circulatory system: a reexamination. *Physiol Zool* 63: 35–71.
- Migaud H, Cowan M, Taylor J, Ferguson HW (2007) The effect of spectral composition and light intensity on melatonin, stress and retinal damage in post-smolt Atlantic salmon, *Salmo salar*. *Aquaculture* 270: 390–404.
- Nagata Y, Koike T (1997) Collapse of the diurnal variation pattern of lobster activity and its causes. *Bull Mar Sci* 61: 129–138.
- Navara KJ, Nelson RJ (2007) The dark side of light at night: physiological, epidemiological, and ecological consequences. *J Pineal Res* 43: 215–224.
- Neumann B, Vafeidis AT, Zimmermann J, Nicholls RJ (2015) Future coastal population growth and exposure to sea-level rise and coastal flooding—a global assessment. *PLoS One* 10: e0118571.
- O'Grady DF, Jury SH, Watson WH III (2001) Use of a treadmill to study the relationship between walking, ventilation and heart rate in the lobster *Homarus americanus*. *Mar Freshwater Res* 52: 1387–1394.
- Parsons DM, Eggleston DB (2005) Indirect effects of recreational fishing on behaviour of the spiny lobster *Panulirus argus*. *Mar Ecol Prog Ser* 303: 235–244.
- Perera E, Díaz-Iglesias E, Fraga I, Carrillo O, Galich GS (2007) Effect of body weight, temperature and feeding on the metabolic rate in the spiny lobster *Panulirus argus* (Latreille, 1804). *Aquaculture* 265: 261–270.
- Perkin EK, Hölker F, Heller S, Berghahn R (2014) Artificial light and nocturnal activity in gammarids. *PeerJ* 2: e279.
- Perkin EK, Hölker F, Richardson JS, Sadler JP, Wolter C, Tockner K (2011) The influence of artificial light on stream and riparian ecosystems: questions, challenges, and perspectives. *Ecosphere* 2: 1–16.
- Pulgar J, Zeballos D, Vargas J, Aldana M, Manriquez PH, Manriquez K, Quijón PA, Widdicombe S, Anguita C, Quintanilla D (2019) Endogenous cycles, activity patterns and energy expenditure of an intertidal fish is modified by artificial light pollution at night (ALAN). *Environ Poll* 244: 361–366.
- Quackenbush LS, Herrnkind WF (1983) Regulation of the molt cycle of the spiny lobster, *Panulirus argus*: effect of photoperiod. *Comp Biochem Physiol Part A Physiol* 76: 259–263.
- Rose RA, MacDougall K, Patel A, Wilkens JL, Walker RL (2001) Effects of walking on ventilatory and cardiac function in intact and cardiac-impaired lobsters. *Physiol Biochem Zool* 74: 102–110.
- Rose RA, Wilkens JL, Walker RL (1998) The effects of walking on heart rate, ventilation rate and acid-base status in the lobster *Homarus americanus*. *J Exp Biol* 201: 2601–2608.
- Ryer CH, van Montfrans J, Orth RJ (1990) Utilization of a seagrass meadow and tidal marsh creek by blue crabs *Callinectes sapidus*. II. Spatial and temporal patterns of moulting. *Bull Mar Sci* 46: 95–104.
- Shepard EL, Wilson RP, Halsey LG, Quintana F, Laich AG, Gleiss AC, Liebsch N, Myers AE, Norman B (2008) Derivation of body motion via appropriate smoothing of acceleration data. *Aquat Biol* 4: 235–241.
- Sherman KD, Shultz AD, Dahlgren CP, Thomas C, Brooks E, Brooks A, Brumbaugh DR, Gittens L, Murchie KJ (2018) Contemporary and emerging fisheries in the Bahamas—conservation and management challenges, achievements and future directions. *Fish Manag Ecol* 25: 319–331.
- Skewes TD, Pitcher RC, Trendall JT (1994) Changes in the size structure, sex ratio and moulting activity of a population of ornate rock lobsters, *Panulirus ornatus*, caused by an annual maturation molt and migration. *Bull Mar Sci* 54: 38–48.
- Smith KN, Herrnkind WF (1992) Predation on early juvenile spiny lobsters *Panulirus argus* (Latreille): influence of size and shelter. *J Exp Mar Biol Ecol* 157: 3–18.
- Smith NS, Zeller D (2013) Bahamas catch reconstruction: fisheries trends in a tourism-driven economy (1950–2010). *Fish Bull* 114: 117–132.
- Srisurichan S, Caputi N, Cross J (2005) Impact of lunar cycle and swell on the daily catch rate of western rock lobster (*Panulirus cygnus*) using time series modelling. *N Z J Mar Freshwater Res* 39: 749–764.
- Sutcliffe WH Jr (1956) Effect of light intensity on the activity of the Bermuda spiny lobster *Panulirus argus*. *Ecology* 37: 200–201.
- Szekeres P, Wilson AD, Haak CR, Danylchuk AJ, Brownscombe JW, Elvidge CK, Shultz AD, Birnie-Gauvin K, Cooke SJ (2017) Does coastal

- light pollution alter the nocturnal behaviour and blood physiology of juvenile bonefish (*Albula vulpes*)? *Bull Mar Sci* 93: 491–505.
- Thums M, Whiting SD, Reisser J, Pendoley KL, Pattiaratchi CB, Proietti M, Hetzel Y, Fisher R, Meekan MG (2016) Artificial light on water attracts turtle hatchlings during their near shore transit. *R Soc Open Sci* 3: 160142.
- Underwood CN, Davies TW, Queirós AM (2017) Artificial light at night alters trophic interactions of intertidal invertebrates. *J Anim Ecol* 86: 781–789.
- Vermeer GK (1987) Effects of air exposure on desiccation rate, haemolymph chemistry, and escape behaviour of the spiny lobster, *Panulirus argus*. *Fish Bull* 85: 45–51.
- De Wachter B, McMahon BR (1996) Haemolymph flow distribution, cardiac performance and ventilation during moderate walking activity in *Cancer magister* (Dana) (Decapoda, Crustacea). *J Exp Biol* 199: 627–633.
- WECAFC (2018) MARPLESCA—The Regional Caribbean Spiny Lobster (*Panulirus argus*) fishery management plan. Western Atlantic Fishery Commission. <http://www.fao.org/fi/static-media/Meeting Documents/WECAFC/SAG2018/6e.pdf>.
- Whiteley NM, Robertson RF, Meagor J, El Haj AJ, Taylor EW (2001) Protein synthesis and specific dynamic action in crustaceans: effects of temperature. *Comp Biochem Physiol Part A Mol Integ Physiol* 128: 593–604.
- Wikelski M, Cooke SJ (2006) Conservation physiology. *Trend Ecol Evol* 21: 38–46.
- Winterbottom M, Haughton M, Mutrie E, Grieve K (2012) Management of the spiny lobster fishery in CARICOM countries: status and recommendations for conservation. Proceedings of the 64th Gulf and Caribbean Fisheries Institute, Puerto Morelos, Mexico.
- Zeng C, Abello P, Naylor E (1999) Endogenous tidal and semilunar moulting rhythms in early juvenile shore crabs *Carcinus maenas*: implications for adaptation to a high intertidal habitat. *Mar Ecol Prog Ser* 191: 257–266.