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Live fast, die young: Behavioural and physiological impacts of light pollution on a marine fish during larval recruitment

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ABSTRACT

Artificial light at night (ALAN) is a recently acknowledged form of anthropogenic pollution of growing concern to the biology and ecology of exposed organisms. Though ALAN can have detrimental effects on physiology and behaviour, we have little understanding of how marine organisms in coastal areas may be impacted. Here, we investigated the effects of ALAN exposure on coral reef fish larvae during the critical recruitment stage, encompassing settlement, metamorphosis, and post-settlement survival. We found that larvae avoided illuminated settlement habitats, however those living under ALAN conditions for 10 days post-settlement experienced changes in swimming behaviour and higher susceptibility to nocturnal predation. Although ALAN-exposed fish grew faster and heavier than control fish, they also experienced significantly higher mortality rates by the end of the experimental period. This is the first study on the ecological impacts of ALAN during the early life history of marine fish.

1. Introduction

In September 1878, while Thomas Edison was devising light bulb technology for the world's first mass-produced electric lighting system, he wrote in his laboratory notes: "With the process I have just discovered, I can produce a thousand – aye, ten thousand – from one machine. Indeed, the number may be said to be infinite" (Friedel and Israel, 2010). Recent satellite data estimates over 80% of the world's human population experiences artificial light at night, with both the extent and brightness of lit areas increasing at a rate of 2.2% per year between 2012 and 2016 (Falchi et al., 2016; Kyba et al., 2017). This phenomenon of anthropogenic light transforming the natural diel light-dark cycle has been linked to widespread biological impacts in a diverse array of taxa including birds, mammals, reptiles, amphibians, insects, and fish, giving rise to the term "light pollution" (Longcore and Rich, 2004; Navara and Nelson, 2007; Riegel, 1973). In contrast to birds and mammals however, impacts on fishes have received comparatively little attention despite indications that they may be more susceptible to deleterious effects due to taxon-specific traits such as a lack of eye lids (Yokogawa et al., 2007).

Biological impacts of light pollution (e.g. metabolic disruption, oxidative stress, immunological dysfunction, sleep loss, energy expenditure and altered growth rate (Bedrosian et al., 2011; Gaston et al., 2015; Navara and Nelson, 2007; Raap et al., 2015; Wyse et al., 2011)) are linked to the disruption of endogenous rhythms driven by daily, seasonal, and lunar light cycles (Gaston et al., 2017). Artificial light at night (ALAN) also impacts species behaviour and inter-species interactions through altering the visual environment around them. Nowhere is this more apparent than in predator-prey interactions involving nocturnal species. These interactions can favour the predator (e.g. through diminishing the effectiveness of anti-predator behaviour, increasing visual acuity or attracting greater prey density (Becker et al., 2013; Bolton et al., 2017; Wakefield et al., 2015)) or the prey (e.g. by reducing foraging activity of nocturnal predators, improving predator avoidance or greater prey density providing safety in numbers (Cerri, 1983; Davies et al., 2013b)). In either scenario, these changes in interspecies dynamics have ecological implications and could lead to trophic cascades with the potential to alter entire communities (Bennie et al., 2015; Bolton et al., 2017; Davies et al., 2012; Longcore and Rich, 2004).

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Although we are becoming increasingly aware of the effects of light pollution in terrestrial systems, we still know little about the effects of light pollution in the marine environment (Davies et al., 2014; Depledge et al., 2010). Sources of artificial light at night illuminating marine areas are numerous, including direct light from point sources (e.g. recreational and commercial shipping, fishing vessels and oil platforms) as well as larger scale continuous lighting (e.g. skyglow from coastal settlements and marine infrastructure). One of our largest knowledge gaps relates to impacts in coral reef environments. While these marine biodiversity hotspots face threats from several natural and anthropogenic stressors, no study to date has investigated how light pollution might impact ecological processes. The presence of light pollution on coral reefs is of particular concern due to the reliance of coral reef fishes on natural lunar cues to regulate reproductive periodicity in adults and the timing of reef-colonization (settlement) by larvae at the end of their pelagic dispersal phase (Besson et al., 2017; Davies et al., 2013a; Naylor, 1999).

During settlement larval fish undergo the most drastic physiological and behavioural transition of their life cycle into juvenile fish more closely representing their adult form, a process known as metamorphosis. The combination of selection pressure and high energetic requirements during this brief window (often < 24 h in coral-reef species) makes it a critical interval in determining population persistence (Doherty et al., 2004; Thorisson, 1994). As replenishment from the survival of larval pulses after settlement (larval recruitment) is also critical to population persistence, any impacts on behaviours and physiological functions relating to ecological fitness during this critical life transition could have unpredictable effects at different levels of biological organisation. Here, we investigate for the first time the impacts of ALAN on 1) behaviour, 2) endocrine function, and 3) growth and survival of a coral reef fish (*Acanthurus triostegus*) during larval recruitment. With the exponential growth of the human population and continuous expansion of infrastructure into marine landscapes, increasing our understanding of how anthropogenic lighting is affecting marine habitats at night is crucial for preserving biodiversity and ecosystem function (Bulleri and Chapman, 2010; Davies et al., 2016).

2. Methods

2.1. Study species & laboratory setup

All experiments were conducted using convict surgeonfish (*Acanthurus triostegus*) collected during settlement to rock pools near Temae Beach, Moorea Island, French Polynesia (17°29′50.7"S 149°45′15.3"W). We identified newly arrived *A. triostegus* larvae as transparent with silver pigmentation over the brain case and alimentary tract (i.e. pre-metamorphosis (McCormick, 1999)). We collected larvae using dip nets during the overnight high tide around the new moon phase in May 2017. Larvae were transported to the laboratory facilities at the Centre de Recherches Insulaires et Observatoire de l'Environnement (CRIOBE) and placed in aquaria (36 cm × 46 cm × 23 cm) supplied with flow-through filtered seawater.

Immediately upon transfer into aquaria, *A. triostegus* larvae were allocated into two treatment groups: a control 12L:12D light-dark cycle, or an artificial light at night cycle (i.e. 12L:12L). Aquaria were lit from overhead with dimmable smd5050 white LED strip lights (6500 k, λp = 450 nm, supplementary material Fig. 1) placed 40 cm above the water's surface, supplying all tanks with a light intensity of 650–700 lx during the day (7 am–7 pm). Importantly, treatment tanks only received an ecologically relevant level of artificial light at night of 20–25 lx from 7 pm–7 am, a range used in previous studies to mimic in situ measurements taken in marine areas exposed to night-time lighting (Davies et al., 2015). We monitored light intensity in aquaria at the water's surface with an EA31 luxmeter (Extech Instruments, MA). Water temperature in the tanks was maintained at 28.7 °C (± 1.1 °C). Rock rubble covered in turf algae collected from the rock platform at Temae reef was placed in the aquaria to provide fish with both shelter and an ad libitum food source. Rocks were replaced to replenish turf algae every two days.

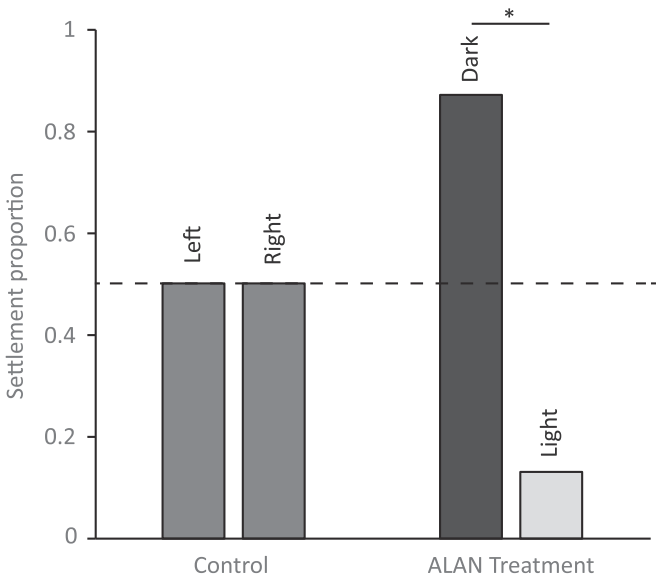

Fig. 1. Preference of *Acanthurus triostegus* larvae for rock rubble settlement habitats with and without artificial light at night compared to left and right sides of the binary choice chamber under control conditions. Dotted line shows distribution expected by chance, asterisk indicates significant difference from expected distribution ($p < 0.05$).

2.2. Experimental procedure

2.2.1. Habitat choice experiments

Habitat choice experiments were conducted to test whether *A. triostegus* larvae preferred to settle to habitat with or without the presence of ALAN. After collection larvae were placed in holding aquaria to acclimate to laboratory conditions and recover from handling, with choice experiments commencing immediately after dusk on day 1 (d1, the day after the night-arrival of larvae). We tested larvae in a binary choice chamber (170 cm × 60 cm × 22 cm) with coral rubble placed at each end (Supplementary material Fig. S1). The chamber itself was delineated into 3 equal sections (i.e. left, centre and right) and randomly applied with either a control (i.e. dark vs. dark habitat choice) or a light treatment (i.e. a dark vs. light habitat) provided by a down-focused LED torch (250 lx) mounted 40 cm above the water's surface above one rubble habitat. To begin each trial, a single larva was introduced into a holding chamber – a vertically standing PVC pipe (12 cm diameter) – in the centre of the middle zone. The holding chamber had two mesh sides facing each end of the choice arena, so that fish could visibly assess the two habitat choices. After an acclimation period of 3 min, the holding chamber was removed allowing the fish to explore the arena. After 2 min we inspected the arena and each habitat, and the position of the larva was noted. Fish were classed as having made a decision if they were within one of the end zones or not having made a decision if they were found within the middle section of the arena. Control and treatment settlement distributions were tested against the distribution expected by chance (50:50) using a G-test for goodness of fit.

2.2.2. Endocrine response

Thyroid hormone levels were measured on fish euthanised (MS222 immersion at 0.4 $mgml^{-1}$) and dry-frozen (−20 °C) at day 2 (d2) and day 5 (d5) post-settlement. Tri-iodothyronine (T_3) and thyroxine (T_4) were extracted following an extraction protocol already established for *A. triostegus* samples (Holzer et al., 2017). Thyroid hormone quantification was performed following the Roche ELICA kit on a Cobas

analyser by a medical laboratory according to the manufacturer's standardized method. Sample sizes of 8 to 10 fish per treatment were used for each sampling point.

2.2.3. Conspecific visual cue response

To test the effect of acute exposure to artificial light at night on the behavioural response of *A. triostegus* larvae to visual stimuli, choice tests were performed using a three-compartment test chamber. Clear Perspex sheets separating the compartments allowed the test fish to receive visual cues from juvenile conspecifics or heterospecifics being held in each of the end compartments. As *A. triostegus* have shown an attraction to visual cues of conspecifics during early life-history (Lecchini et al., 2014), our null hypothesis was that individuals would spend significantly more time close to conspecifics in the test chamber. A detailed description of test protocol including a diagram of the test chamber (Fig. S2) is provided in the supplementary material. Briefly, visual cue response trials were conducted on day 10 of exposure to light and control treatments in the lab. Each trial began with the introduction of a single *A. triostegus* larva from one of the two treatments into an opaque cylindrical holding chamber standing vertically in the centre of the central compartment for an acclimation period of 1 min. After the acclimation period, the pipe was removed and the position of the larva in one of three equal-sized visually-delineated zones (i.e. central, by conspecifics or by heterospecifics) was recorded every 5 s for a period of 2 min. Each larva was tested only once (n = 40), and after each trial the test chamber was emptied and washed with fresh water. The positions of the conspecific and heterospecific treatment fish were switched between each end of the test chamber after every 10 runs to account for a potential side bias in the experimental apparatus. Furthermore, we tested a subset of larvae using the same procedure, but with opaque screens placed between the central compartment and the cue fish compartments to eliminate stimuli and test for tank/arena effects (n = 20). The time spent by light (ALAN) and control treatment larvae near conspecifics and heterospecifics, and the time spent in left and right sides of the test chamber during control runs was compared with non-parametric Wilcoxon Signed Rank tests, which is a suitable test for time proportion data of this kind (O'Connor et al., 2016). We also compared the time a larva took to first move to a sub-compartment at either side of the chamber after release from the holding chamber (i.e. the time to make an initial choice) between ALAN and control treatment fish using Wilcoxon Rank Sum tests.

2.2.4. Post-settlement growth and survival

To examine the effects of artificial light at night on growth rates of fish, we measured weight and examined growth histories of *A. triostegus* larvae after 10 days (d10) of exposure to light (ALAN) or control treatments in the lab, the period in which metamorphosis is completed in this species (Holzer et al., 2017). Larvae were euthanized (as per above), and their wet weights (n = 80) were recorded. The sagittal otoliths were extracted from all 80 fish, and growth histories were successfully quantified for 60 of these individuals. Transverse sections through the nucleus of the otoliths were produced to expose daily growth increments across the transverse plane (Wilson and McCormick, 1997). A detailed description of otolith imaging and preparation is provided in the supplementary material. Briefly, polished samples were observed in immersion oil and a set of digital images was collected for each otolith to measure growth increments along the dorsal axis. Individual increment widths from the settlement mark to the edge of the otolith were recorded to the nearest 0.001 μm. This section of the otolith represented the experimental period (10 days), as fish were collected immediately upon settlement and otoliths were harvested on Day 10.

Otolith increment width was used as a proxy for daily fish growth, which is based on the generally held assumption that there is a strong relationship between somatic and otolith growth (Thorrold and Hare, 2002). The 10 daily increments closest to the otolith's edge were summed to calculate the total post-settlement growth of individuals over the duration of the experiment. Samples were read only once by a single observer who was blind with respect to metadata associated with each sample. Where daily increments were difficult to identify, but a mark corresponding to settlement was clearly visible (Victor, 1982), a measurement from the settlement mark to the otolith edge was taken along the dorsal axis to give a measure of total post-settlement growth over 10 days. To evaluate whether exposure to artificial light at night had an effect on post-settlement growth rates and mean weight of *A. triostegus*, we used Welch two-sample *t*-tests to compare control and treatment groups.

To analyse how mortality was affected by ALAN we recorded any mortality of fish discovered during routine inspections of aquaria during the experimental period. We then used this data to generate Kaplan-Meier survival curves for each treatment and compared them to investigate differences in survival probability over time using the "survival" package in R (Diez, 2013).

2.2.5. Predator-prey interaction

To test how exposure to ALAN affects post-settlement predation risk, predation experiments on *A. triostegus* (n = 7) were conducted at 10 days post-settlement (d10). Circular tanks (85 cm diameter, 40 cm depth) were used as test arenas; PVC pipe sections (15 cm diameter) were placed in the arena for predator shelter, and pieces of rock rubble (4–6 cm diameter) were included for prey shelter. At least 24-h prior to being used in a predation experiment, *A. triostegus* individuals were tagged with a subcutaneous coloured elastomer tag (Northwest Marine Technology) on their dorsal side, in one of two different colours to identify the two treatment groups. On the afternoon of d10, we simultaneously released groups of fish from each treatment (ALAN vs. Control, n = 8–10 per group per trial) into the test arena containing a pair of nocturnal predators (clearfin lionfish *Pterois radiata*, 15–20 cm SL), starved for 48 h prior to testing. Trials began during the afternoon between 12 and 2 pm to allow *A. triostegus* acclimation time in the test arena conditions before exposure to nocturnal predation.

Predation was visually evaluated every 2 h during the afternoon by counting the number of *A. triostegus* individuals remaining in the arena. No predation was observed during these periods. Prey and predators were left overnight in the test arena and visually evaluated haphazardly to assess predation. Trials were ended when 50% of larvae were eaten, or at 24-h after introduction of fish into the arena. We then calculated the survival rate in each group (number of survivors/initial number for each group) and overall (total number of survivors/initial number for both groups) for each trial, giving us the relative survival rate for each treatment (survival rate of each treatment - overall survival rate). No trials were ended during nightly observations (i.e. at least 50% of the prey fish survived until dawn observations the next day). Predator pairs used for trials were alternated between test days to allow their appetite to regenerate.

2.3. Ethics statement

This study was carried out in accordance with the guidelines of the French Polynesia committee for animal ethics, and all experiments were approved by the CRIOBE-IRCP animal ethics committee (IRCP-2018). This study did not involve endangered or protected species.

3. Results

3.1. Settling larvae selected darker habitats

At the end of the habitat choice experiment runs, all *A. triostegus* larvae were located nestled within a settlement habitat, with exception of one individual which was found in the centre section after both habitats had been searched. As the initial position of the larva at the end of the experimental period was uncertain we excluded it from the

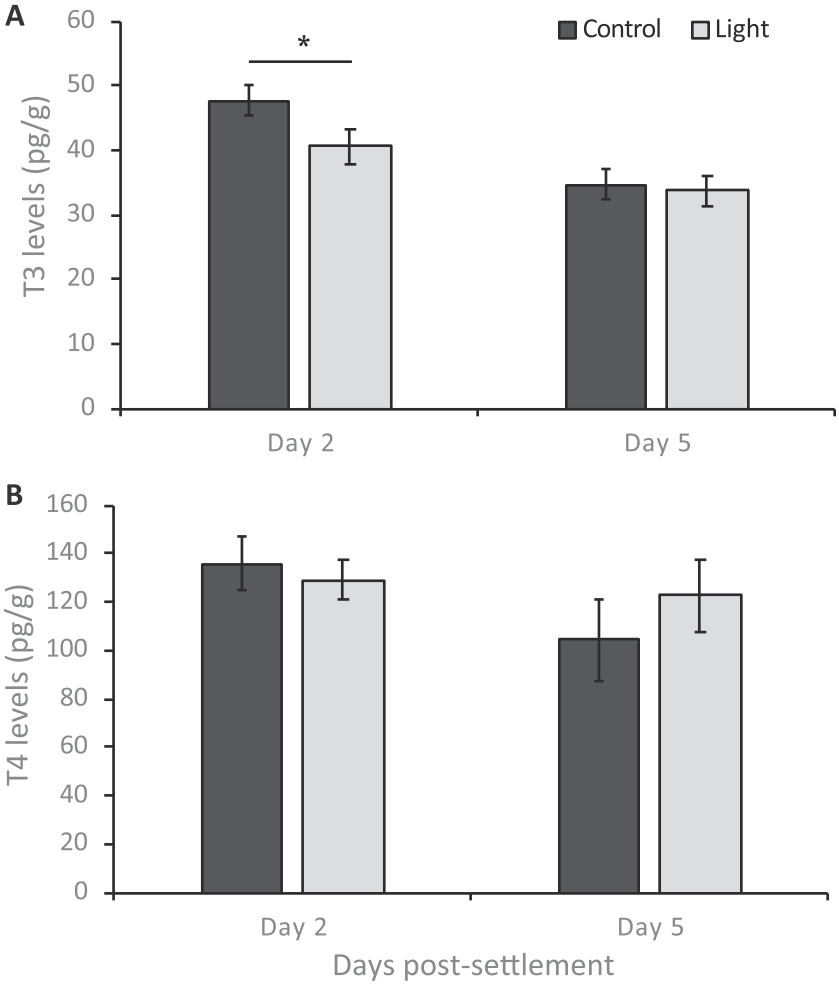

Fig. 2. Impact of artificial light at night exposure of thyroid hormone T_3 (A) and T_4 (B) levels in *Acanthurus triostegus* larvae during post-settlement metamorphosis compared to control treatments.

analysis. No larvae were observed freely swimming in the chamber at the end of the experimental period and were therefore assumed to have completed their initial settlement choice. While larval habitat preferences did not differ from that expected by chance during control trials ($G = 0.07$, df = 1, p = 0.80), larvae showed a significant preference for settlement to the dark habitat over the habitat lit with the LED light at night (G = 9.01, df = 1, p = 0.0027, Fig. 2).

3.2. ALAN lowered thyroid hormone levels during metamorphosis

Exposure to artificial light at night significantly reduced T_3 levels in *A. triostegus* at day 2 post-settlement compared to the control treatment fish ($W = 67$, p = 0.039, Fig. 3A). By day 5 post-settlement T_3 levels evened out between the two treatments ($W = 39$, p-value = 0.81). We did not find a difference in T_4 levels at day 2 ($W = 41$, p-value = 0.351) or at day 5 ($W = 20$, p-value = 0.3969).

3.3. ALAN exposed fish swam faster but did not alter visual cue response

During control runs, larvae showed no bias for one side of the choice chamber (V = 33, p = 0.53) or the middle sub-compartment (V = 60, p = 0.59). Exposure to artificial light at night did not affect choice behaviour in *A. triostegus*, with 75% of individuals from both ALAN and control treatments preferring the compartment closest to conspecific fish over heterospecific fish (i.e. fish spent > 50% of the observation period in the compartment closest to conspecifics). There was however a significant difference in the amount of time taken to make a choice.

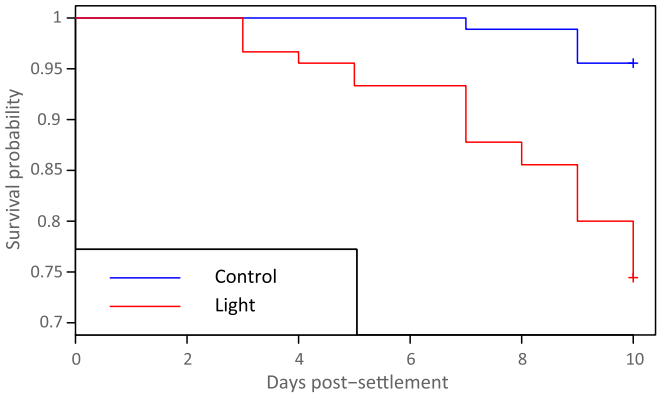

Fig. 3. Kaplan-Meier survival curves for *Acanthurus triostegus* larvae during the experimental period (10 days post-settlement) comparing exposure to artificial light at night (12L:12L cycle) with a control treatment (12L:12D). X – axis has been restricted to 0.7 probability for clarity.

Fish from the ALAN treatment that swam towards cue fish (18 of the 20 fish tested; 2 fish remained in the central compartment for the duration of the experiment) did so immediately after release with an average time of 1.2 s (± 0.89) to reach the cue fish compartment. Control fish displayed distinctly different behaviour in the choice chamber, spending significantly longer time observing the cue fish before making a choice (21.4 s, W = 127.5, p = 0.035).

3.4. ALAN exposed fish grew faster and heavier but with decreased probability of survival

Over the 10-day experimental period, *A. triostegus* grew faster when exposed to artificial light at night post-settlement, compared to control fish exposed to a normal light/dark cycle ($t = 2.12$; $df = 57.99$; $p = 0.038$). Light exposure resulted in a mean of 7.1% greater growth over the 10-day post-settlement period. Fish exposed to artificial light at night also showed significantly greater mean weight than the control group ($t = 2.35$; $df = 79.66$; $p = 0.021$). However, post-settlement mortality over 10-day period was increased by exposure to ALAN ($\chi^2 = 15.9$, $df = 1$, $p < 0.0001$). Survival was comparable for the first 3 days post-settlement in both treatments, before a significant dissociation between the survival curves becomes apparent, driven by decreasing survival probability for fish in the ALAN treatment. Overall, 4% of control fish experienced mortality by day 10, compared to 26% ($n = 90$ per treatment) in the ALAN treatment.

3.5. ALAN exposure increased probability of predation

Fish exposed to ALAN experienced higher rates of predation compared to control fish with relative mortality ratios as high as 9:1 (Fig. 4). Relative mortality was significantly different between fish which had been exposed to ALAN during metamorphosis and control fish ($W = 7$, $p = 0.98$).

4. Discussion

This study provided significant evidence that the presence of ALAN changes the behaviour and physiology of a coral-reef fish during larval recruitment. These changes, including habitat avoidance, endocrine disruption, altered growth and increased mortality rates, may have negative implications for the fitness and post-settlement survival of fish at this critical life stage. Indeed, factors affecting survival during settlement and metamorphosis of larvae can greatly influence larval recruitment success and therefore subsequent population dynamics (Pepin and Myers, 1991; Searcy and Sponaugle, 2001). Even sub-lethal effects on fish during recruitment, where selection through competition and predation is at its highest, may indirectly affect the composition of coral reef assemblages (Hoey and McCormick, 2004; Jones, 1990). The broad range of ecological impacts we observed suggests a need for better understanding of how light pollution is affecting increasingly impacted coastal areas, which act as nursery habitats for the majority of marine fishes (Davies et al., 2014).

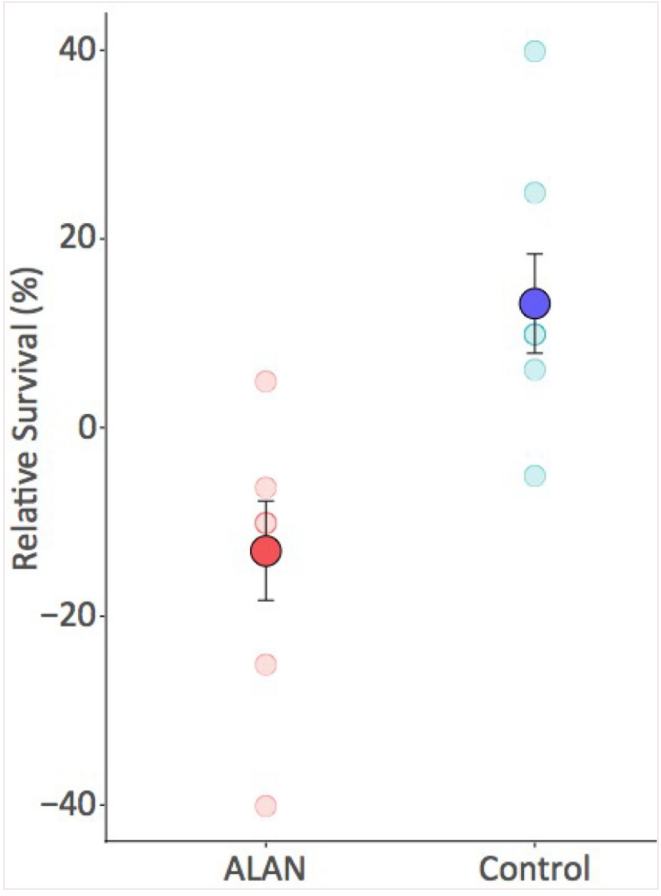

Fig. 4. Impact of exposure to artificial light at night (ALAN) on *Acanthurus triostegus* on relative survival rates when exposed to nocturnal predators at night, 10 days post-settlement.

Fish larvae avoided settling to lit habitats when given the choice between lit and dark structures. Positive phototactic behaviour is common in marine organisms during the larval stage, encouraging vertical movement of planktonic organisms in the pelagic environment and attracting nekton into light-baited traps for collection (but see Bardonnet et al., 2005; Doherty, 1987; Moore et al., 2000; Okera, 1974; Porter et al., 2008). Phototaxis often varies between species and with ontogeny, with the strength of the response generally decreasing later in the larval stage (Bulkowski and Meade, 1983; Forward and Costlow, 1974; Gehrke, 1994; Marchesan et al., 2005). This suggests the impact of ALAN on the fitness of recruiting larvae could disproportionately affect species with positive phototaxis at the settlement stage, skewing community compositions (Davies et al., 2012). Furthermore, selection on reproductive phenology has resulted in the recruitment of many fishes to coral habitat during the new moon when it is darkest in an attempt to avoid the predation gauntlet awaiting them on the reef (Almany and Webster, 2006). Indeed, there is evidence that developmental plasticity during the larval stage has evolved in some species in order to avoid settlement during bright lunar periods in favour of dark periods (Shima et al. 2018). Future studies are needed to investigate how the presence of ALAN, potentially masking lunar cues around the time of spawning and settlement, affects patterns of reproductive phenology and settlement in situ.

In fishes, the majority of knowledge on the known biological effects of artificial light intensity and periodicity come from aquaculture, where optimal photic conditions for growth during early life history are prioritised (reviewed in Villamizar et al., 2011). This research may be less ecologically relevant to most marine fishes as they are less likely to encounter chronic exposure to artificial light before they settle to coastal habitat, as dispersal during the pelagic larval phase often transports larvae hundreds of meters to thousands of kilometres offshore (Green et al., 2015). Considering the ecological effects of light pollution on fishes, the few previous studies that exist have primarily investigated impacts of ALAN on mature, freshwater species, focusing on melatonin expression (but see Barker and Cowan, 2018; Brüning et al., 2016, 2017; Brüning et al., 2015).

We found physiological evidence for the fitness benefit of light avoidance behaviour at settlement in the significant endocrine disruption experienced by *A. triostegus* exposed to ALAN during metamorphosis. Larvae experiencing ALAN upon settlement and throughout the post-settlement metamorphic stage showed depressed levels of T_3, an important hormone for metamorphosis (Holzer et al., 2017), at day 2 post-settlement. Such an endocrine disruption at this critical life stage could impair fish development as individual turn from larvae to juveniles (Holzer et al., 2017). This is further demonstrated here with the decreased relative survival of the ALAN-exposed group compared to dark control group at day 2 post-settlement when facing predators. Mortality of coral reef fishes due to predation is estimated to be highest around the time of larval settlement and recruitment (Almany and Webster, 2006), and the further effect of ALAN exposure in increasing predation risk may even decrease recruit survival, impacting population

persistence.

We observed that *A. triostegus* exposed to ALAN swam in rapid erratic bursts during visual cue response trials, lacking the cautious assessment behaviour of control fish when presented with conspecific and heterospecific visual cues. Changes in the swimming behaviour of fishes are commonly used as indicators of sublethal toxicity in response to external pollutants (reviewed in Little and Finger, 1990). Although behavioural responses to toxins can vary between species, life stage and chemical compound used, hyperactivity and increased burst swimming are common symptoms of physiological toxicity (Jordaan et al., 2013; Saglio et al., 2003; Williams et al., 2012). As degradation of visual acuity due to ALAN was not detected during visual cue choice tests, increased vulnerability to predation may relate to changes in swimming behaviour as a result of physiological stress. For example, increased activity and boldness of coral reef fish during recruitment has been shown to elevate predation risk (Ferrari et al., 2011). In addition, as acute stress can reduce metabolic scope in fish, the physiological cost of hyperactivity may have played a role in the reduced survival rate of ALAN exposed fish during the exposure period (Barton and Schreck, 1987).

Despite the physiological impacts of ALAN exposure, we found that fish grew faster and were heavier under ALAN conditions compared to control fish. Fish larvae settling to coral reefs show natural variation in growth rate which can influence fitness and survival immediately post-settlement (Shima and Findlay, 2002). In coral reef fish ecology, growth rates are often used as a proxy for predicting recruitment success, with faster-growing individuals contributing more to population replenishment than slower-growing individuals (Bergenius et al., 2002; Wilson and Meekan, 2002). However, our results indicate that exposure to light pollution may override innate growth patterns of settling fish. From aquaculture studies, we know that growth rates in fish larvae can be influenced by altering regimes of light exposure, with longer photoperiods often beneficial to growth, particularly early on in the larval stage (e.g. Olivotto et al., 2003; Puvanendran and Brown, 2002). In most species however, a constant lighting regime (i.e. 24L:0D) negatively affects development and survival during early life stages (Villamizar et al., 2011). In short, despite increased growth shown by ALAN treated individuals, the net result of ALAN exposure in wild-caught larvae at the settlement stage was decreased fitness.

ALAN-exposed *A. triostegus* were also heavier than the control fish, which under natural circumstances can be an indicator of increased fitness in coral-reef fish recruits. Weight positively affects estimates of body condition (e.g. Fulton's k condition index), a selective trait positively correlated with post-settlement survival (Booth and Hixon, 1999; Searcy and Sponaugle, 2001). However, in some cases post-settlement predation can be selective for fish with higher standardized weight (Hoey and McCormick, 2004), indicating another potential contributor to increased predation rates in ALAN-exposed *A. triostegus*. The increased mortality we observed in settlement-stage coral-reef fish larvae exposed to ALAN, both during the exposure period and predation trials, suggests that recruitment to habitats experiencing light pollution may have negative effects on post-settlement survival, with unknown flow on consequences for coral-reef community structure.

Sleep deprivation due to ALAN exposure is another potential driver of the physiological and behavioural changes we observed in *A. triostegus* during metamorphosis. Sleep states in fish share fundamental similarities with those of mammals (Zhdanova et al., 2001). The sleep/wake regulator hypocretin/orexin (Hrct, linked to locomotive activity) is also shared, with robust locomotive sleep/wake behaviours exhibited in fish larvae as young as 5 days post-hatch (Prober et al., 2006). Sleep deprivation in humans, often caused by ALAN exposure via the disruption of circadian systems, has been shown to increase metabolic requirements and weight gain via appetite upregulation (Knutson et al., 2007; Touitou et al., 2017). As other impacts of sleep deprivation are shared between mammals and fish (e.g. disruption of cognitive performance (Pinheiro-da-Silva et al., 2017)), metabolic impairment due to sleep deprivation may be a pathway for some of the impacts we observed here.

This is the first study to provide a multi-faceted, ecologically-relevant examination of how ALAN in coral reef habitats may affect fishes during the critical larval recruitment stage. We found significant evidence that light pollution can result in changes to behaviour, physiological function and post-settlement survival. These results raise concerns about how coastal ecosystems will fare with increasing coastal development and the loss of natural darkness in the night skies. To better understand the mechanisms behind the impacts reported here, future studies should look across a broad range of taxa and habitats to investigate: 1) the impacts of ALAN on recruitment dynamics in situ, 2) how ALAN affects sensory development across multiple modalities, 3) how ALAN affects the behaviour and physiology of predators, and perhaps most importantly 4) quantify the underwater light field in impacted areas, and determine threshold values for intensity and wavelengths related to negative impacts. This information is vital for informing mitigation measures and management of our coastal areas where human activities are significantly re-shaping marine communities (Ruppert et al., 2018).

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.marpolbul.2019.05.038.

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