

## Moonlight enhances growth in larval fish

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**Abstract.** Moonlight mediates trophic interactions and shapes the evolution of life-history strategies for nocturnal organisms. Reproductive cycles and important life-history transitions for many marine organisms coincide with moon phases, but few studies consider the effects of moonlight on pelagic larvae at sea. We evaluated effects of moonlight on growth of pelagic larvae of a temperate reef fish using “master chronologies” of larval growth constructed from age-independent daily increment widths recorded in otoliths of 321 individuals. We found that daily growth rates of fish larvae were enhanced by lunar illumination after controlling for the positive influence of temperature and the negative influence of cloud cover. Collectively, these results indicate that moonlight enhances growth rates of larval fish. This pattern is likely the result of moonlight’s combined effects on foraging efficiency and suppression of diel migrations of mesopelagic predators, and has the potential to drive evolution of marine life histories.

**Key words:** *chronobiology; developmental history; larval dispersal; larval growth; life history variation; lunar periodicity; marine ecosystems; reef fish.*

### INTRODUCTION

Moonlight affects behavior and demographic rates of a wide range of organisms (Kronfeld-Schor et al. 2013, Palmer et al. 2017). Moonlit nights can enhance foraging activity, but may also increase predation risk (Prugh and Golden 2014). Moonlight can synchronize reproduction (Foster et al. 2018), shape trophic cascades (Mukherjee et al. 2009), drive carbon flux and sequestration within ecosystems (Hernandez-Leon et al. 2010), and mediate dispersal and connectivity across ecosystems (Thomsen and Green 2016).

Lunar effects are not limited to moonlight; the moon shapes geomagnetic fields and tidal cycles (Stolov 1965), with important consequences for many organisms, particularly those found in marine ecosystems (Connell 1961, Lohmann et al. 2008). Most marine reef organisms have a complex life cycle involving a dispersive larval stage and a relatively sedentary adult stage (Caley et al. 1996). Lunar periodicity in spawning and larval settlement back to reef habitat is common (Claydon et al. 2014, Foster et al. 2018, Shima et al. 2018). These

lunar (or semi-lunar) cycles are frequently attributed to risk minimizing strategies for spawning adults (Robertson 1991), or for their offspring that must traverse a gauntlet of predators during outbound and return journeys (Bailey and Houde 1989, Acosta and Butler 1999, Shima et al. 2018). Alternative hypotheses attribute lunar periodicity in spawning and/or settlement to tidally driven currents that maximize dispersal of offspring away from reefs (Johannes 1978, Robertson et al. 1990, Sponaugle and Pinkard 2004), or transport back to reefs (Forward and Tankersley 2001). Few studies have considered the effects of moonlight on pelagic larvae while at sea, and the extent to which such effects may contribute to dispersal, fitness, and the evolution of life-history strategies.

Most larvae of marine reef organisms must actively forage to complete larval development (Thorson 1950); many of these taxa (particularly fish and cephalopods) are visual predators at an early developmental stage (Leis 2010). Moonlight may extend foraging times and/or improve foraging success of marine larvae. In contrast to many terrestrial systems (where moonlight often enhances risk for the forager; Prugh and Golden 2014), predation risk for pelagic larvae at sea may decrease on bright, moonlit nights. This is because diel vertical migrations of mesopelagic predators are suppressed during full moons (Drazen et al. 2011, Last et al. 2016,

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Prihartato et al. 2016). During darker periods of the lunar cycle, this assemblage of predators (primarily myctophid lanternfish) undergoes a nocturnal migration into shallow (epipelagic) water containing larval stages of reef organisms (Cowen 2002). Consequently, moonlight may simultaneously and substantially increase the foraging opportunities and decrease the predation risk for larvae of marine reef organisms.

Moonlight may become decoupled from the lunar cycle due to masking effects of cloud cover. This situation facilitates a natural experiment that enabled us to evaluate the specific effects of moonlight, as opposed to other environmental variables (tidal cycles, etc.) that may be linked to the lunar cycle. We hypothesized that growth rates of pelagic larval stages of a reef fish will be enhanced by moonlight; specifically, that daily growth should increase with lunar illumination and decrease with cloud cover (using appropriate statistical approaches to control for the interactive effects of these and other important sources of variation in growth). We capitalized on high resolution chronologies (i.e., daily growth rates) recorded within the otoliths (“ear stones”) of a reef fish. We integrated information from 321 individuals sampled from two distinct developmental environments to construct detrended master chronologies (Black et al. 2008) of larval fish growth. We evaluated temporal variation in these master chronologies against daily variation in lunar illumination, cloud cover derived from satellite sensors, and water temperature. We identified novel effects of moonlight on marine larvae that shed fundamentally new insights on larval biology, and potentially, the evolutionary drivers of life-history variation in the sea.

## MATERIAL AND METHODS

### *Study system*

We evaluate the effects of moonlight on growth rates of dispersing larvae of the common triplefin (*Forsterygion lapillum*), sampled from a metapopulation in central New Zealand. Adults inhabit shallow rocky reefs (Feary and Clements 2006), have small home ranges (Shima et al. 2012), and spawn and defend benthic eggs (Moginie and Shima 2018) that hatch and develop as pelagic larvae for ~52 d (Shima and Swearer 2009a). Our previous work used daily records of growth and chemical composition recorded within the otoliths of common triplefin to infer patterns of dispersal (Shima and Swearer 2009a, Swearer and Shima 2010) and developmental history (Shima and Swearer 2009b) that have important consequences for connectivity (Shima et al. 2015), demographic performance (Shima and Swearer 2010, Shima et al. 2015), and population dynamics (Noonburg et al. 2015, Shima et al. 2015). Descriptions of the collection, preparation, and analyses of common triplefin otoliths used in this study can be found in (Shima and Swearer 2009a,b).

We constructed master chronologies (sensu Black et al. 2008) of daily larval otolith growth (a proxy for

somatic growth) over a ~3 month period and use these to explore the consequences of moonlight and cloud cover on daily growth. Corroboration of our hypothesis that nocturnal illumination enhances larval growth would be evidenced by (1) a positive relationship between lunar illumination and larval growth (controlling for variation in water temperature and cloud cover) and (2) a negative relationship between cloud cover and larval growth (controlling for variation in water temperature and lunar illumination).

### *Constructing master chronologies*

Otolith growth (as estimated by widths of successive daily otolith increments) often varies with an individual's age (Ashworth et al. 2015). We removed age-related trends in the sequence of daily increment widths for each individual by (1) fitting an appropriate model of otolith growth to the full set of data (i.e., otolith growth trajectories for 321 fish; mean larval duration 51.76 d, SD = 9.33, range = 33–101) and (2) obtaining the residuals for each observation as a measure of detrended daily growth. We evaluated four candidate models to characterize the ontogenetic pattern of larval otolith growth for common triplefin. Specifically, we modeled the relationship between otolith increment width and larval age with (1) a linear function, (2) a von Bertalanffy growth function, (3) a logistic growth function, and (4) a quadratic function (see Appendix S1). We used the Akaike information criterion (AIC; estimated with the NLMIXED procedure, SAS v9.4, Cary, NC, USA) to identify the best model. Although we used a mixed modeling framework, our models did not include a random effect to identify individuals because doing so would likely remove a meaningful component of temporal variation (e.g., differences in average larval growth resulting from differences in water temperature rather than intrinsic differences among individuals). A characteristic ontogenetic pattern of larval otolith growth was apparent across our 321 fish and was best approximated by a quadratic model (otolith increment width =  $\text{age}^2 + \text{age} + \text{intercept}$ ; AIC = 53,807, Appendix S1). This unimodal model of otolith growth outperformed a linear growth model (AIC = 56,728), a von Bertalanffy growth model (AIC = 54,441), and a logistic growth model (AIC = 54,120; Appendix S1), and was used to estimate residual (i.e., detrended) otolith growth for all individuals.

We used the residuals from the best-fit model to construct detrended master chronologies of otolith increment growth, for common triplefin with one of two distinct developmental histories: (1) fish that had probable development within nearshore waters and (2) fish that had probable development in offshore waters (developmental histories inferred from distinct trace element profiles; Shima and Swearer 2009a,b, Shima et al. 2015). We constructed separate master chronologies for these two developmental histories because we speculated that the effects of realized lunar illumination might vary

with developmental environment. For example, if the effects of lunar illumination on larval growth are mediated primarily by suppression of vertical migration of mesopelagic predators into surface waters, then larvae in offshore locations (i.e., with a putatively greater exposure to mesopelagic predators given a deeper water column) might manifest this effect more strongly than fish developing in shallower waters close to shore.

We aligned otoliths by calendar date and evaluated only dates for which  $\geq 20$  measures of residual growth (i.e.,  $\geq 20$  individual fish alive on a given calendar date) were available, because a measure of variance stabilized at  $\sim 20$  fish. This approach resulted in the exclusion of some dates at the beginning and end of the time series for each developmental history (see *Results*). We estimated daily medians of residual increment growth (calculated across all individuals growing in a particular developmental environment on a given day) to construct master chronologies.

#### *Environmental variables*

We estimated daily lunar illumination as the proportion of moon surface illuminated (data *available online*).<sup>4</sup> We obtained daily nocturnal cloud cover data estimated by the Atmospheric Infrared Sounder (AIRS Science Team/Joao Teixeira 2013; data *available online*).<sup>5</sup> We measured daily averages of water temperature with HOBO TidBit loggers (Onset Corporation., Bourne, MA, USA) deployed at two locations within Wellington Harbour. We used daily estimates of sea surface temperature (SST) from NOAA's High-resolution Blended Analysis (Earth System Research Laboratory; data *available online*)<sup>6</sup> to estimate in situ temperature for two moderate gaps in our time series (due to instrument failure, 29 November–20 December 2003; 1–7 January 2004). A strong linear relationship between in situ temperature and SST ( $F_{1,194} = 837.47$   $P < 0.0001$ ,  $r^2 = 0.81$ ) enabled us to reconstruct missing values of in situ temperature with high confidence, using the formula in situ temperature =  $0.97 \times \text{SST} + 1.05$ .

We used an ARIMA procedure (SAS ETS v13.2; SAS Institute, Cary, North Carolina, USA) to identify time lags in otolith growth in response to water temperature, lunar illumination, and nocturnal cloud cover. Environmental variables were lagged independently (by up to 5 d), and the time lag that gave the strongest correlation with otolith growth was used for subsequent analyses (see Appendix S2). We used a general linear model (PROC GLM, SAS v9.4) to evaluate the effects of temperature (with a 1-d lag), lunar illumination (with no lag), nocturnal cloud cover (with a 2-d lag), and developmental history (a categorical variable with two levels) on master chronologies of detrended larval fish growth. We assumed that our construction of master chronologies

(i.e., derivation of a system-wide estimate of growth from multiple individuals of different ages) effectively resulted in independent estimates of larval growth potential on any given day. We modeled all interaction terms, and sequentially removed non-significant, higher order interactions to determine a reduced model that best explained daily variation in the growth rate of larval fish. We evaluated sensitivity of our statistical inferences to Type I error using a subsequent analysis that accounted for autocorrelated error structures (PROC AUTOREG, SAS v9.4, using the BACKSTEP option [a stepwise selection procedure to identify autoregressive parameters]).

#### RESULTS

Master chronologies of residual growth exhibited a unimodal pattern across the growing season that was similar for fish with nearshore vs. offshore developmental histories, peaking in January (Fig. 1a, b). Residual otolith growth followed variation in water temperature (Fig. 1c): otolith growth and temperature were generally lowest from late November through mid-December; they reached a maximum in mid-January, and exhibited greater temporal variability near the end of the sequence. Lunar illumination followed a sinusoidal pattern corresponding to the lunar cycle (Fig. 1d). Realized lunar illumination was likely to be heavily moderated by nocturnal cloud cover, which varied from near zero to 100% in a seemingly haphazard pattern (Fig. 1d). An ARIMA procedure indicated that residual otolith growth was most strongly correlated with (1) nocturnal cloud cover 2 d previously (i.e., a 2-d lag effect), (2) temperature on the previous day (i.e., a 1-d lag), and (3) lunar illumination on the same day (i.e., no lag; see Appendix S2).

The final (reduced) model that best explained variation in residual growth contained only the main effects, because all interaction terms were nonsignificant. Controlling for other main effects in the model (i.e., using Type III SS), residual growth (1) increased with water temperature ( $F_{1,194} = 311.14$   $P < 0.0001$ , Fig. 2a), (2) increased with lunar illumination ( $F_{1,194} = 19.72$   $P < 0.0001$ , Fig. 2b), and (3) decreased with cloud cover ( $F_{1,194} = 5.87$   $P = 0.0163$ , Fig. 2c). Residual growth did not vary significantly between inshore and offshore ( $F_{1,194} = 2.02$   $P = 0.16$ ), and the absence of significant interactions indicates that fish with different developmental histories were similarly influenced by temperature, moonlight, and cloud cover (Fig. 2). We note that these results were robust to the inclusion/exclusion of time lags in environmental variables, and to the inclusion/exclusion of water temperature estimated from SST (i.e., our results were qualitatively identical in all cases).

Parameter estimates from our GLM suggest that a 1-degree increase in temperature was correlated with a 0.25 unit increase in residual otolith growth. This effect on growth is similar to the growth advantage afforded by a full moon (larval fish experience a 0.22-unit increase in

<sup>4</sup> <http://aa.usno.navy.mil>

<sup>5</sup> <https://giovanni.gsfc.nasa.gov/giovanni/>

<sup>6</sup> <https://www.esrl.noaa.gov>

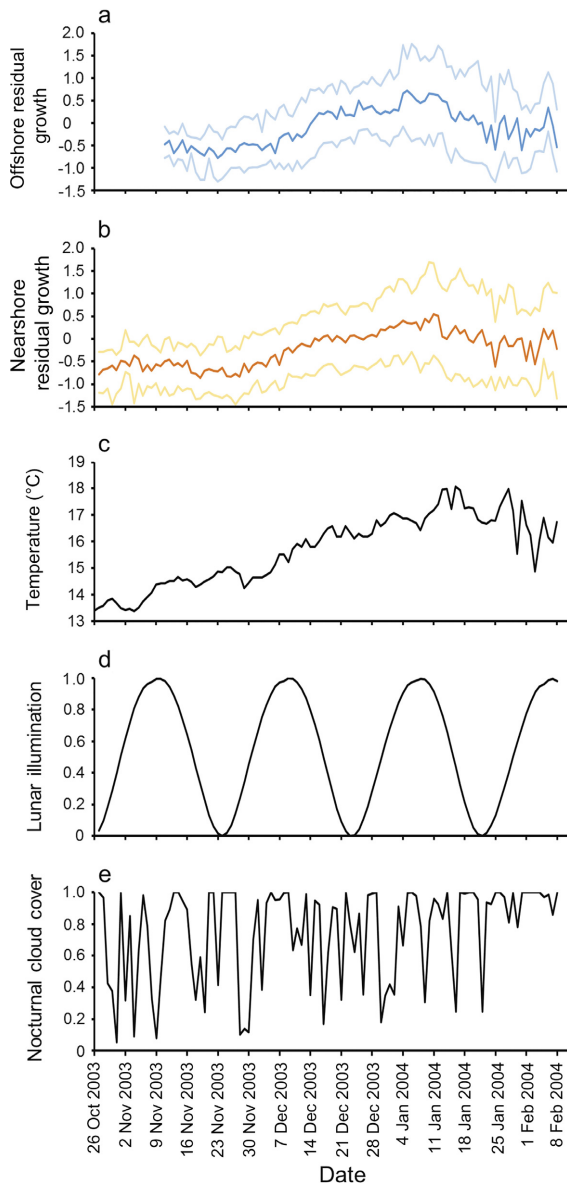


FIG. 1. Temporal variation in larval growth for the common triplefin (*Forsterygion lapillum*) in relation to environmental variables. We estimated daily otolith growth of 321 fish during their larval development. We removed an ontogenetic pattern of growth, aligned otolith increments by calendar date, and constructed “master chronologies” of residual growth over ~3 months (median [dark lines] and interquartile range [light lines]) for fish with otolith chemical signatures consistent with (a) offshore larval development (blue lines) and (b) nearshore larval development (orange lines). Environmental variables include (c) water temperature, (d) lunar illumination (proportion of moon surface illuminated), and (e) nocturnal cloud cover (proportion of the sky covered by cloud overnight).

residual otolith growth during full moons relative to new moons). A night with full cloud cover reduces residual otolith growth by 0.14 units relative to a cloudless night (roughly equivalent to the effect of a 0.5-degree reduction in water temperature). Slopes of the fitted lines in Fig. 2

(showing relationships analogous to partial regression plots) approximate these effect sizes.

Results from an autoregressive error model were qualitatively similar to the GLM in most respects. This model supported the inferences of no significant effect of developmental location (i.e., growth in nearshore vs. offshore waters:  $t = 1.07$ ,  $P = 0.28$ , parameter estimate = 0.06), a positive effect of temperature ( $t = 6.94$ ,  $P < 0.0001$ , parameter estimate = 0.16) and a positive effect of lunar illumination ( $t = 2.42$ ,  $P = 0.0163$ , parameter estimate = 0.16) on residual otolith growth. However, the effect of nocturnal cloud cover was not significant ( $t = -0.64$ ,  $P = 0.52$ , parameter estimate =  $-0.03$ ) when an autocorrelated error structure was included in the model.

## DISCUSSION

Construction of master growth chronologies enabled us to integrate demographic information from many individuals and evaluate new sources of variation in larval performance over a temporal period that greatly exceeded the lifespan of any individual. This approach revealed the novel result that moonlight enhances growth of pelagic larval reef fish. Controlling for the well-known effect of temperature on larval growth (Morales-Nin 2000), and for cloud cover (which obscures moonlight), we found a highly significant positive correlation between larval growth and lunar illumination. A larval fish developing on a cloudless full moon night will have a growth advantage that is roughly equivalent to a 1-degree increase in temperature. This effect is substantial, because temperature variation on this order can greatly affect larval growth, survival and developmental duration (Houde 1989, Pepin 1991, Byrne 2011), and hence dispersal probabilities (O'Connor et al. 2007), size-at-settlement, and post-settlement performance (Sponaugle et al. 2006). Our previous work on the common triplefin suggests that such differences can affect intraspecific interactions in the adult habitat (Shima and Swearer 2010, Noonburg et al. 2015, Shima et al. 2015), with potential carry-over effects on adult fitness (Moginie and Shima 2018).

A negative correlation between larval growth and nocturnal cloud cover (while controlling for other effects in our model) further corroborates our inference that moonlight enhances growth. This pattern is consistent with clouds obscuring moonlight and reducing the positive effects of lunar illumination. However, we note that this inference is sensitive to the GLM assumption of independent error terms through time. In an analysis that incorporated autocorrelated error terms, the cloud effect ceases to be significant. Collectively, these results suggest that a significant component of variability in daily larval growth of common triplefin may be attributable to moonlight, and not simply to other processes that may covary with lunar periodicity (e.g., tidal variation; Campana 1984).

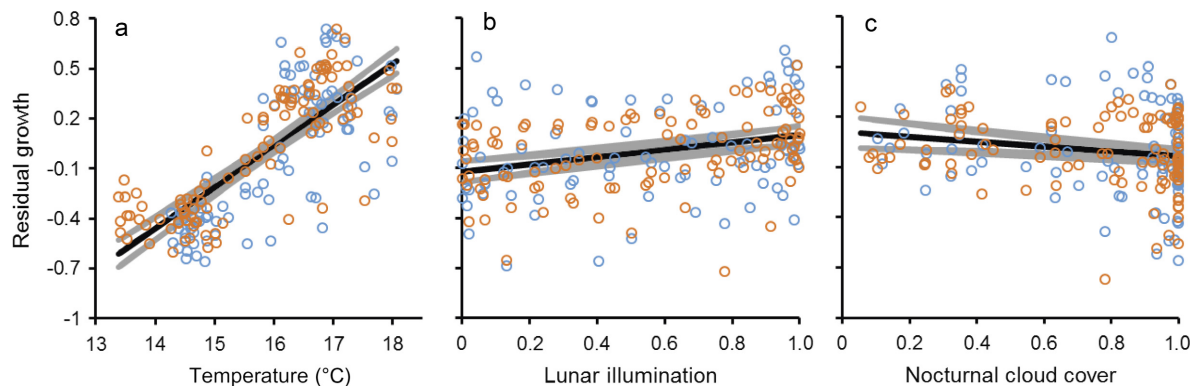


FIG. 2. Partial regression plots illustrating larval fish growth that (a) increases with temperature ( $P < 0.0001$ ), (b) increases with lunar illumination ( $P < 0.0001$ ), and (c) decreases with nocturnal cloud cover ( $P = 0.016$ ). Growth does not vary with developmental history ( $P = 0.16$ ; orange symbols, nearshore development; blue symbols, offshore development). Given are estimates of residual otolith growth (after removing an ontogenetic pattern, and controlling for other variables in the full GLM) plotted against predictor variables (best-fit lines  $\pm 95\%$  CI shown for presentation purposes; slopes closely approximate parameter estimates from our formal GLM analysis that are given in the Results). Results of an autoregressive error model suggest that the effect of nocturnal cloud cover may be sensitive to Type 1 error; all other inferences are robust to autocorrelated error structures.

After controlling for the strong effects of temperature, residual variation in the growth rate of a planktotrophic (i.e., feeding) larva is likely determined by foraging efficiency. Foraging efficiency is a function of prey availability, successful prey capture rate, and foraging time (MacArthur and Pianka 1966). The latter may increase if foragers can devote more hours in any given day to feeding, and/or if they can increase the proportion of time devoted exclusively to this task (and not, for example, spending time evading their own predators; Thomson and Green 2016). Larvae of many species of reef fish develop primarily in the top 100 m of the pelagic environment (Cowen 2002). They have excellent vision and are visual predators of smaller zooplankton (Leis 2010). We speculate that increased moonlight may enable larvae to enhance their growth rates by (1) extending their time spent foraging, (2) increasing their probability of detecting prey at night, and/or (3) improving their prey capture rates.

Moonlight also has a well-known effect on diel vertical migration of mesopelagic predators (Drazen et al. 2011, Last et al. 2016), which appears to be a global phenomenon (Prihartato et al. 2016). Few studies have connected vertical migrations of mesopelagic predators to the distribution and performance of pelagic larval stages of reef organisms. The mesopelagic predator assemblage (composed mainly of myctophid lanternfishes) can reach the surface waters (where larval reef fish are found) during dark nights (i.e., during new moons; Drazen et al. 2011, Prihartato et al. 2016). During brighter nights (i.e., when the moon is wholly or partially full), this upward migration is attenuated, and mesopelagic predators generally do not migrate into the shallow depths (Drazen et al. 2011, Prihartato et al. 2016) that are the nocturnal domain of larval reef organisms (Cowen 2002). A study by Tarling et al. (1999) found that upward migrations of mesopelagic predators resumed when a bright moon was

temporarily obscured by a lunar eclipse, suggesting that the assemblage can respond directly and quickly to light cues (and migration is not simply controlled by an endogenous process; Forward 1988). This inference is supported by other studies (e.g., Staby and Aksnes 2011), and is important because it indicates that mesopelagic predators respond in real time and likely migrate into shallow waters when nocturnal cloud cover obscures lunar illumination. Several important mesopelagic predators (all myctophids) exhibit lunar periodicity in growth that is consistent with enhanced feeding in surface waters during new moons (Linkowski 1996, Hayashi et al. 2001). Mesopelagic predators such as myctophids have a global distribution, are among the most numerous vertebrates on Earth, and are reported to consume larvae of reef organisms (Catul et al. 2011). Combining these observations from a wide range of studies with our own findings, we speculate that an influx of predators on dark nights may increase predation rates on larval fish (a hypothesis that our data cannot evaluate), and reduce the growth rates of those individuals that manage to escape predation (a pattern that is evident in our data). We further speculate that effects on growth are mediated by “fear effects” (e.g., Palmer et al. 2017). If our speculations are true, then we suggest that moonlight may have important (and until now, unappreciated) indirect effects on dispersing larvae of reef associated organisms, mediated by induced changes to the migratory behavior of these mesopelagic predators.

Our analyses are based on otolith growth, and we assume this is indicative of somatic growth. Strong relationships between fish length and otolith size have been documented for many species (Harvey et al. 2000) including triplefins (Plaza et al. 2012). Even for our collection of recently recruited fish (which do not vary greatly in size), we note a significant positive relationship between total length of fish and otolith radius

( $F_{1,318} = 58.26$ ,  $P < 0.0001$ ), suggesting that otolith growth is a good proxy for somatic growth.

We failed to detect an effect of developmental history (i.e., putative nearshore vs. offshore locations of larval cohorts) on larval growth. This outcome was somewhat surprising given that our previous analyses found that these developmental histories affect developmental duration (Shima and Swearer 2009*a,b*), stage-specific individual growth rates (Shima and Swearer 2009*a,b*), post-settlement performance (Shima and Swearer 2010, Shima et al. 2015) and intraspecific interactions (Noonburg et al. 2015, Shima et al. 2015). We had expected that fish with traits consistent with larval development in nearshore coastal environments (orange symbols in our figures) might have an attenuated response to moonlight relative to fish that were likely to develop in offshore environments (blue symbols). This expectation was predicated on the following (untested) assumptions: (1) inshore waters are comparatively turbid, and this may limit light penetration, moderating the effects of moonlight, and (2) offshore waters experience a greater influx of mesopelagic predators on dark nights (due to a comparatively deep water column). The absence of significant interactions between dispersal history and effects related to moonlight (i.e., any combination of effects containing lunar illumination and/or nocturnal cloud cover) may be due to limited statistical power, or may suggest that our underlying assumptions were incorrect. At least one study suggests diel vertical migrations of important predators are not limited to offshore waters; these organisms infiltrate offshore, shelf, and nearshore waters equally well and on a schedule linked to the moon (Last et al. 2016). Turbidity may not vary greatly across the shelf (particularly in Cook Strait, where currents are highly advective). Last, our previous identification of larval rearing locations (Shima and Swearer 2009*a,b*) may be incorrect. None of this changes our conclusion that moonlight enhances larval growth of survivors. Instead, the absence of significant interactions with developmental history suggests that moonlight effects on larval performance may be widely manifested.

Growth is a fundamental demographic trait that underlies many ecological and evolutionary processes (Arendt 1997, Sogard 1997, Metcalfe and Monaghan 2001). Our study stitches chronological information from otoliths of many individuals to reveal moonlight as a novel source of variation in growth rates of marine larvae. Our findings have potential implications for spatial and temporal variation in realised connectivity (e.g., Shima et al. 2010, Trembl et al. 2015), if particular geographic locations and/or times experience differential cloud cover. Cloud cover during bright periods of the lunar cycle may reduce larval growth, survival, and successful dispersal between locations. Artificial light at night (ALAN; Gaston et al. 2017) may disrupt moonlight effects on pelagic larvae, yet the effects of cloud cover may be context-dependent, as clouds can amplify

the effects of ALAN near urban centers (Kyba et al. 2011). Variation in moonlight and its effects on growth may also contribute to phenotypic variation among individuals that settle to a common location. Phenotypic variation mediated by moonlight may have wholly unappreciated effects that carry-over to benthic life stages, shaping competitive interactions (Noonburg et al. 2015) and alternative life-history strategies (Moginie and Shima 2018).

Many species that exhibit lunar periodicity in spawning and/or settlement may adopt these strategies, at least in part, to target moonlight conditions that maximize growth potential and/or reduce predation risk for pelagic larval stages. Our work contributes importantly to an influential body of literature (e.g., match-mismatch hypothesis [Cushing 1975], ocean-stability hypothesis [Lasker 1981], member-vagrant hypothesis [Sinclair 1988], bigger-is-better hypothesis [Sogard 1997]) that attempts to understand and predict the drivers of variation in growth of fish larvae. Moonlight may explain much of the variation in larval growth that is not well explained by existing conceptual frameworks.

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