



# Juvenile reef fish growth and survival related to subregional patterns of primary production

E. D. Goldstein<sup>1,2</sup> · S. Sponaugle<sup>3</sup>

Received: 14 April 2019 / Accepted: 25 November 2019 / Published online: 9 January 2020  
© Springer-Verlag GmbH Germany, part of Springer Nature 2019

## Abstract

For coral reef organisms with bipartite lifecycles, the ontogenetic shift from the pelagic larval stage to the benthic environment is often associated with high mortality that may be influenced by the local environment as well as individual traits that alter vulnerability to predation. Habitat variability such as food availability and competition for resources can influence traits such as growth and size, ultimately affecting mortality rates as well as the strength or direction of trait-mediated mortality. In this study, we examined subregional patterns of early life-history traits (ELHTs) of a model coral reef fish (bicolor damselfish: *Stegastes partitus*) in environmentally and oceanographically distinct regions of the Florida Keys, USA: the relatively more productive lower Keys (LK) and the more oligotrophic upper Keys (UK). Fish arrived to reef habitats with similar larval ELHTs (larval growth, pelagic larval duration, settlement size) but experienced higher mortality in the LK. Despite variability in mortality rates, patterns of selective mortality were similar between the UK and LK. For juvenile fish, growth during the first 4 days post-settlement was significantly faster in the LK compared to the UK, potentially linked to higher productivity and food availability. Results of this study indicate that environmental variability in settlement habitat at subregional spatial scales can affect post-settlement growth and survival of young fish soon after they transition to the demersal juvenile stage in coral reef environments.

## Introduction

For a coral reef fish, successful settlement and recruitment to the reef requires survival through multiple life stages and environments. During the pelagic larval stage,

hydrodynamic features and oceanographic processes affect growth, survival, condition, and transport of larvae prior to settlement (Botsford et al. 1994; Sponaugle et al. 2011; Shulzitski et al. 2015). Subsequently, fish undergo a critical ontogenetic shift from the pelagic environment to the benthic reef habitat. This transition often coincides with high mortality rates (Sogard 1997) that are influenced by dynamic and spatially variable environmental processes such as productivity and food availability that affect growth and condition of individuals (Jones 1986; Levin et al. 1997; Booth and Hixon 1999; Leahy et al. 2015). For territorial reef fishes, growth, energy allocation, and survival are also linked to interactions between competition and resource availability that vary spatially or temporally as a result of local habitat and population density (Holbrook et al. 2000; Brokovich et al. 2006; Johnson 2008). Such habitat-driven variability in critical traits affects individual survival and can also scale-up to affect broader subpopulation demographics and dynamics.

High mortality associated with the transition from pelagic to benthic environments creates the potential for trait-mediated selective processes to alter spatial patterns in fish traits (Sponaugle and Grorud-Colvert 2006; Rankin

---

Responsible Editor: D. Goulet.

---

Reviewed by undisclosed experts.

---

**Electronic supplementary material** The online version of this article (<https://doi.org/10.1007/s00227-019-3627-9>) contains supplementary material, which is available to authorized users.

---

✉ E. D. Goldstein  
Esther.D.Goldstein@gmail.com

<sup>1</sup> Department of Marine Biology and Ecology, University of Miami Rosenstiel School of Marine and Atmospheric Science, Miami, FL 33149, USA

<sup>2</sup> Present Address: Age and Growth Program, Resource Ecology and Fisheries Management Division, Alaska Fisheries Science Center, NOAA Fisheries, 7600 Sand Point Way NE, Seattle, WA 98115, USA

<sup>3</sup> Department of Integrative Biology, Hatfield Marine Science Center, Oregon State University, Newport, OR 97365, USA

and Sponaugle 2011; Di Franco et al. 2013). Upon arrival to the reef, larval traits including growth rate, condition, and size at settlement can carry over to influence post-settlement survival and fitness (Searcy and Sponaugle 2001; Hamilton et al. 2008; Shima and Swearer 2010). The direction or strength of this trait-mediated selective mortality may vary depending on settlement habitat. Extrinsic habitat variation such as resource availability and predation risk, that are also influenced by population density (Johnson 2008; Hixon et al. 2012), can affect the extent to which particular traits confer a selective advantage (Smith and Shima 2011) and thus influence spatial patterns in survivorship. Spatial variation in selective mortality can have broader consequences to fish populations and connectivity among subpopulations by creating local trait adaptations that differentially affect mortality rates and survival advantages (Figueira 2009; Clarke et al. 2010).

The upper and lower Florida Keys (UK, LK) are influenced by dynamic oceanography that may affect habitat suitability for reef fish populations. Mesoscale eddies, with horizontal scales of ~ 100–200 km, are prevalent oceanographic features that are typically associated with major boundary currents, and in the Straits of Florida, mesoscale cyclonic eddies often form and propagate along the Florida Current front. These features influence larval transport and delivery to reefs (Sponaugle et al. 2005; D'Alessandro et al. 2007) and also induce upwelling of nutrient-rich water that increases primary and secondary productivity and food availability for marine organisms (Lee et al. 1994; Hitchcock et al. 2005). Eddy properties differ across the Florida Keys: eddies propagate slowly along the Florida Current front in the LK, and then speed up and shear apart into sub-mesoscale eddies as they move through the UK (Lee et al. 1994; Fratantoni et al. 1998). Subregional variability in eddy dynamics may be linked to enhanced delivery of larval reef fishes to settlement habitats in the LK compared to the UK (Sponaugle et al. 2005) and high survival (Shulzitski et al. 2016). Yet, biophysical modeling using a model coral reef fish species, *Stegastes partitus* (bicolor damselfish), indicates that while oceanography alone can explain temporal fluctuations in larval supply, it does not explain subregional incongruencies in the magnitude of larval supply, settlement, and recruitment (Sponaugle et al. 2012). This decoupling between oceanographic processes and recruitment suggests that other factors such as reproductive output, larval condition or survival, or post-settlement processes such as regional differences in growth or mortality underlie the observed patterns.

We focused on the critical period of metamorphosis from the pelagic larval stage to the reef-associated juvenile stage in a common coral reef fish (bicolor damselfish) to assess whether subregional habitat variability can influence spatial patterns in early life-history traits (ELHTs: larval growth,

pelagic larval duration, settlement size, post-settlement growth), recruitment, and survival. We hypothesized that in the LK, higher productivity, induced by eddy upwelling, would lead to faster larval growth as well as post-settlement growth of young fish. However, higher densities of new recruits to the reef environment in the LK may also increase density-dependent competition and increase the strength or alter the direction of trait-mediated selective mortality. Spatial patterns of fish traits and survival at subregional spatial scales would provide insight into the potential effects of habitat variation and environmental variability on post-settlement survival, local population replenishment, and realized population connectivity for coral reef fishes.

## Methods

### Study species

*Stegastes partitus* (bicolor damselfish) is a common demersal reef fish found throughout the Florida Keys, the Bahamas, and the Caribbean Sea (Emery 1973). Adults and juveniles are territorial, with high site fidelity and a home range of 1–2 m (Johnson and Hixon 2010). Demersal eggs are spawned year-round with peak spawning during the summer ~3 d after the full moon (Schmale 1981; Robertson et al. 1988). Peak reef settlement is between the third quarter and the new moons, during which time larvae settle to reef habitats and metamorphose into demersal juveniles (Sponaugle and Cowen 1996; D'Alessandro et al. 2007). As juveniles, bicolor damselfish consume plankton and benthic algae, undergoing an ontogenetic diet shift to an adult diet of predominantly plankton and some benthic and planktonic algae (Emery 1973; Booth and Hixon 1999; Goldstein et al. 2017). The primarily planktivorous diet of bicolor damselfish makes it an ideal study species to assess the impacts of subregional productivity on reef fish.

### Subregional productivity and temperature

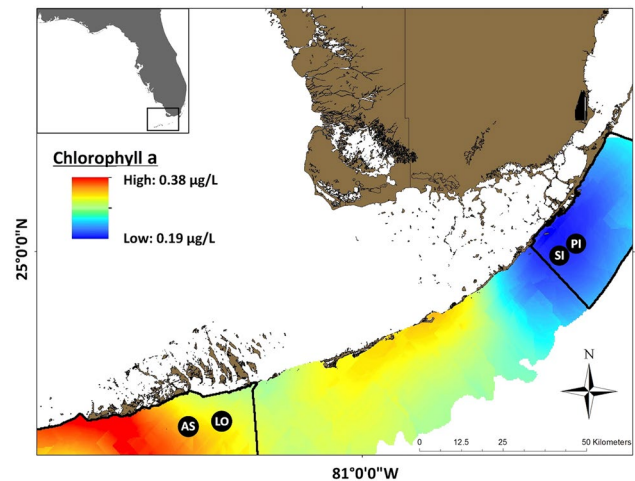
Chlorophyll a (henceforth chlorophyll) data, used as a proxy for primary productivity, were obtained from discrete sample collections as well as satellite data to provide information for seasons and years without discrete collections. Discrete sample collections were from the SERC-FIU Water Quality Monitoring Network (<http://serc.fiu.edu/wqmnetwork/>) for the years 1995–2011 to overlap with the survey and collection years used for this study. Discrete water samples were collected throughout the year with general agreement between sampling months in the UK and the LK (ESM 1). For the analysis, chlorophyll values were averaged across depths (surface to ~60 m), years, and seasons at each of the 87 sample sites in the Florida Keys. After verifying the

assumptions of a normal distribution, stationarity, and isotropy, discrete chlorophyll data were interpolated using ordinary kriging in ArcGIS using the semivariogram method to fit the best model. Sea surface chlorophyll satellite data were obtained from MODIS-Aqua using the monthly 4-km resolution chlorophyll product for the years 2003–2011 ([https://oceansci.gsfc.nasa.gov/MODIS-Aqua/Mapped/Monthly/4km/chlor\\_a/](https://oceansci.gsfc.nasa.gov/MODIS-Aqua/Mapped/Monthly/4km/chlor_a/)). Time series were constructed for both datasets by averaging chlorophyll values within each season (Spring: March–May, Summer: June–August, Fall: September–November, Winter: December–February) and year. For the discrete sample data, values were averaged across stations within the UK and LK spatial designations (ESM 1). Chlorophyll values may differ throughout the water column, and surface satellite data may not reflect the demersal environment of a coral reef fish, particularly in deeper and more offshore environments where the water column is not well-mixed (Leichter et al. 2003). Therefore, for satellite-based analyses, regional designations were constrained to shallow locations near the coral reef study sites by averaging across six 4-km grid cells (96 km<sup>2</sup> area) that were selected in each the LK and the UK in closest proximity to the fish sample collection sites at American Shoal (24°31.241, –81°31.041) and Looe Key (24°32.528, –81°24.891) in the LK and Pickles Reef (24°59.17, –80°24.94) and Sand Island (25°01.109, –80°22.044) in the UK.

Temperature has a significant influence on bicolor damselfish growth (Rankin and Sponaugle 2011). Therefore, we compared subregional differences in surface temperatures in the UK and LK from the first hatch date through the final collection date for all fish cohorts using averaged satellite-derived sea surface temperature from NOAA Coast Watch (daytime Aqua-MODIS, NASA, <https://oceancolor.gsfc.nasa.gov/data/aqua/>). We also compared daytime satellite sea surface temperature (<http://oceansci.gsfc.nasa.gov/MODIS-Aqua/Mapped/Monthly/4km/sst>) averaged across grid cells (aforementioned 96 km<sup>2</sup> area) near collection sites in the LK and the UK to subsurface temperature data using the same set of discrete water samples from SERC-FIU Water Quality Monitoring Network that are described above (ESM 1).

### Field fish collections

Fish collections took place from June–August in 2007 and June–July in 2008 in the UK and LK at two replicate coral reef sites within each subregion of the Florida Keys, Florida, United States (Fig. 1). Light traps were deployed to intercept late-stage larvae as they settled to the reef (Sponaugle and Cowen 1996; Rankin and Sponaugle 2011) during 15 day time periods of peak settlement encompassing the new and third quarter lunar phases (D'Alessandro et al. 2007). At each site, up to four replicate light traps were deployed 1 m



**Fig. 1** Ordinary kriging interpolation of chlorophyll a in the Florida Keys. Values were averaged at each sample site from 1995 to 2011 (ESM 1). *Stegastes partitus* (bicolor damselfish) samples were collected from the lower Florida Keys (LK) at American Shoal (AS; 24°31.241, –81°31.041) and Looe Key (LO; 24°32.528, –81°24.891). Samples from the upper Florida Keys (UK) were collected from Pickles Reef (PI; 24°59.17, –80°24.94) and Sand Island (SI; 25°01.109, –80°22.044). Black outlines show the delineation of UK and LK subregions. Chlorophyll a data were provided by the SERC-FIU Water Quality Monitoring Network which is supported by EPA Agreement #X994621-94-0 and NOAA Agreement #NA09NOS4260253

below the surface and 50 m apart at sunset and then collected the next day at sunrise. Following the appearance of late-stage larvae in the light traps, juvenile fish up to 3 weeks post-settlement were counted and collected weekly by divers along 15 haphazardly placed 5 m × 1 m transects at each of the sites in the UK and LK. Upon arriving to a site, divers swam several meters away from the small boat (in different directions each survey period) before beginning transect surveys and collections to ensure that the exact same location was not resampled with each subsequent collection.

### Otolith analysis

Four cohorts of bicolor damselfish collected during June and July of 2007 and 2008 were aged using otolith microstructure analysis. The standard length of each fish was measured to the nearest 0.01 mm using a Leica MZ12 dissecting microscope and Image-Pro Plus 7.0 image analysis software (Media Cybernetics). The lapillus was used for otolith analyses rather than the sagitta based on the precedence set by previous studies (Sponaugle and Cowen 1996; Rankin and Sponaugle 2011) and the ease of daily increment enumeration. Left and right lapilli were extracted from each fish and stored in immersion oil, and one otolith per fish was selected for microstructure analysis based on clarity and ease of reading. Daily otolith growth increments of bicolor damselfish

have been validated by Robertson et al. (1988) and bicolor damselfish show a distinct mark between the larval and juvenile stages that denotes settlement (Nemeth 2005). Daily growth and settlement marks were identified and enumerated using a Leica DMLB microscope at 400× magnification, a digital camera, and Image-Pro Plus software (Sponaugle 2009). Each otolith was read up to three times, and fish were included in analyses if a minimum of two otolith reads were within a 5% margin of error. The final otolith read used in the analysis was then selected randomly from the replicate reads.

### Early life-history traits and selective mortality

Otolith increment widths were used as a proxy for somatic growth after verifying a significant relationship between fish standard length and otolith radius for pooled sites and cohorts (Linear regression,  $r^2 = 0.87$ ,  $F_{1,791} = 5213$ ,  $P < 0.0001$ ). Each cohort was defined using a 14-d back-calculated settlement window for early life-history trait and selective mortality analyses. Fish were divided into three age groups to assess trait-based selective mortality: (1) settlers collected in light traps on the night of settlement, (2) recruits that were 1–10 days post-settlement, and (3) juveniles that were 11–20 days post-settlement. Daily otolith-derived growth corresponding to the pelagic larval stage was averaged across two larval growth periods from 1 to 10 days and 11–20 days post-hatch. Post-settlement growth was averaged during the first 4 days following settlement to the reef. Therefore, the analysis of post-settlement growth included only fish that were > 4 days post-settlement, resulting in slightly smaller sample sizes.

For all analyses, fish collected from the two replicate sites within each subregion were combined for analysis to correspond to the subregional scale of productivity patterns. Subregional differences in otolith-derived traits and selective mortality were compared using two-factor General Linear Mixed Models with cohort as a random factor and subregion and age group as fixed factors (R Statistical Software, lme4 package). Candidate models with and without interaction terms were compared using AIC to select the most parsimonious models, and Tukey post hoc tests were used when significant differences emerged among main effects (R Statistical Software, multcomp package).

### Population density and mortality

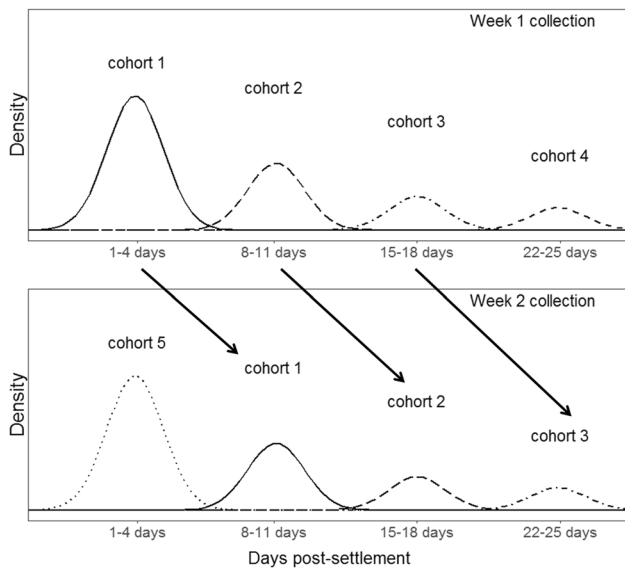
To obtain fish density and comparative mortality estimates in the UK and LK, fish surveys and collections of fish up to ~20 mm total length, along the aforementioned 15 m × 1 m transects at each site, from June–August 2007 and June–July 2008 were used to calculate juvenile fish

population densities and to track bicolor damselfish cohorts through time. Total average density of bicolor damselfish (fish m<sup>-2</sup>) up to 4 weeks post-settlement in each subregion was calculated using total counts of fish from weekly survey data that incorporated transects in which no fish were observed. For mortality calculations, we used size–age relationships to calculate the relative decline in abundance of cohorts through time. Using the least squares regression relationships between otolith-derived post-settlement age ( $y$ ) and standard length ( $x$ ) from the four primary study cohorts (June and July 2007 and 2008) in the UK (Linear regression,  $r^2 = 0.74$ ,  $F_{1,362} = 1025$ ,  $P < 0.0001$ ,  $y = 2.25x - 24.76$ ) and LK (Linear regression,  $r^2 = 0.72$ ,  $F_{1,427} = 1076$ ,  $P < 0.0001$ ,  $y = 2.73x - 27.51$ ), we converted the standard lengths of all fish counted along transects to post-settlement age. SCUBA divers aimed to collect all fish that were censused on each transect; however, along each transect, there were small differences in the number of fish collected compared to those observed. With the assumption that visual counts provide a better estimate of fish densities, proportional age values from collected and aged fish were applied to counts from visual surveys for each respective survey to obtain a corrected age distribution. Mortality calculations rely on a decline in abundance with time, and study sites were visited weekly. Therefore, for mortality analyses, cohorts were tracked based on weekly settlement windows. Due to uncertainty in the length to age relationship (root mean-squared error: UK and LK = 3.49) used for age conversions, cohorts were further constrained to a 4-day window such that a cohort during week 1 was defined as containing fish between age 1–4 days, week 2 as 8–11, week 3 as 15–18, and week 4 as 22–25 days. Density values were then averaged among 4-day windows to obtain cohort-based weekly density estimates (see Fig. 2 for schematic). This resulted in a total of 27 cohorts that were observed during the sampling period. Weekly declines in cohort densities were used to estimate mortality rates across all fish cohorts from June–August 2007 and June–July 2008 with the catch curve method. This method uses a linearized exponential mortality equation:

$$\ln(N_t) = a + Mt$$

where  $N_t$  is the fish abundance or catch per unit effort at time  $t$ ,  $a$  is the intercept,  $M$  is the natural mortality rate, and  $t$  is time calculated in weeks for this study (Pauly 1984; Beverton and Holt 1993). The method assumes that there are no temporal trends in recruitment magnitude, and that levels of recruitment fluctuate around a mean value. However, the method is robust to some variation in recruitment magnitude (Meekan et al. 2001). Mortality rate, or the slope of the linear regression line, was compared between sites within subregions and then between subregions using ANCOVA (R Statistical Software version 3.1.2).





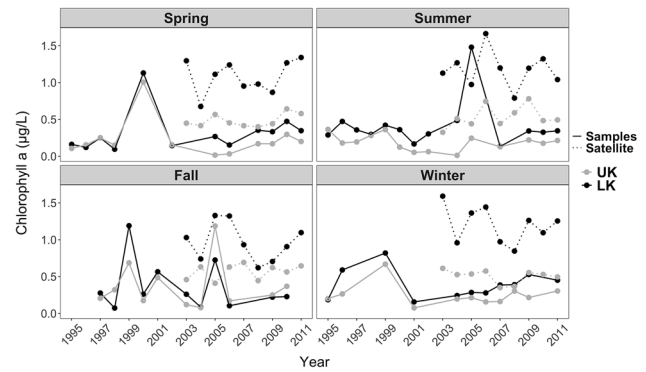
**Fig. 2** Schematic of mortality calculations based on two sample collections. Cohorts were defined based on 4-day time intervals and density values were averaged within each interval to obtain cohort densities (ex: cohort 1, cohort 2, cohort 3, cohort 4 during week 1 collection). These cohorts were then repeatedly sampled based on otolith-derived age-length relationships in the subsequent week (arrows designate cohort re-sampling between week 1 and week 2 collections). The decline in cohort densities between weeks was used to calculated mortality

## Results

### Subregional productivity and temperature

Ordinary kriging interpolations of chlorophyll from discrete sample data (root mean square = 0.06) revealed that long-term (1995–2011) patterns of primary productivity were likely higher in the LK compared to the UK. On average, chlorophyll concentrations were ~1.75 times higher in the LK than the UK (Fig. 1). Time series of chlorophyll also suggest higher primary productivity in the LK compared to the UK across seasons and years, particularly based on surface satellite data (Fig. 3). During 2007 and 2008, when fish collections and surveys took place, the two datasets together indicate higher chlorophyll in the LK. Based on the discrete sample data, chlorophyll was higher in the spring in the LK in 2008 (no data from spring 2007) and similar during the summer in 2007 (no data from summer 2008), but the surface satellite data consistently shows higher chlorophyll in the LK across all seasons and years (Fig. 3).

Subregional sea surface water temperatures were within 0.5 °C during each cohort sample month, and there was < 2 °C temperature range across the entire study period (Table 1). Sea surface satellite data and discrete sample data throughout the water column indicate that there was no major subregional pattern in water temperature. These



**Fig. 3** Chlorophyll a in the upper (UK) and lower (LK) Florida Keys using discrete sample (Samples) and satellite-based data (Satellite). For discrete sample data, values were averaged across sites and depths from 1995 to 2011 using the UK and LK subregional designations (ESM 1). Values were averaged for satellite data across six 4-km grid cells that were selected in each the LK and the UK in closest proximity to the fish sample collection sites at American Shoal (24°31.241, -81°31.041) and Looe Key (24°32.528, -81°24.891) in the LK and Pickles Reef (24°59.17, -80°24.94) and Sand Island (25°01.109, -80°22.044) in the UK. Seasons are designated as: (1) Spring: March–May, (2) Summer: June–August, (3) Fall: September–November, (4) Winter: December–February. Discrete sample chlorophyll a data were provided by the SERC-FIU Water Quality Monitoring Network which is supported by EPA Agreement #X994621-94-0 and NOAA Agreement #NA09NOS4260253. Satellite data were MODIS-Aqua 4-km resolution monthly data (<http://oceandata.sci.gsfc.nasa.gov/MODIS-Aqua/>)

data also confirm that temperatures in the UK and LK were similar in 2007 and 2008, particularly during the summer months (ESM 2).

**Table 1** Summary of *Stegastes partitus* (bicolor damselfish) cohorts used in otolith analyses

Cohort	Subregion	Temperature (°C)	N (settlers, recruits, juveniles)
June 2007	UK	27.13	29, 26, 14
	LK	27.57	29, 33, 13
July 2007	UK	28.66	27, 36, 12
	LK	29.01	29, 37, 11
June 2008	UK	27.78	58, 32, 29
	LK	27.97	59, 33, 39
July 2008	UK	28.87	30, 24, 32
	LK	29.09	57, 34, 43

The “Cohort” column refers the settlement month and year of each cohort. Subregion refers to the upper Florida Keys (UK) and lower Florida Keys (LK) and N is the number of fish in each age group used in the analyses

## Fish traits and selective mortality

A total of 766 fish were used in the analysis after excluding 232 fish that were either outside of the 14-day cohort settlement window, or had otolith reads that did not meet the 5% margin of error criteria (Table 1). Patterns of traits and selective mortality were similar in the UK and LK, with no subregional differences in ELHTs associated with the pelagic larval stage (larval growth, pelagic larval duration (PLD), or settlement size; Table 2, Fig. 4a–c). Recruits (1–10 days post-settlement) in both subregions experienced selection for faster larval growth during days 1–10 post-hatch (i.e., survivors had significantly faster growth during this period). This selective survival was reversed such that juvenile fish (11–20 days post-settlement) with slower growth during days 1–10 post-hatch preferentially survived (Table 2; Fig. 4a). There was no apparent selective mortality related to growth over days 11–20 post-hatch (Table 2). In both subregions, there was also consistently higher survival of individuals with longer PLDs and larger settlement sizes (Table 2; Fig. 4b, c). Selection for settlement size was apparent for recruits, whereas selection for longer PLD show incremental increases between settlers, recruits, and juveniles (Fig. 4b, c). Both the recruit and the juvenile age categories grew significantly faster in the LK compared to the UK during the first 4 days after settlement to the reef (Table 2; Fig. 4d). Accordingly, this faster growth in the LK was not associated with selective survival of faster growing individuals following settlement to the reef.

## Population density and mortality

Densities of fish up to ~1 month post-settlement were significantly higher in the LK (density  $\pm$  SE =  $0.59 \pm 0.05$  fish  $m^{-2}$ ) compared to the UK (density  $\pm$  SE =  $0.34 \pm 0.03$  fish  $m^{-2}$ ) throughout the study ( $T$  test,  $t_{48,72} = -4.2$ ,  $P < 0.0001$ ). There were no significant differences in mortality between

sites within each subregion (ANCOVA;  $P > 0.05$ ), thus, site-specific fish densities were averaged within each the UK and LK. Mortality comparisons among subregions showed significantly higher mortality in the LK than the UK (ANCOVA,  $r^2 = 0.20$ ,  $F_{2,95} = 12.16$ ,  $P < 0.0001$ ). The slope of the mortality regression in the LK was significant (Linear regression,  $r^2 = 0.15$ ,  $F_{1,47} = 8.4$ ,  $P = 0.006$ ,  $y = 1.15 - 0.14x$ ), with a weekly mortality estimate of 0.14, whereas in the UK, fish densities did not decrease with age sufficiently precipitously to generate a significant slope (Linear regression,  $P = 0.47$ ; Fig. 5).

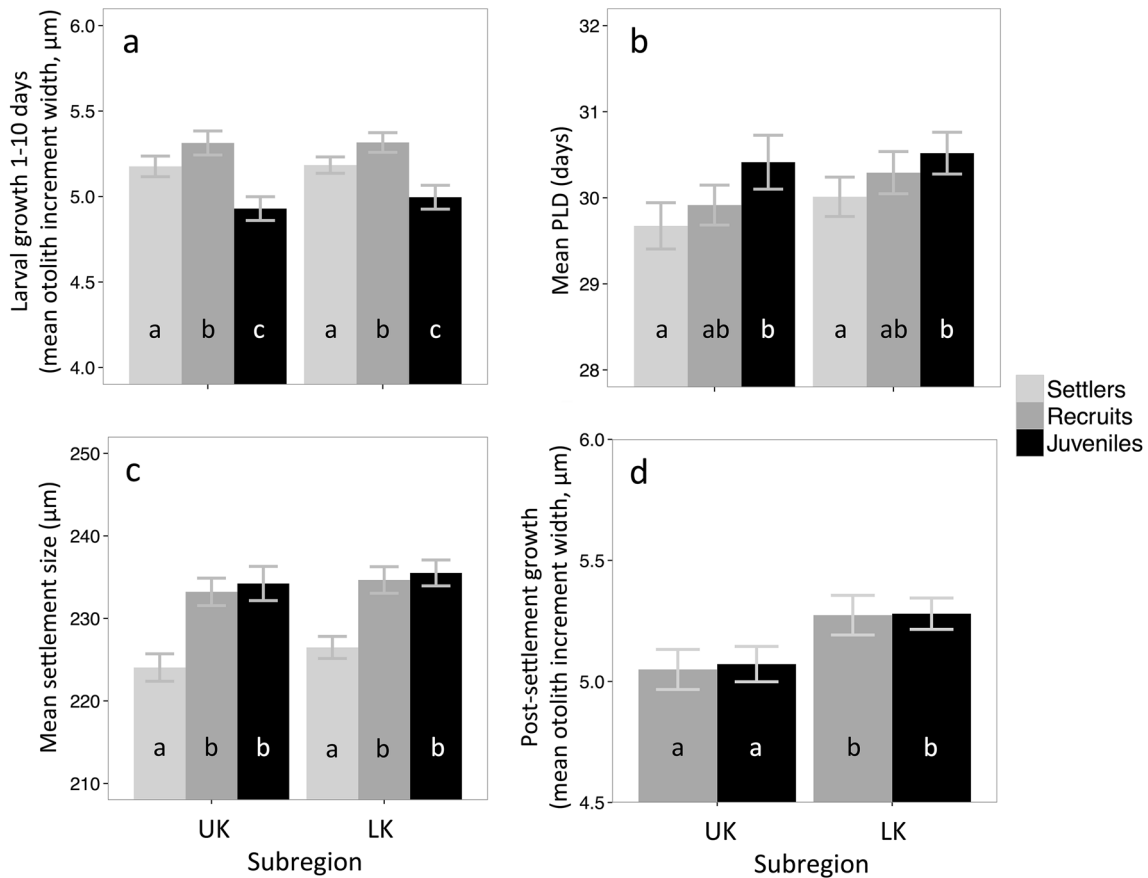
## Discussion

Local oceanographic differences between the UK and LK result in subregional variability in chlorophyll, with the potential to influence patterns in traits and survival of coral reef organisms. Subregional oceanography such as longer residence times of cyclonic eddies that likely enhance upwelling and nutrients in shallow coral reef environments (Lee et al. 1994; Wolanski and Delesalle 1995; Leichter et al. 2003) may augment primary and secondary production and create spatial patterns in food availability for fish (Hitchcock et al. 2005). Indeed, our results indicate that despite arriving to reefs with similar traits, and consistencies in trait-mediated selective mortality, juvenile bicolor damselfish grew faster in the LK where productivity, and likely food availability, are higher. Subregional enhancement of pelagic productivity may increase food availability for demersal reef organisms, and create local patterns in juvenile fish growth, survival, and local population replenishment. However, despite the potential for the LK to be a favorable settlement habitat with higher food availability supporting faster growth, mortality was higher for young fish in the LK following settlement to the reef.

**Table 2** Results of General Linear Mixed Models for otolith-derived traits of *Stegastes partitus* (bicolor damselfish) with subregion (UK and LK) and age level ( $S$  settlers,  $R$  recruits,  $J$  juveniles) as fixed factors, and cohort as a random factor

	Subregion	Age group	Pairwise comparisons
Larval growth 1–10 days ( $\mu$ m)	ns	$P < 0.0001$ $F(2,759) = 24.33$	$J < S < R$ $5.0 \pm 0.05 < 5.2 \pm 0.04 < 5.3 \pm 0.04$
Larval growth 11–20 days ( $\mu$ m)	ns	ns	–
PLD (days)	ns	$P = 0.01$ $F(2,759) = 4.39$	$S < J$ $29.9 \pm 0.17 < 30.5 \pm 0.19$
Settlement size ( $\mu$ m)	ns	$P < 0.0001$ $F(2,759) = 35.15$	$S < R$ and $S < J$ $225.4 \pm 1.05 < 234.0 \pm 1.16$ and $225.4 \pm 1.05 < 235.0 \pm 1.27$
Post-settlement growth ( $\mu$ m)	$P = 0.006$ $F(1,392) = 7.51$	ns	$LK > UK$ $5.3 \pm 0.05 < 5.1 \pm 0.06$

Test statistics and  $P$  values are reported for significant tests comparing subregions and age groups and “ns” denotes non-significant tests. Multiple pairwise comparisons are results of Tukey HSD, and inequality values are mean  $\pm$  SE



**Fig. 4** Significant differences in mean otolith-derived early life-history traits among age groups (settlers, recruits, juveniles) of *Stegastes partitus* (bicolor damselfish) in the upper Florida Keys (UK) and lower Florida Keys (LK), reflecting selective mortality. Traits are mean **a** larval growth during days 1–10 post-hatch, **b** pelagic larval

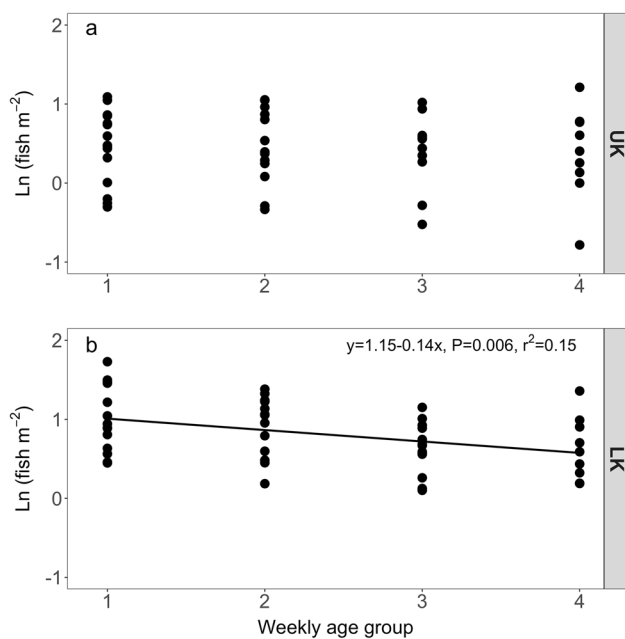
duration, **c** settlement size, and **d** daily juvenile growth during the first 4 days post-settlement. Letters denote significant differences among pairwise comparisons. All pairwise comparisons are shown for visual purposes even when there was no significant difference

### Pelagic larval traits

Bicolor damselfish that settled to reefs in the UK and LK had similar pelagic ELHTs with respect to larval growth, pelagic larval duration, and settlement size. With the assumption that the ELHTs of larvae that develop in similar water masses are expected to be analogous (Hamilton et al. 2008; Shima and Swearer 2009), the absence of spatial patterns in larval ELHTs suggests that late-stage larvae collected in the UK and LK experienced comparable pelagic environments as larvae. The locations of larvae throughout the pelagic stage during this study were unknown and there is evidence that bicolor damselfish populations are well mixed throughout the Bahamas (Christie et al. 2010) and the Caribbean Sea (Purcell et al. 2009), suggesting that late-stage larvae collected in the UK and LK may originate from either proximal or distant sources, and consequently experience a range of pelagic environments. Similarities in larval traits may be a result of a shared pelagic habitat, or bicolor damselfish may be robust to environmentally driven growth variability

during the larval stages (Shulzitski et al. 2015, 2016). Thus, similarities in pelagic ELHTs of bicolor damselfish in the UK and LK may be influenced by relatively invariant growth patterns as well as by larval mixing and transport.

Regardless of post-settlement habitat, all juveniles exhibited a similar directional shift in ELHTs associated with survival. Across the study region, survival of young bicolor damselfish in the reef environment was associated with slow growth during the first 10 days of life as pelagic larvae. This pattern shifted for older fish in the reef environment where survival was lower for individuals that grew slowly as larvae. Such shifts in the direction of selection may ultimately serve to maintain phenotypic variation in ELHTs and support bet-hedging strategies for larval traits (Gagliano et al. 2007), but similarities among the UK and LK suggest that selective predation favors similar pelagic growth histories regardless of subregional differences in settlement habitat. In addition to growth, selection for longer PLDs and larger settlement sizes was consistent in both the UK and the LK, in concert with the “bigger is better” component of the Growth



**Fig. 5** Relationship between the natural log of the mean density (fish m<sup>-2</sup>) of young bicolor damselfish weekly age groups, based on otolith-derived length-age relationships of *Stegastes partitus* (bicolor damselfish) repeatedly sampled in 2007 and 2008 in the **a** upper (UK) and **b** lower (LK) Florida Keys. The slope of the regression equation corresponds to an estimated weekly mortality rate. The regression equation and  $r^2$  value is included for significant relationships

Mortality Hypothesis that links larger size to reduced susceptibility to predation (Anderson 1988; Rankin and Sponaugle 2011). Selective mortality is primarily the result of predation (Sogard 1997; Hixon and Jones 2005), and can be influenced by water temperature, competition, and the composition and size of predators (Hoey and McCormick 2004), thus varying among species, locations, and seasons (Sponaugle and Grorud-Colvert 2006; Rankin and Sponaugle 2011). Co-linearity of traits can also disguise the role of particular ELHTs in survival (Johnson et al. 2012). Despite these interacting drivers of mortality, and a consistent sub-regional pattern of productivity, subregional congruence in the direction of selective mortality across the Florida Keys reflects the overwhelming strength of selection for particular larval growth rates, larger settlement sizes, and longer PLDs for this species. Habitat-mediated and predator-related carry-over effects of larval traits on post-settlement survival have been identified at smaller spatial scales (McCormick and Hoey 2004; Smith and Shima 2011); however, the impacts of such processes may not scale-up to subregional patterns. Consistent patterns of selective mortality across the ~160 km between the UK and LK suggest that survival across the Florida Keys is influenced by large-scale, common ecological pressures and is not restricted by selection for locally adapted ELHTs.

## Post-settlement traits and survival

Following the arrival and settlement of fish with similar larval traits to the reefs of the UK and LK, variability in post-settlement reef habitat resulted in differences in sub-regional juvenile growth. Bicolor damselfish in the LK grew 4% faster during the first 4 days post-settlement than fish in the UK. Although this value is small, differences in growth were apparent after only 4 days in the reef environment despite potential physiological lags related to assimilation efficiency between feeding and growth (Elliott and Persson 1978; Armstrong et al. 2013), and potential carry-over from the larval stage (Shima and Swearer 2010; Smith and Shima 2011; D'Alessandro et al. 2013). Substantial differences in subregional productivity in some years also underscore the potential for greater divergences in growth. Similarities between subregional temperatures in comparison to the magnitude of difference between chlorophyll in the UK and LK suggest the influence of productivity on growth rather than temperature (Rankin and Sponaugle 2011). Young fish in the LK grew faster despite higher population densities that could potentially enhance density-dependent processes such as access to food and competition (White et al. 2010). We did not measure other processes that interact with density-dependent competition such as shelter availability or predation (White et al. 2010; Ford et al. 2016), but the lack of post-settlement growth-related selective mortality, as well as higher densities coupled with faster growth in the more productive LK, suggests that access to higher food availability likely enhances growth rates of young planktivorous fish in the LK.

While higher juvenile growth in the LK suggests potential regional variability in settlement habitat quality, mortality was also significantly higher in the LK, creating conflicting risks and benefits of each settlement subregion. Interestingly, subpopulation densities of young bicolor damselfish were consistently higher in the LK, indicating that higher mortality did not entirely suppress the effects of the larger influx of settlement-stage larvae (Sponaugle et al. 2012). Modeling and time-series light trap collections of settling larvae demonstrate that subpopulations in the LK experience consistently higher recruitment to the juvenile population than UK populations (Sponaugle et al. 2012) despite enhanced mortality.

The absence of selective mortality related to post-settlement growth in this study was in contrast to a previous study showing higher survival linked to slower post-settlement growth across 13 cohorts of bicolor damselfish collected in the UK (Rankin and Sponaugle 2011). Potential explanations for the difference in findings include: (1) the comparison of different periods of juvenile growth. Due to sample limitations in the present study, we compared growth over the first 4 days of post-settlement life and it is



possible that patterns of selective mortality only become evident after 6 days of growth (the period examined previously); or (2) additional cohorts may be required for small but consistent differences in traits to become significant. This discrepancy highlights the intricacies of selective processes, and the value of the present study in comparing paired temporal cohorts across a broad spatial scale.

## Conclusions

Our results revealed patterns of post-settlement growth and mortality of young bicolor damselfish across subregions with spatially variable oceanography and productivity. Newly settled fish in the LK grew more quickly than fish in the UK, suggesting that high food availability may mitigate the effects of higher juvenile densities and resource competition. This faster post-settlement growth in the LK was not a result of selective mortality differences between subregions and was detectable after just a few days in the reef environment. Rapid subregional differences in growth and mortality highlight the potential compounding impacts of habitat variation on fish populations throughout ontogeny to influence subregional population sizes and source-sink dynamics (Goldstein et al. 2016). These patterns suggest that oceanographically driven higher productivity in the LK not only enhances fish recruitment (Sponaugle et al. 2012; Shulzitski et al. 2016) and post-settlement growth rates, but also supports large population sizes despite higher mortality rates. Interactions between dynamic oceanographic conditions and benthic habitats ultimately create spatial patterns of recruitment, favorable habitats, and alter food availability with consequences to subpopulation traits, abundance, and survival of demersal reef organisms.

**Acknowledgements** We thank T. Rankin, E. D'Alessandro, K. Shulzitski, K. Huebert, K. Walter, and numerous volunteers for field and laboratory assistance and expertise. We also thank the anonymous reviewers for their constructive feedback.

**Author contributions** SS and EG conceived of the study. EG conducted the laboratory work and data analysis. EG wrote the paper with input from SS.

**Funding** Collection of samples was supported by National Science Foundation (NSF) OCE Grant 0550732, and during manuscript preparation, SS received support from National Oceanic and Atmospheric Administration Award NA11NOS4780045 and NSF Grant OCE 14119987.

## Compliance with ethical standards

**Conflict of interest** The authors declare that they have no conflict of interest.

**Ethical standards** All collections and fish handling procedures were carried out with the approval of the University of Miami under UM-ACUC Permit #01-056. Fish were collected under permits #00S-524 and 02R-524 from the Florida Fish and Wildlife Conservation Commission, and permits #2001-004 and 2002-025A from the Florida Keys National Marine Sanctuary. All applicable international, national, and institutional guidelines for the care and use of animals were followed.

## References

- Anderson JT (1988) A review of size dependent survival during pre-recruit stages of fishes in relation to recruitment. *J Northwest Atl Fish Sci* 8:55–66
- Armstrong JB, Schindler DE, Ruff CP, Brooks GT, Bentley KE, Torgersen CE (2013) Diel horizontal migration in streams: Juvenile fish exploit spatial heterogeneity in thermal and trophic resources. *Ecology* 94:2066–2075
- Beverton RJH, Holt SJ (1993) On the dynamics of exploited fish populations. *Fish and Fisheries Series*, vol 11. Chapman & Hall, London (**Facsimile reprint of the 1957 book, UK Stationary Office**)
- Booth DJ, Hixon MA (1999) Food ration and condition affect early survival of the coral reef damselfish, *Stegastes partitus*. *Oecologia* 121:364–368
- Botsford LW, Moloney CL, Hastings A, Largier JL, Powell TM, Higgins K, Quinn JF (1994) The influence of spatially and temporally varying oceanographic conditions on meroplanktonic metapopulations. *Deep Sea Res Part II Top Stud Oceanogr* 41:107–145
- Brokovich E, Baranes A, Goren M (2006) Habitat structure determines coral reef fish assemblages at the northern tip of the Red Sea. *Ecol Indic* 6:494–507
- Christie MR, Johnson DW, Stallings CD, Hixon MA (2010) Self-recruitment and sweepstakes reproduction amid extensive gene flow in a coral-reef fish. *Mol Ecol* 19:1042–1057
- Clarke LM, Munch SB, Thorrold SR, Conover DO (2010) High connectivity among locally adapted populations of a marine fish (*Menidia menidia*). *Ecology* 91:3526–3537
- D'Alessandro EK, Sponaugle S, Lee T (2007) Patterns and processes of larval fish supply to the coral reefs of the upper Florida Keys. *Mar Ecol Prog Ser* 331:85–100
- D'Alessandro E, Sponaugle S, Cowen R (2013) Selective mortality during the larval and juvenile stages of snappers (Lutjanidae) and great barracuda *Sphyrna barracuda*. *Mar Ecol Prog Ser* 474:227–242. <https://doi.org/10.3354/meps10114>
- Di Franco A, Qian K, Calò A, Di Lorenzo M, Planes S, Guidetti P (2013) Patterns of variability in early life traits of a Mediterranean coastal fish. *Mar Ecol Prog Ser* 476:227–235. <https://doi.org/10.3354/meps10117>
- Elliott JM, Persson L (1978) The estimation of daily rates of food consumption for fish. *J Anim Ecol* 47:977–991. <https://doi.org/10.2307/3682>
- Emery AR (1973) Comparative ecology and functional osteology of fourteen species of damselfish (Pisces: Pomacentridae) at Alligator Reef, Florida Keys. *Bull Mar Sci* 23:649–770
- Figueira WF (2009) Connectivity or demography: defining sources and sinks in coral reef fish metapopulations. *Ecol Model* 220:1126–1137
- Ford JR, Shima JS, Swearer SE (2016) Interactive effects of shelter and conspecific density shape mortality, growth, and condition in juvenile reef fish. *Ecology* 97:1373–1380. <https://doi.org/10.1002/ecy.1436>
- Fratantoni PS, Lee TN, Podesta GP, Muller-Karger F (1998) The influence of Loop Current perturbations on the formation and evolution

- of Tortugas eddies in the southern straits of Florida. *J Geophys Res* 103:24759–24779
- Gagliano M, McCormick MI, Meekan MG (2007) Survival against the odds: ontogenetic changes in selective pressure mediate growth-mortality trade-offs in a marine fish. *Proc R Soc B Biol Sci* 274:1575–1582
- Goldstein ED, D'Alessandro EK, Reed J, Sponaugle S (2016) Habitat availability and depth-driven population demographics regulate reproductive output of a coral reef fish. *Ecosphere* 7:11. <https://doi.org/10.1002/ecs2.1542>
- Goldstein ED, D'Alessandro EK, Sponaugle S (2017) Fitness consequences of habitat variability, trophic position, and energy allocation across the depth distribution of a coral-reef fish. *Coral Reefs* 36:957–968. <https://doi.org/10.1007/s00338-017-1587-4>
- Hamilton SL, Regetz J, Warner RR (2008) Post settlement survival linked to larval life in a marine fish. *Proc Natl Acad Sci* 105:1561–1566
- Hitchcock GL, Lee TN, Ortner PB, Cummings S, Kelble C, Williams E (2005) Property fields in a tortugas eddy in the southern straits of Florida. *Deep Sea Res Part Oceanogr Res Pap* 52:2195–2213
- Hixon MA, Jones GP (2005) Competition, predation, and density-dependent mortality in demersal marine fishes. *Ecology* 86:2847–2859
- Hixon M, Anderson T, Buch K, Johnson D, McLeod JB, Stallings C (2012) Density dependence and population regulation in marine fish: a large-scale, long-term field manipulation. *Ecol Monogr* 82:467–489
- Hoey A, McCormick M (2004) Selective predation for low body condition at the larval-juvenile transition of a coral reef fish. *Oecologia* 139:23–29
- Holbrook SJ, Forrester GE, Schmitt RJ (2000) Spatial patterns in abundance of a damselfish reflect availability of suitable habitat. *Oecologia* 122:109–120
- Johnson DW (2008) Combined effects of condition and density on post-settlement survival and growth of a marine fish. *Oecologia* 155:43–52. <https://doi.org/10.1007/s00442-007-0882-0>
- Johnson DW, Hixon MA (2010) Ontogenetic and spatial variation in size-selective mortality of a marine fish. *J Evol Biol* 23:724–737
- Johnson DW, Grorud-Colvert K, Rankin T, Sponaugle S (2012) Measuring selective mortality from otoliths and similar structures: a practical guide for describing multivariate selection from cross-sectional data. *Mar Ecol Prog Ser* 471:151–163
- Jones GP (1986) Food availability affects growth in a coral reef fish. *Oecologia* 70:136–139
- Leahy SM, Russ GR, Abesamis RA (2015) Pelagic larval duration and settlement size of a reef fish are spatially consistent, but post-settlement growth varies at the reef scale. *Coral Reefs* 34:1283–1296. <https://doi.org/10.1007/s00338-015-1330-y>
- Lee TN, Clarke M, Williams E, Szmant AF, Berger T (1994) Evolution of the Tortugas Gyre and its influence on recruitment in the Florida Keys. *Bull Mar Sci* 54:621–646
- Leichter JJ, Stewart HL, Miller SL (2003) Episodic nutrient transport to Florida coral reefs. *Limnol Oceanogr* 48:1394–1407
- Levin P, Petrik R, Malone J (1997) Interactive effects of habitat selection, food supply and predation on recruitment of an estuarine fish. *Oecologia* 112:55–63
- McCormick MI, Hoey AS (2004) Larval growth history determines juvenile growth and survival in a tropical marine fish. *Oikos* 106:225–242. <https://doi.org/10.1111/j.0030-1299.2004.13131.x>
- Meekan MG, Ackerman JL, Wellington GM (2001) Demography and age structures of coral reef damselfishes in the tropical eastern Pacific Ocean. *Mar Ecol Prog Ser* 212:223–232
- Nemeth RS (2005) Linking larval history to juvenile demography in the bicolor damselfish *Stegastes partitus* (Perciformes: Pomacentridae). *Rev Biol Trop* 53:155–163
- Pauly D (1984) Fish population dynamics in tropical waters: a manual for use with programmable calculators. ICLARM Studies and Reviews 8. International Center for Living Aquatic Resources Management, Manila
- Purcell JFH, Cowen RK, Hughes CR, Williams DA (2009) Population structure in a common Caribbean coral-reef fish: implications for larval dispersal and early life-history traits. *J Fish Biol* 74:403–417. <https://doi.org/10.1111/j.1095-8649.2008.02078.x>
- Rankin TL, Sponaugle S (2011) Temperature influences selective mortality during the early life stages of a coral reef fish. *PLoS One* 6:e16814
- Robertson DR, Green DG, Victor BC (1988) Temporal coupling of production and recruitment of larvae of a Caribbean reef fish. *Ecology* 69:370–381
- Schmale MC (1981) Sexual selection and reproductive success in males of the bicolor damselfish, *Eupomacentrus partitus* (Pisces: Pomacentridae). *Anim Behav* 29:1172–1184
- Searcy SP, Sponaugle S (2001) Selective mortality during the larval-juvenile transition in two coral reef fishes. *Ecology* 82:2452–2470
- Shima JS, Swearer SE (2009) Larval quality is shaped by matrix effects: implications for connectivity in a marine metapopulation. *Ecology* 90:1255–1267. <https://doi.org/10.1890/08-0029.1>
- Shima JS, Swearer SE (2010) The legacy of dispersal: larval experience shapes persistence later in the life of a reef fish. *J Anim Ecol* 79:1308–1314
- Shulzitski K, Sponaugle S, Hauff M, Walter K, D'Alessandro EK, Cowen RK (2015) Close encounters with eddies: oceanographic features increase growth of larval reef fishes during their journey to the reef. *Biol Lett* 11:20140746
- Shulzitski K, Sponaugle S, Hauff M, Walter KD, Cowen RK (2016) Encounter with mesoscale eddies enhances survival to settlement in larval coral reef fishes. *Proc Natl Acad Sci* 113:6928–6933. <https://doi.org/10.1073/pnas.1601606113>
- Smith AC, Shima JS (2011) Variation in the effects of larval history on juvenile performance of a temperate reef fish: larval history and population dynamics. *Austral Ecol* 36:830–838. <https://doi.org/10.1111/j.1442-9993.2010.02223.x>
- Sogard SM (1997) Size-selective mortality in the juvenile stage of teleost fishes: a review. *Bull Mar Sci* 60:1129–1157
- Sponaugle S (2009) Gathering information from otoliths of tropical fishes. In: Green BS, Mapstone BD, Carlos G, Begg GA (eds) *Tropical fish otoliths: information for assessment, management, and ecology*. Springer, Netherlands, pp 93–132
- Sponaugle S, Cowen RK (1996) Larval supply and patterns of recruitment for two Caribbean reef fishes *Stegastes partitus* and *Acanthurus bahianus*. *Mar Freshw Res* 47:433–447
- Sponaugle S, Grorud-Colvert K (2006) Environmental variability, early life-history traits, and survival of new coral reef fish recruits. *Integr Comp Biol* 46:623–633
- Sponaugle S, Lee T, Kourafalou V, Pinkard D (2005) Florida current frontal eddies and the settlement of coral reef fishes. *Limnol Oceanogr* 50:1033–1048
- Sponaugle S, Boulay J, Rankin T (2011) Growth and size-selective mortality in pelagic larvae of a common reef fish. *Aquat Biol* 13:263–273
- Sponaugle S, Paris C, Walter K, Kourafalou V, D'Alessandro EK (2012) Observed and modeled larval settlement of a reef fish to the Florida Keys. *Mar Ecol Prog Ser* 453:201–212. <https://doi.org/10.3354/meps09641>
- White JW, Samhoury JF, Stier AC, Wormald CL, Hamilton SL, Sandin SA (2010) Synthesizing mechanisms of density dependence in reef fishes: behavior, habitat configuration, and observational scale. *Ecology* 91:1949–1961
- Wolanski E, Delesalle B (1995) Upwelling by internal waves, Tahiti, French Polynesia. *Cont Shelf Res* 15:357–368

**Publisher's Note** Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.