

AN ABSTRACT OF THE DISSERTATION OF

Miram Rayzel Gleiber for the degree of Doctor of Philosophy in Integrative Biology
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Title: PLANKTON FOOD WEB DYNAMICS AND LARVAL FISH SUCCESS:
INFLUENCE OF PREY AND PREDATOR DISTRIBUTIONS ON LARVAL FISH DIET,
GROWTH, AND ASSEMBLAGES IN THE STRAITS OF FLORIDA

Abstract approved: _____

Su Sponaugle

Survival of marine fishes during their early life history stage is tightly related to prey availability and predation pressure. Yet, our understanding of how individual larvae to entire assemblages are constrained by these factors is limited. We integrated biological sampling of larval fishes with fine-scale *in situ* imaging to relate patterns of larval fish feeding, growth, abundance, and assemblage structure to a gradient of fine- to regional-scale prey and predator conditions in the Straits of Florida. Otolith microstructure analysis showed that larval fish growth patterns reflected distributions of their preferred prey. Slower-growing reef fish (wrasses) larvae that are adapted to feed on patchy prey had faster growth at high prey densities, but also benefitted from dense patches of prey in otherwise low-density regions. In contrast, a fast-growing tuna species had faster larval growth at higher prey densities, but did not respond to prey patchiness, as their prey were consistently abundant. However, temperature appeared to strongly constrain larval tunas, evident from growth-temperature relationships that peaked at an optimum temperature, below their thermal limit. Further exploration of larval diet and growth of the abundant *Thunnus atlanticus* (blackfin tuna) revealed the combined consequences of poor prey availability and high temperatures. Larvae in high prey-low temperature conditions had fuller guts from eating higher quality prey and 30% faster growth rates, and were larger, older, and an order of magnitude more abundant, in

comparison to fish in warmer temperatures. Predators had a strong effect on larval growth for both tunas and wrasses, evident by increasing strength of growth-selective mortality with predator densities or availability of dense patches of predators. Quantification of the entire plankton and larval fish community illustrated contrasting patterns of how larval fishes in coastal-upwelling compared to oligotrophic conditions respond to interannual prey variability. In the upwelling-influenced region larval fishes were tightly linked to fluctuations in prey, with overall 350% higher densities of larval fishes in high-prey versus low-prey conditions. This was due to numerous key larvae (e.g., tunas) having dramatic changes in abundance associated with fluctuations in their preferred prey. In contrast, larvae in the oligotrophic oceanic region were more consistent, as many larvae (e.g., wrasses) have flexible life history traits suggesting adaptive tolerance to a poor prey environment. Consistently strong predation pressure by gelatinous zooplankton may compound the effects of variable prey conditions in the continental region, as larvae in a poor-prey year experienced similar predation pressure as in high-prey conditions. Our results illustrate the importance of considering food web dynamics when predicting the response of larval fishes, and thus marine fish population replenishment, to ecosystem variability, particularly in light of ongoing global climate change.

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GROWTH, AND ASSEMBLAGES IN THE STRAITS OF FLORIDA

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I understand that my dissertation will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my dissertation to any reader upon request.

Miram Rayzel Gleiber, Author

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CONTRIBUTION OF AUTHORS

Chapter 2, 3 & 4: Miram Gleiber conducted all laboratory analyses, data analysis, and manuscript preparation; Su Sponaugle was a co-PI, advised Miram Gleiber in analyses, and edited manuscript drafts; Robert Cowen was a co-PI and chief scientist; all authors participated in fieldwork.

Chapter 2 & 4: See above; Kelly Robinson facilitated image processing.

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CHAPTER 1: GENERAL INTRODUCTION

The need to understand food web dynamics is increasingly urgent to enable accurate predictions of the biological responses of our planet's ecological communities to ongoing and future conditions. Climate change is increasing environmental variability, with implications for ecological interactions within and across systems. In marine ecosystems, rising global temperatures are driving changes in productivity (Behrenfeld et al. 2006) and restructuring planktonic food webs (Richardson 2008), with consequences for higher trophic levels (Beaugrand et al. 2003). As changes in prey availability impact feeding success, the combined effects of increased metabolic rates at higher temperatures and resource limitation can exacerbate the effects of warming on marine communities (Buckley et al. 2004, Tewksbury et al. 2008). Therefore, it is a critical time to be examining the effect of trophic interactions across scales from individuals to communities.

The pelagic larval phase of most marine fishes is especially sensitive to food web variability, as survival during this phase (weeks to months) depends on the ability of larvae to find food and avoid predation (Houde 2008). Since mortality rates are typically very high during the larval phase, successful feeding and growth influence patterns of recruitment and subsequent adult population dynamics (Hjort 1914, Castonguay et al. 2008). However, fine-(meters) to large-scale (kilometers) physical oceanographic processes (e.g., currents, upwelling, stratification, eddies, fronts) locally enhance biological production in the pelagic environment, structuring distributions of larval fishes and their planktonic prey and predators (Steele 1978, Bakun 2006, Greer et al. 2013). Aggregations of prey due to such physical processes enhance larva-prey encounter rates that optimize foraging in an often prey-limited pelagic environment (Lasker 1975, Houde 1987). Yet favorable feeding conditions can be risky scenarios for fish larvae due to a high co-occurrence of predators (Purcell & Arai 2001, Garrison et al. 2002), as both are frequently concentrated by physical oceanographic processes that enhance biological productivity (McGillicuddy 2016). Consequently, factors that regulate larval fish survival, such as feeding and growth, are closely linked to prey and predator concentrations and distribution patterns.

Individual larval fish traits (e.g., diet, growth, size-at-age) are valuable tools for understanding how success is related to variability in the prey (or predator) environment. Enhanced prey availability has been consistently linked to greater larval fish feeding success

which generally translates to faster growth rates and higher condition (Sponaugle et al. 2009, Dower et al. 2009). Favorable larval growth and condition increases the probability of larval survival by reducing vulnerability to gape-limited predation via size and shorter larval duration (Miller et al. 1988, Hare & Cowen 1997) and can carry over to influence metamorphosis and juvenile survivorship (Searcy & Sponaugle 2001, Sponaugle & Grorud-Colvert 2006). The effect of predators on larval survivorship is often evident in the characteristics of survivors, as predators generally consume smaller, slower-growing individuals (Anderson, 1988; Takasuka *et al.*, 2003). However, directly relating larval fish traits to predator concentrations has been difficult due to sampling limitations. High resolution *in situ* imaging now makes it possible to quantify the gelatinous predator field together with the prey of larval fishes (Greer et al. 2013, Luo et al. 2014).

In this study, we combine fine-scale *in situ* imaging with biological net sampling of larval fishes to explore the relationship between larval traits and prey/predator distributions across a gradient of conditions. We conducted high-resolution imaging with the *In Situ* Ichthyoplankton Imaging System (*ISIIS*; Cowen and Guigand, 2008), an oceanographic tool that simultaneously samples fine-scale distributions of the entire plankton community and the surrounding physical conditions. *In situ* imaging studies with the *ISIIS* have revealed locally enhanced zooplankton abundances, including prey and predators of larval fishes, along physical gradients associated with productive frontal features (Luo et al. 2014, Greer et al. 2015). Further, a recent study showed tight coupling between the fine-scale distributions of larval fishes and their prey across a productive mesoscale eddy (Schmid et al. 2020). Larvae associated with such productive oceanographic features can experience faster growth and higher condition likely due to prey enrichment (Nakata et al. 2000, Sponaugle et al. 2009, Shulzitski et al. 2015), increasing larval fish survival (Logerwell & Smith 2001, Shulzitski et al. 2016). For the first time we will directly explore such patterns of individual larval traits across a wide gradient of prey and predator concentrations and fine-scale structure in the highly oceanographically dynamic Straits of Florida.

The Straits of Florida

The Straits of Florida (SOF) is a region well suited to the examination of the influence of prey and predator variability on larval fish success. The SOF is mostly

oligotrophic, but dynamic nearshore processes enhance productivity and contribute to a high abundance and diversity of larval fishes (Llopiz et al. 2010, Shulzitski et al. 2018). Flow through the SOF is dominated by the rapid Florida Current, which links the waters from the Gulf of Mexico and Caribbean to the Gulf Stream in the North Atlantic. The Florida Current is stronger along the western (continental) side of the SOF generating western boundary upwelling and enriching eddies (Olson 2001, Hitchcock et al. 2005). These physical processes result in regional gradients in nutrients, primary productivity, zooplankton, and larval fishes, with generally higher values in western compared to eastern (oceanic) waters (Lee *et al.*, 1991; Llopiz *et al.*, 2010). Furthermore, regional physical processes that elevate prey concentrations translate to higher gut fullness and growth in larval fishes on broad scales (Sponaugle et al. 2009, Llopiz et al. 2010, Shulzitski et al. 2015). This faster growth during the larval phase have been shown to enhance survival to settlement (Shulzitski et al. 2016) and to ‘carry over’ and lead to increased survival of juveniles on reefs (Grorud-Colvert & Sponaugle 2006). While our understanding of the effect of predator densities on larval fish growth is limited, strong selective mortality has been documented in coral reef larvae with selection against both slow-growing (Shulzitski et al. 2016) and fast-growing individuals (Sponaugle et al. 2011), hypothesized to be due to strong predation pressure in the western SOF. This accumulated wealth of knowledge on larval fishes in the SOF, as well as cross-strait gradient in prey and predator conditions, enables an examination of larval fish responses to variability in resources and mortality from predation.

Understanding how larvae respond across a range of conditions in the SOF is critical to predicting how these low-latitude marine fish populations will be influenced by climate change. In warm, oligotrophic oceans, projected increases in stratification with global warming will further reduce nutrient enrichment of surface waters, with enhanced oligotrophy and microbial loop processes (Behrenfeld et al. 2006). In the SOF, unprecedented warming is already occurring (1°C from 2010-2015; Domingues *et al.*, 2018), and future warming is predicted to decrease the strength of enriching physical processes (eddies, current-driven upwelling) in the region (Liu et al. 2015). Subtropical and tropical fish larvae have specialized diets and feeding strategies adapted for planktonic food webs in low-productivity systems (Llopiz & Cowen 2009, Llopiz & Hobday 2015). However, increased food intake is required to support basic functions (e.g., growth) at higher metabolic

rates associated with warmer temperatures (Houde 1989, McLeod et al. 2013). Given that subtropical fishes already exist near their thermal limits (Rummer et al. 2014) in low-productivity systems, building a greater understanding of how they respond to prey and predator conditions with present variability is key in predicting future population dynamics.

Objectives

My dissertation explores how prey and predator distributions influence feeding, growth, and success of larval fishes in the Straits of Florida and the implications for structuring larval assemblages. To examine these topics, I integrate two sampling methods (*in situ* imaging, biological samples) and various analysis techniques on individual larvae (diet and growth analysis, modeling) across a range of scales (fine-, meso-, regional, interannual). Chapter 2 examines the influence of fine-scale prey and predator abundance and patchiness on larval fish growth for two slower-growing coral reef fish species compared to a fast-growing tuna. In Chapter 3, I examine how interannual variability in prey, predators, and temperature conditions influence larval diet and growth of the fast-growing and abundant *Thunnus atlanticus* (blackfin tuna). Chapter 4 explores how variability in the planktonic food web influences larval fish assemblage structure through predator-prey relationships. The overarching goal of these studies is to further our understanding of larval ecology by connecting across scales, from traits of individual larvae and fine-scale distributions of their prey and predators to broader regional and interannual patterns of communities across a gradient of planktonic food web conditions. Knowledge of how variability in resource utilization and mortality influence larval fishes is critical to sustainable fisheries management and predicting the consequences of global climate change for marine fish populations.

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**FOOD WEB CONSTRAINTS ON LARVAL GROWTH IN SUBTROPICAL
CORAL REEF AND PELAGIC FISHES**

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CHAPTER 2: FOOD WEB CONSTRAINTS ON LARVAL GROWTH IN SUBTROPICAL CORAL REEF AND PELAGIC FISHES

Abstract

Prey availability and predation pressure are thought to be key constraints on larval growth, especially in low-productivity, subtropical environments. Yet, measuring their effects on larval fishes has been challenging, given the dynamic biophysical drivers of plankton distributions and small scales of interactions. We integrated fine-scale net tows (10's m) with *in situ* imaging to explore how predator-prey interactions influence larval fish growth in the Straits of Florida. Otolith-derived recent growth was analyzed for three ecologically important fishes: two coral reef labrids (*Thalassoma bifasciatum* and *Xyrichtys novacula*) and one tuna (*Katsuwonus pelamis*), with differing mean growth rates (labrids 0.25 mm d⁻¹, *K. pelamis* 0.44 mm d⁻¹) and prey (labrids-copepods; tuna-appendicularians). We used generalized additive models to examine the interactive effect of background density and frequency of elevated (>2SD above background) prey and predators on recent (last 3 d) larval growth. For all taxa, recent growth increased with prey background density. Recent growth of labrids was also higher when copepod densities were more often elevated (14% of transect >20 ind. m⁻³) above otherwise low background densities (2 ind. m⁻³). Predators (chaetognaths and hydromedusae) had a growth-selective effect: stronger selection in transects with high-density predator patches, although the direction of the effect was species-specific. The effect of temperature was taxa specific: growth increased with temperature for the labrids, and peaked at an optimum (28°C) for the rapidly growing tuna. Integration of these fine-scale sampling methods improves our understanding of the variable influence of prey and predators on larval growth, and consequently, larval survival.

2.1 Introduction

The pelagic larval phase of most marine fishes is characterized by high mortality rates that influence patterns of recruitment and subsequent adult population dynamics (Hjort 1914). Larval survival and growth during this phase (weeks to months) depends on the ability of larvae to find food and avoid predation (Houde 1987). Their success doing so often impacts cohort strength (Ringuette et al. 2002, Castonguay et al. 2008). Studies have suggested that patches of dense aggregations of prey, as opposed to average densities, are key to larval survival due to increased larva-prey encounter rates that optimize foraging in an often prey-limited pelagic environment (Lasker 1975, Houde 1987, Rothschild & Osborn 1988).

Prey and predator aggregations, from fine- (meters) to large-scales (kilometers), occur along biological gradients formed by physical processes such as fronts, eddies, stratification, and upwelling (Mackas et al. 1985, Owen 1989, Richardson et al. 2009, Greer et al. 2013). While decades of research points to the critical role of patchiness of planktonic prey to larval fishes (Mackenzie et al. 1990, Davis et al. 1991, Young et al. 2009), we lack empirical studies examining relationships between prey patchiness and larval fish growth and survival. Furthermore, understanding the direct effects of predator distributions on larval fishes has been difficult, if not impossible, given the small scale of the interactions and dynamic biophysical drivers of predator and prey distributions (Greer et al. 2013). Traditional net sampling has previously limited the scale over which these questions can be asked (but see Bils et al. 2017), as integrating prey over large spatial scales obscures relationships between prey availability, larval feeding success, and predation pressure (Pepin 2004, Young et al. 2009). However, advances in sampling technology now allow us to use *in situ* measurements (high-resolution imaging) to look beyond “average” scenarios to examine consequences of spatial variability in zoo- and ichthyoplankton aggregations to trophic interactions (Greer et al. 2013, 2016, Greer & Woodson 2016).

Larval fish growth is a valuable tool for understanding how variability in the prey (or predator) environment relates to success. Growth is recorded via the daily deposition of concentric increments in fish otoliths (ear stones) in proportion to their somatic growth, with wider increments indicating faster growth (Pannella 1971). High larval growth rates increase the probability of survival by reducing vulnerability to gape-limited predation and duration of

larval stage (Miller et al. 1988, Houde 1989, Hare & Cowen 1997), but can also influence juvenile survivorship by determining condition at metamorphosis/settlement (Searcy & Sponaugle 2001, Hamilton 2008). Larval growth has been consistently linked to feeding success across taxa and environments (Sponaugle et al. 2009, Dower et al. 2009, Pepin et al. 2014), but few studies have examined how larval growth is directly related to prey availability (Wexler et al. 2007, Satoh et al. 2013). Over larger scales, productive oceanographic physical features (e.g., fronts, mesoscale eddies) have been shown to enhance larval growth (Shulzitski et al. 2015), condition (Nakata et al. 2000), and survival to settlement (Shulzitski et al. 2016), likely due to increased prey availability. Additionally, studies on individual larvae have demonstrated that variability in feeding and growth rates due to stochastic feeding events play a key role in larval success within cohorts (Pepin 2004, Dower et al. 2009, Pepin et al. 2014, Robert et al. 2014), suggesting prey patchiness as an essential component of larval growth and survival. However, the examination of larval growth with regard to variation in natural prey patchiness has not been possible.

In addition to the importance of prey availability for larval fishes, predator densities have the potential to influence larval survivorship. Mortality is often selective, with predators removing smaller, slower growing individuals from the population (Anderson 1988, Bailey & Houde 1989, Hare & Cowen 1997, Takasuka et al. 2003), although the opposite direction of selective mortality has been also documented (Sponaugle et al. 2011, Takasuka et al. 2016). Non-random predation can obscure the effect of variable prey conditions on larval growth (Meekan & Fortier 1996, Robert et al. 2007), so quantifying this effect is important. While it is difficult to study the direct role of predation on larval fishes in nature, the selective influence of predators can be inferred through the examination of otolith-based growth trends in a larval population. For example, predator removal of small or slow growers increases the apparent average growth and size-at-age of a sampled population (survivors). High-density patches of predators have the potential to exert a strong selective pressure on a larval fish population, but fine-scale examination of larval growth trends, and corresponding predator and prey densities are required to tease apart the influence of predators and prey on larval growth.

We used coupled fine-scale *in situ* imaging with biological sampling to examine how local prey and predator densities and patchiness influence larval fish growth for two coral

reef fishes and one tuna in the Straits of Florida (SOF). The SOF is a region characterized by a high abundance and diversity of larval fishes imbedded within a fast-flowing major western boundary current. Regional physical processes (cyclonic mesoscale eddies and upwelling) that elevate prey concentrations translate to higher gut fullness and growth in larval fishes on broad scales (Sponaugle et al. 2009, Llopiz et al. 2010, Shulzitski et al. 2015). Assuming high density prey patches similarly influence larval traits on fine scales, we expected high prey availability in frequent patches (reduced prey search time) to enhance growth. While our understanding of the effect of predator densities on larval growth is limited, modeling studies suggest high predation pressure, such as high-density patches of predators, is needed to see evidence of size-selective losses (Paradis et al. 1999). Studies of selective mortality on coral reef larvae in the SOF have shown selection against both slow-growing (Shulzitski et al. 2016) and fast-growing larvae (Sponaugle et al. 2011). Therefore, it is difficult to predict the direction of selective loss, but we hypothesized that the strength of selective mortality (regardless of direction) will increase with high densities, and more frequent patches, of predators.

2.2 Methods

2.2.1 Study area

The SOF is bordered by the Florida Keys to the west and the Bahamas to the east (Figure 2.1). Flow through the SOF is dominated by the rapid Florida Current (average speed = 160 cm s^{-1} ; Lee et al. 1991), which links the Gulf of Mexico and Caribbean to the Gulf Stream in the North Atlantic. The Florida Current is stronger and more dynamic along the northwest/west (Florida Keys) side of the SOF and generates cyclonic mesoscale and sub-mesoscale eddies in addition to western boundary current upwelling (Hitchcock et al. 2005). These physical processes result in cross-strait variability in nutrients, primary productivity, zooplankton, and larval fishes, with generally higher values in western waters compared to the eastern SOF (Lee et al. 1991, Richardson et al. 2010, Shulzitski et al. 2018).

2.2.2 Field sampling

To examine otolith-derived growth in larval fishes and fine-scale distributions of their prey and predators, we collected biological samples together with *in situ* plankton imagery.

Sampling was conducted on two cruises in the SOF aboard the R/V *FG Walton Smith* from 28 May - 14 June, 2014 and 10 - 28 June, 2015. Each year, we sampled eight stations encompassing the north-south and cross-strait variability in the SOF (Figure 2.1). At each station we used the *In Situ* Ichthyoplankton Imaging System (*ISIIS*; Cowen & Guigand 2008) to measure zooplankton distributions. We sampled the water column at each station with two 8-16 km transects sampling at discrete depths of 15m and 30m (Figure 2.1). Towed at a speed of 2.5 m s^{-1} , the *ISIIS* imaged the water column at $\sim 140 \text{ L s}^{-1}$ with a pixel resolution of 55-68 μm , imaging particles from $\sim 200 \mu\text{m}$ to 13 cm. Sensors on *ISIIS* simultaneously measured conductivity, temperature, and depth.

Larval fishes were collected at each station using a Multiple Opening/Closing Net and Environmental Sensing System (MOCNESS) with a 4 m^2 opening and 1-mm mesh nets. The MOCNESS is equipped with sensors that simultaneously measured conductivity, temperature, and depth. To capture larval fishes and mesozooplankton on a fine horizontal spatial scale, we sequentially fired each MOCNESS net every $\sim 125 \text{ m}$. Traveling at a speed of 1 m s^{-1} each MOCNESS net sampled $\sim 500 \text{ m}^3$. We fired a total of five nets per tow; one net was open from the surface to depth (net zero; not included in analysis), and the four remaining nets sampled sequentially at the same depth, either 15 or 30 m. At every station, this fine-scale net sampling was repeated with two complete MOCNESS tows (depth determined in randomized order), yielding eight replicate nets per depth (Figure 2.1). Once onboard, the nets were rinsed with seawater and the contents of each cod end preserved in 95% ethanol. To reduce degradation of otoliths, ethanol was changed after 24-48 h, and again after 2-3 mo for high biomass samples. All larval fishes were separated out of the samples in the laboratory, and identified to the lowest possible taxonomic grouping following Richards (2005).

To ensure all *ISIIS* and MOCNESS transects sampled the same water mass, transects and tows at each depth were centered on a GPS Lagrangian drifter at 10 m depth, moving with the Florida Current (Figure 2.1). Each replicate MOCNESS tow (four nets) per depth at each station corresponded with one half of the *ISIIS* transects (half-transects = 4-8 km). All sampling occurred during daylight hours, approx. 0600 – 1800 to minimize diel effects, and because larval fish typically feed during daylight hours in the SOF (Llopiz & Cowen 2009,

Llopiz et al. 2010).

2.2.3 Otolith analysis

We used otolith microstructure analysis to obtain data on larval age and daily growth (increment widths) for individual larvae. Based on sample size, confirmation of daily increment deposition (Victor 1982, Radtke 1983, Hare & Cowen 1991, Tanabe et al. 2003) and our ability to morphologically identify larvae to species, two coral reef wrasses and one tuna were selected for otolith analyses: *Thalassoma bifasciatum* (bluehead wrasse), *Xyrichtys novacula* (pearly razorfish) and *Katsuwonus pelamis* (skipjack tuna). All larvae collected of *T. bifasciatum* (n = 339), *X. novacula* (n = 479), and *K. pelamis* (n = 295) were measured for standard length (SL) using a Leica dissecting microscope with camera and image analysis software (Image-Pro Plus 7.0 and Premier 9.3). We analyzed the otolith microstructure on a subset of larvae (n = 6-19) from a subset of replicate tows at different stations/depths (n = 14 - 19; depending on availability of each species). The size distribution of the subset of larvae used for otolith analysis (*T. bifasciatum*: n = 147, *X. novacula*: n = 156, *K. pelamis*: n = 134) was proportional to all larvae of that species in each tow (Figure 2.2).

Sagittal otoliths were extracted and stored in immersion oil on a glass slide to facilitate reading (Sponaugle 2009). Prepared otoliths were read along the longest axis at 1000x (oil immersion) magnification using a Leica compound microscope with a camera attachment and Image-Pro Premier 9.3. Otoliths were read 2-3 times by the same reader, and if reads differed by $\leq 5\%$, one read was randomly chosen for analysis. Otoliths where three reads all differed by $>5\%$ were removed from further analysis (Sponaugle 2009).

2.2.4 ISIIS image analysis

Zooplankton taxa were sorted into image classes based on taxonomy and morphology with an automated algorithm. ISIIS raw image files were flat-fielded and segmented with methods described in Luo et al. (2018). Segmented images were classified using a Sparse Convolutional Neural Network (Graham 2014), following the methods developed in Luo et al. (2018). The algorithm was implemented with training sets (different for each sampling year) comprised of 124 classes representing 40 broader groups (e.g., classes of different shapes or orientations of chaetognaths combined into a single “Chaetognath” group; Schmid

et al. *in review*). Automated image classifications were corrected for mis-classifications with scaling factors determined by confusion matrices. The confusion matrices were created separately for each year from a random subset of images (0.005% of all ~ 100 million classified images) that were manually classified (Luo et al. 2018, Schmid et al. *in review*).

Physical data and biological counts from image analyses were synchronized using the sample time stamp and quantified by 1-m horizontal distance bins. Corrected counts (see above) of organisms in each classification group were used to estimate plankton densities (ind. m⁻³) based on the volume of water sampled by *ISIIS* in each 1-m horizontal bin.

2.2.5 Fine-scale prey/predator availability

Environmental prey/predator availability and fine-scale distributions from *ISIIS* imagery were summarized with two variables for comparison with recent larval growth: *background density (BD)* and *frequency elevated (FE)*. *BD* was calculated as the mean of the 1-m horizontal bin densities (ind. m⁻³) in each *ISIIS* half-transect. *FE* was calculated as the percentage of 1-m horizontal bins in an *ISIIS* half-transect where the density was >2 standard deviations (SD) above the *BD*. Prey groups from *ISIIS* considered in this study were determined from previous gut content analyses in the SOF: “appendicularians” for *K. pelamis* (Llopiz et al. 2010) and “copepod other” (a morphological classification including copepods without visible antennae) for *T. bifasciatum* and *X. novacula*. The wrasses consume a mixed diet of harpacticoid and cyclopoid (e.g., *Oncaea* sp., *Farranula* sp., but not *Oithona* sp.) copepods (Llopiz & Cowen 2009, Sponaugle et al. 2009), but because *ISIIS* imagery cannot distinguish between some taxa with similar morphologies, these groups were combined in the “copepod other” group. Predator groups from *ISIIS* included “chaetognaths” and “hydromedusae”, the most abundant potential predators of larval fishes in the SOF (Bailey & Houde 1989, Purcell & Arai 2001 and references therein; unpubl. data). The two predator groups were combined for *BD* and *FE* calculations since separately, chaetognath and hydromedusae densities were strongly correlated ($r = 0.88$).

2.2.6 Recent growth analysis

We compared variability in larval growth with prey/predator availability by computing ‘recent growth’ (as a detrended growth index) for all species from average of the

last three complete otolith increment widths. As it is unknown how long the larvae had been associated with the sampled prey/predator conditions (days to weeks), we used recent growth as a proxy for the last three full days of growth prior to capture (Sponaugle et al. 2010, Shulzitski et al. 2015). This is also the amount of time for feeding to influence nutritional condition (Clemmesen 1994).

Since increment width and variability increases with age, we detrended the last three increment widths by age to allow for the comparison of recent growth of different aged larvae (Baumann et al. 2003). A detrended growth index was computed using:

$$DG_{ij} = (G_{ij} - G_j) SD_j^{-1}$$

where DG_{ij} is the detrended growth of individual i at age j , G_{ij} is otolith growth (increment width) for individual i at age j , G_j is the mean of otolith growth of all individuals at age j , and SD is the standard deviation of G (Sponaugle et al. 2010). For each species, we compared detrended recent growth across prey densities, predator densities, temperatures, depths, and years using separate analysis of covariance (ANCOVA) with age as a covariate, to confirm there was not a significant interaction between age and each variable.

2.2.7 Modeling approach

We examined the effect of local prey and predator availability on recent growth for each larval fish species using generalized additive models (GAMs) with a Gaussian distribution. These non-parametric regression techniques allow for non-linear relationships between dependent and independent covariates (Wood 2006). GAMs are modeled using smoothing functions with additive techniques where all covariates are independent, allowing for easy inference, as the effect of each covariate is the same regardless of the values of the remaining covariates. The model for each species included detrended recent growth from 147 (*T. bifasciatum*), 156 (*X. novacula*), or 134 (*K. pelamis*) larvae and their associated prey/predator *BD* and *FE* from *ISIIS* half-transects corresponding to each MOCNESS tow ($n = 18, 19, 14$, respectively). Temperature, depth, and otolith-derived early growth (for wrasses) were included as covariates. Since larval fishes can have serial correlation in daily otolith-derived growth (Dower et al. 2009, Pepin et al. 2014, Robert et al. 2014), an early growth variable (average increment width from days 5-10) was included in the model. Early growth was not included for *K. pelamis* since their ages ranged from only 4 to 11 d (mean =

7.1 d), thus mean recent growth (last three full days of life) of the younger larvae included the earliest days of growth. Temperature was from MOCNESS environmental data, averaged across each tow. While larval density can influence growth due to competition for resources, density dependence was not appropriate to consider in the models since larval fishes in the SOF are rare compared to their planktonic prey and predators. In fact, the copepod and appendicularian prey are, on average, ~500 and ~9000 times more abundant than their respective larval fish predators (wrasses, tuna).

We examined the additive and interactive effects of prey or predator *BD* and *FE* on recent larval fish growth with two model formulations for each species: a GAM and an interactive GAM (Table 2.1). Fixed covariates were *prey BD* (continuous), *prey FE* (continuous), *predator BD* (continuous), *predator FE* (continuous), *temperature* (continuous), *early growth* (continuous), and *depth* (categorical with two levels). The interaction terms in the interactive GAM were *prey BD* $\times$ *prey FE* and *predator BD* $\times$ *predator FE*. Smoothing functions were applied to continuous variables and tensor product smoothers were included for interactions as they are more appropriate for interactions fitted to covariates with different units. To avoid model overfitting, the number of knots used in the smoothers and tensor product smoothers were restricted to 4 and 8, respectively. Density variables were log transformed since prey and predator densities each range over an order of magnitude. Prior to the GAM analyses, we used variance inflation factor (VIF) analysis to detect collinear variables and removed those variables above a VIF cut-off of 3. For *K. pelamis*, there was collinearity between prey and predator *BD*, and predator *BD* and *FE*. Therefore, we formulated separate prey and predator models for *K. pelamis* and were unable to include an interactive GAM for predators (Table 2.1).

Model selection was performed using a backward stepwise approach. Full and reduced versions of the models were compared using Akaike Information Criterion (AIC) as a measure of goodness of fit, and the Generalized Cross Validation (GCV) as a measure of the model's predictive performance. The best model was identified by minimizing both AIC and GCV. We incorporated the dependency of growth on larvae collected from the same MOCNESS tow by including a random intercept in the fixed model, but AIC determined models without a random effect were best. Model diagnostics and residuals were checked for potential deviations from normality assumption, homogeneity of variance, and other

anomalies. All calculations and models were coded in R software (Version 3.6.0; R Core Team 2019) using the *mgcv* library.

2.3. Results

2.3.1 Larval fish characteristics

Larval densities of *T. bifasciatum*, *X. novacula*, and *K. pelamis* from all tows were 2.94 ± 6.92 , 3.89 ± 11.21 , and 2.37 ± 3.89 ind. 1000 m^{-3} , respectively (mean $\pm$ SD, $n = 64$). Mean densities from the subset of replicate tows included in otolith analyses for each species were 8.41 ± 8.58 ($n = 18$), 10.05 ± 16.71 ($n = 19$), 7.39 ± 3.21 ($n = 14$). All three species had a roughly similar size range (Figure 2.2). However, because *K. pelamis* is a rapidly growing species with somatic growth rates of 0.44 mm d^{-1} (linear regression), compared to the wrasses (*T. bifasciatum*: 0.21 mm d^{-1} , *X. novacula*: 0.27 mm d^{-1}), tuna larvae were substantially younger (4-11 d; mean = 7.1 ± 1.4 d) than either wrasse (15-45 d; *T. bifasciatum*: mean = 26.0 ± 6.1 d, *X. novacula*: 25.8 ± 4.1 d). Mean size of *X. novacula* ($6.74 \pm 1.32 \text{ mm SL}$) tended to be larger than *T. bifasciatum* ($4.96 \pm 1.36 \text{ mm}$) and *K. pelamis* ($4.79 \pm 0.76 \text{ mm}$).

2.3.2 Fine-scale prey/predator availability

The appendicularian prey of *K. pelamis* were more abundant and pervasive compared to the copepod (cyclopoid and harpacticoid) prey of the wrasses (*T. bifasciatum*, *X. novacula*). Appendicularian background densities (*BD*) ranged from 30-111 ind. m^{-3} , 5-10 times greater than the copepod *BD* ranging from 2-20 ind. m^{-3} (Table 2.2). The copepods had more variability in their fine-scale distribution with frequent high-density patches of prey in some regions, where up to 14% of the transect had elevated densities (frequency elevated, *FE*; Table 2.2). When copepod prey were elevated, their densities were 3-27 times greater than *BD*. In contrast, the appendicularians had lower and less variable *FE* with only 2-5% of the transect having elevated densities (Table 2.2). When elevated, densities were only 2-5 times greater than *BD*. The *BD* of the predators (chaetognaths and hydromedusae, combined) ranged from 6-73 ind. m^{-3} (Table 2.2). Predators were pervasive and less variable in distribution, similar to appendicularians, with elevated densities in only 3-6% of the transect. When elevated, densities were 2-19 times greater than *BD*.

2.3.3 Modeled relative recent growth

Both the GAMs and interactive GAMs revealed clear influences of prey, predators, and temperature on larval fish recent growth. For all species, both types of models performed similarly, but we focus primarily on the interactive GAMs (Figs. 3, 4) since they provide additional insights on the multiplicative effect of *BD* and *FE* of prey and predators. However, we had to focus on GAM results for *K. pelamis* (predator model) since an interactive GAM was unable to be performed due to collinearity between predator *BD* and *FE* (Figure 2.4c, d). GAM results are provided for other species in Supplementary materials to illustrate the more simple, univariate responses (Supplementary Figure A1-3).

Recent growth of *T. bifasciatum* significantly increased across gradients of both prey (copepods) *BD* and *FE* (Table 2.3, Figure 2.3a). The effect of predators on recent growth was significant and bimodal, with faster growth at high (>25 ind. m^{-3}), as well as at low (<12 ind. m^{-3}) *BD*, but only when predators were more frequently elevated ($>4\%$; Table 2.3, Figure 2.3b). Recent growth was lowest at mid-range predator *BD* (12-25 ind. m^{-3}), regardless of the *FE*. There was a significant increasing relationship between recent growth and temperature (Table 2.3, Figure 2.3c).

X. novacula had similar trends as *T. bifasciatum* in recent growth with prey (copepods) and temperature, but the relationship was non-significant for both ($p < 0.1$; Table 2.3, Figure 2.3d, f). Predators significantly affected recent growth of *X. novacula*, with the lowest growth occurring when predators had both high *BD* (>25 ind. m^{-3}) and *FE* ($>4\%$; Table 2.3, Figure 2.3e). Otherwise, recent growth was fairly consistent across the gradients of predator *BD* and *FE*.

For *K. pelamis*, recent growth increased significantly with prey (appendicularian) *BD* (Table 2.3, Figure 2.4a). Recent growth increased slightly with prey *FE* at the highest range of the gradient (5%), but *BD* had the strongest effect on recent growth. Recent growth was strongly affected by temperature, increasing to a peak at 28°C before decreasing at higher temperatures (Table 2.3, Figure 2.4b). The univariate predator model indicated that recent growth increased significantly with predator *BD*, and peaked at mid-temperatures, similar to the other *K. pelamis* models (Table 2.3, Figure 2.4c, d).

2.4. Discussion

2.4.1 Prey availability and larval growth

The wrasses, *T. bifasciatum* and *X. novacula*, occupy a substantially different ecological niche than skipjack tuna, *K. pelamis*. The wrasses are slower-growing (~ 0.25 mm d⁻¹) larvae that prey on cyclopoid and harpacticoid copepods (Sponaugle et al. 2009) and range from moderately abundant to rare and patchy. In contrast, skipjack tuna larvae are fast-growing (0.44 mm d⁻¹) and prey on highly abundant, ubiquitous appendicularians (Llopiz et al. 2010). This variability in prey selection and larval growth sets the stage for a comparison in the relationship between recent growth and prey availability.

For all three species, recent larval growth increased with prey background density (*BD*), with the fastest growth occurring on transects with the highest average prey densities. But average densities do not fully explain the effect prey has on larval fish growth. High-density patches of prey on otherwise low prey density transects can also support faster larval growth. For larvae of both wrasse species, recent growth increased with the frequency of elevated patches of prey (frequency elevated; *FE*). Both wrasses had high recent growth at high prey *BD* (20 ind. m⁻³), but also at low *BD* (2 ind. m⁻³) when prey was more frequently elevated (higher *FE*). In fact, at low *BD*, prey were elevated to 21 - 82 ind. m⁻³ in 13% of the transect, indicating that dense patches of prey can be as beneficial for growth as consistently high prey. Yet, larvae collected from regions of low prey *BD*, without high *FE*, did not experience the same growth advantage. In comparison to the wrasses, *K. pelamis* growth increased primarily with prey *BD* and less so with prey *FE*. This pattern reflects the natural distributions of their prey in the SOF: appendicularians are consistently highly abundant, with elevated prey densities present in only 2-5% of the transect.

Patchiness of plankton has been well documented (Mackas et al. 1985, Davis et al. 1991), and frequently hypothesized to be important for larval fish growth and survival especially in regions with low prey concentrations (Houde & Schekter 1978, Pepin et al. 2014). However, logistical sampling challenges have made testing these hypotheses in the wild near impossible. Here, the coupling of fine-scale plankton sampling with fine-scale otolith growth analysis has enabled us to examine larval fish growth in the context of the fine-scale distributions of their prey. By quantifying the prey *FE* in 1-m horizontal bins across a transect we estimated the probability of a larval fish encountering high densities of

prey on the scale of a larval fish. Additionally, the application of a multiplicative modeling approach revealed how these high-density patches of prey can further benefit larval growth beyond relationships with average concentrations of prey.

The contrast in the relative importance of patchy prey to recent growth for the wrasses versus the tuna is consistent with experimental evidence suggesting that not all larvae may benefit from patchy prey (Houde & Schekter 1978, 1981). Additionally, recent studies examining relationships between larval feeding success and growth also suggest a difference in prey utilization between fast and slow-growing larval fishes (Dower et al. 2009, Pepin et al. 2014, Robert et al. 2014). Fast-growers (i.e. scombrids) had a strong correlation between larval growth and gut contents, as well as a higher degree of autocorrelation in daily growth, suggesting consistently high feeding rates and highly important early feeding success (Pepin et al. 2014). In comparison, slow-growers (including *T. bifasciatum*) had weaker correlations between larval growth and gut contents, indicative of feeding on more variable or patchy prey, and potential resilience to episodes of poor feeding success (Pepin et al. 2014). In our study, variation in larval growth with prey patchiness further reinforces the existence of diverse larval strategies that include different suites of larval traits and foraging on distinctly different prey. The slow-growing wrasses and fast-growing skipjack tuna reflect two contrasting evolutionary adaptations to exploit resources in an oligotrophic planktonic food web (Llopiz 2013).

Slow-growing wrasses with patchy prey

T. bifasciatum and *X. novacula* in the SOF exhibit highly selective feeding for cyclopoid and harpacticoid copepods (Llopiz & Cowen 2009, Sponaugle et al. 2009), yet calanoids (2-8 times more abundant; unpubl. data) are the dominant copepods in the plankton. While such specialization may reduce competition for resources, it likely increases energy expended as larvae search for prey and is thus counter to optimal foraging theories (Pyke et al. 1977). Yet, diet analyses of *T. bifasciatum* and *X. novacula* larvae in the SOF indicate survivors are successfully feeding, with almost all collected larvae having full guts (Llopiz & Cowen 2009, Sponaugle et al. 2009). Interestingly, our results suggest that larvae can successfully exploit high-density patches of prey, when present, to enhance growth. For species with relatively slow larval growth, periods of elevated growth may be sufficient to

allow survival in an otherwise food-limited environment. This may be a strategy that these subtropical larvae have evolved to survive in this oligotrophic region. *T. bifasciatum* has a highly variable pelagic larval phase, with individuals within and among cohorts varying in growth, pelagic larval duration (PLD), and size-at-settlement (Searcy & Sponaugle 2000, 2001). With similar prey, growth rates, and relationships to prey availability as *T. bifasciatum*, *X. novacula* larvae have a similarly plastic early life history strategy (Hare & Cowen 1991). Previous studies have hypothesized that the slow growth rate, low daily rations, and plasticity in larval traits for *T. bifasciatum* larvae enable them to survive in a highly variable pelagic environment with patchy prey (Sponaugle & Pinkard 2004). The increase in larval growth these species exhibit across a strong gradient of cyclopoid and harpacticoid copepod *BD* and *FE* is consistent with this hypothesis.

Larval growth has previously been shown to vary with prey abundance for coral reef fishes in the SOF, but only over broad regional scales or across mesoscale physical features. Sponaugle et al. (2009) found *T. bifasciatum* to have faster growth, larger size-at-age, and fuller guts in the more productive western SOF where prey abundances are generally higher compared to the eastern regions. Further, *T. bifasciatum* and *X. novacula* associated with productive mesoscale eddies had faster growth and larger sizes-at-age compared to larvae outside of the eddies, likely due to higher prey availability (Shulzitski et al. 2015, 2016). Our results echo these patterns, but are the first to demonstrate a direct relationship between larval growth and prey availability across a gradient of prey densities, and importantly, prey patchiness. Previous studies have shown that faster larval growth not only enhances larval survival (Shulzitski et al. 2016) but also can “carry-over” to increase the survival of juveniles (Sponaugle et al. 2006). Faster-growing *T. bifasciatum* undergo metamorphosis at younger ages (Grorud-Colvert & Sponaugle 2011) and smaller sizes, but in a higher condition (Searcy & Sponaugle 2000), and these smaller, higher condition juveniles can swim faster to evade predators (Grorud-Colvert & Sponaugle 2006). Such growth-related traits are key to survival of early stages and our findings point to the importance of examining larval fish traits over gradients of not only prey density, but also prey patchiness, especially in larvae with slower growth and more variable larval traits.

Fast-growing tuna with ubiquitous prey

K. pelamis in the SOF feed almost exclusively on appendicularians prior to a rapid (at ~7 mm, SL) switch to piscivory (Llopiz et al. 2010). Studies of other fast-growing fish larvae have shown that such rapid growth is not resilient to periods of poor feeding success so reliance on a consistently abundant prey is critical (Pepin et al. 2014, Robert et al. 2014). Based on growth rates measured in our study, *K. pelamis* larvae in the SOF only have 7-10 d to develop the predation capabilities (e.g., digestive system, eyes, swimming abilities) to achieve piscivory. Therefore, there is a premium on their ability to efficiently find, attack, and capture prey, without expending much additional energy (optimal foraging theory; Pyke et al. 1977). High densities of appendicularians in the SOF substantially reduce predator search time. Appendicularian feeding by larval tunas is suggested as a nutritional “loophole” for larvae to gain sufficient resources in an oligotrophic region by exploiting energy from the microbial loop (Bakun & Broad 2003, Llopiz et al. 2010). Our results demonstrate that appendicularians are ubiquitous in the SOF, occurring in consistently high densities, likely making them a reliable prey fueling the rapid growth and development of tuna larvae.

Comparison of these data on the natural variation in growth of *K. pelamis* in relation to environmental prey densities to other studies of larval tuna growth reinforces the concept that the fast growth of *K. pelamis* is due to their efficient feeding on appendicularians. Locally in the SOF, larval tuna success has been related to appendicularian densities: both co-occur in the upper 50 m, and gut evacuation experiments with *Auxis* sp. across seasons and years revealed that the highest feeding rates were associated with the highest environmental abundance of appendicularians (Llopiz et al. 2010). Elsewhere, fast growth in yellowfin tuna larvae was associated with the highest zooplankton volumes in the Panama Bight (Wexler et al. 2007) and bullet tuna larvae grew faster in the Mediterranean Sea where prey were more abundant, compared to the Atlantic Ocean (Laíz-Carrión et al. 2010).

Fast larval growth in high prey conditions can translate to higher survival during the larval and even juvenile phases, which can have important consequences for recruitment. For Pacific bluefin tuna larvae, faster growth leads to higher survival: survivors were larger-at-age and grew faster than the initial population in studies that either tracked cohorts (Satoh et al. 2013) or compared old and young larvae (Tanaka et al. 2006). Satoh et al. (2013) additionally showed that faster growth of survivors was significantly related to prey densities

and sea surface temperature. Lack of sufficient prey can lead to starvation and reduced survival in these fast growing species (see for example, Tanaka et al. 2008), although slow-growth in Atlantic bluefin tuna can be advantageous in low prey conditions (Blanco et al. 2018). But larval tunas in the SOF, including *K. pelamis*, have some of the highest feeding incidences worldwide for tunas, with 99% of collected larvae having prey in their gut (Llopiz et al. 2010, Llopiz 2013). Prey depletion by larvae is also unlikely, since even at lower densities appendicularians in the SOF were 4000-22000 times more abundant than *K. pelamis*, and appendicularian generation times in warm water are very rapid (1-2 days; Hopcroft & Roff 1995), so their populations can withstand strong predation pressure (Llopiz et al. 2010). Therefore, the slower-growing *K. pelamis* larvae in lower density prey conditions may not experience significantly reduced feeding, but this slow growth could result in reduced survival as larvae switch to piscivory and eventually metamorphose into juveniles. The switch to piscivory in tunas is a critical period in their larval phase; faster larval growth enables an earlier switch to piscivory and delays in the shift due to slow growth can reduce growth rates even further (Reglero et al. 2014).

2.4.2 Predation pressure and larval growth

The partial effect of predators on growth was important for all three species, and recent growth varied with both predator *BD* and *FE*. The strength and direction of the predation effect was species-specific with evidence of selective loss of both fast- and slow-growing larvae. Variability in the direction of the effect of predation on growth is not unexpected. The conventional Growth-Survival Paradigm (GSP; Houde 1987, Anderson 1988, Cushing 1990) posits that faster-growing larvae have a higher probability of survival through larger size and reduced vulnerability to gape-limited predators (Miller et al. 1988), shorter time spent vulnerable to predation (Houde 1989), and higher growth and condition, thus enhanced predator detection abilities (Takasuka et al. 2003, 2007). But there is accumulating evidence contrary to this paradigm (Takasuka et al. 2016), and broad recognition that selective mortality patterns can vary widely and be dependent on fish species, habitat, and size and type of predators.

For *T. bifasciatum*, there was an increase in the strength of selective mortality (as measured by growth patterns) with an increase in predator density: the fastest larval growth

occurred at the highest *BD* of predators (>25 ind. m^{-3}). This suggests selective loss of the slow-growing larvae due to strong predation pressure, evident from apparent faster growth among the survivors (Meekan & Fortier 1996). High-density patches of predators, at otherwise low *BD*, also have a growth-selective effect on larval *T. bifasciatum*, with growth increasing with the *FE* of predators. This further suggests selection against slow-growers in locations (patches) where predation pressure may be elevated 2-44 times higher than *BD*. While this is in agreement with the GSP, it contrasts prior findings in the SOF. Previous studies comparing young *T. bifasciatum* larvae in the SOF to older survivors has suggested that larvae experience selection against fast-growers (Sponaugle et al. 2011, Shulzitski et al. 2016). But these studies did not distinguish individual effects of prey and predators, and either averaged multiple cohorts over broad time scales (Sponaugle et al. 2011) or sampled when water temperatures were 2°C warmer than our study, when metabolic demands may make fast growth a liability (Shulzitski et al. 2016).

Growth of *K. pelamis* also increased with the *BD* of predators, suggesting a greater proportion of slower-growing larvae were culled from the population in locations with high (>30 ind. m^{-3}) compared to low (<10 ind. m^{-3}) predator densities. In another scombrid, the Atlantic mackerel, strong selection predation against slow growers in some years was evident by fast larval growth of surviving larvae, and this had significant implications for annual recruitment (Robert et al. 2007). We note that prey (appendicularian) and predator *BD* for *K. pelamis* were collinear and we were only able to model the partial effect of predators (and temperature) on recent growth, therefore it is possible that the fast larval growth of *K. pelamis* is due to co-occurring high densities of predators and prey.

Most of the stations used to examine *X. novacula* growth had high predator *BD* (24-72 ind. m^{-3}) and among these locations, the predator *FE* had a stronger effect on recent larval growth than *BD*. Slower larval growth was associated with more frequent high-density (77-330 ind. m^{-3}) patches of predators (higher *FE*). This pattern suggests that predators selectively preyed upon fast growers, resulting in the preponderance of slower growers among the survivors we sampled, in contrast to the GSP and predation effect on *T. bifasciatum* and *K. pelamis*. Higher predation on faster-growing, larger larvae is thought to be due to heightened foraging activity and, consequently, higher encounter rates with predators, compared to smaller, less active larvae (Litvak & Leggett 1992, Paradis et al.

1999). Within the wrasses, *X. novacula* was larger-at-age and had a higher mean somatic growth rate (0.26 mm d^{-1}) compared to *T. bifasciatum* (0.21 mm d^{-1}). The larger size ($\sim 7 \text{ mm SL}$) and potentially greater swimming activity may make larger *X. novacula* more vulnerable to predation mortality than *T. bifasciatum* ($\sim 5 \text{ mm SL}$). *X. novacula* was also substantially larger than *K. pelamis* ($\sim 5 \text{ mm SL}$), which may further account for these contrasting vulnerability patterns.

Quantifying larval mortality from predation is challenging and our study is among the first to directly relate larval fish growth to environmental predator densities and spatial distributions in any marine environment. Locally in the SOF, predation pressure on larval fishes has been predicted to be regionally strong in the more productive western SOF (Sponaugle et al. 2009, Llopiz 2013), but quantification of the distribution and abundance of predator populations has been limited by sampling technology. *In situ* imaging now enables enumeration of gelatinous zooplankton, especially those of smaller sizes (mm to cm) that can be important predators on larval fishes (Bailey & Houde 1989), but have previously been too small and fragile to properly be estimated with conventional net sampling (Luo et al. 2014). Additionally, the modeling approach we used enables the contrasting effects of prey, predators, and temperature on larval growth to be disentangled by examination of the partial effects of each component. However, a full examination of the direct impacts of predation on larval fish growth is difficult in a dynamic pelagic ecosystem due to the wide array of predator sizes, types, and other prey choices (Bailey & Houde 1989). For example, growth-selection is dependent on the size ratio of prey to predators ($\sim 10\%$; Paradis et al. 1999). While the predators considered in our study (chaetognaths and hydromedusae) vary in size, we assumed that the relative proportions of predator sizes are consistent across sampling locations. Additionally, we recognize that chaetognaths and hydromedusae also feed on common zooplankton in the SOF (e.g., copepods, crustacean larvae, smaller hydromedusae; Baier & Purcell 1997, Regula et al. 2009), but with the densities of predators exceeding larval fishes by 100-26,000 times, a strong growth-selective effect by predators was present.

2.4.3 Temperature and larval growth

For all three species, temperature had a significant effect on recent larval growth. For both wrasses, growth was positively related to temperature, similar to many larval fishes

(Houde 1989). This is consistent with prior studies that demonstrated a strong effect of temperature on larval growth for coral reef fishes, despite the relatively small seasonal variation in temperature in these regions (McCormick & Moloney 1995, Sponaugle et al. 2006, D'Alessandro et al. 2013). High plasticity in growth-related traits in these species suggests they may be resilient to variable environmental conditions. Hindcasted larval growth from 13 cohorts of juveniles indicated that larval growth in *T. bifasciatum* varies directly with temperature, with faster growing larvae in warmer water spending up to 15 fewer days in the plankton before settling to the reef (Sponaugle et al. 2006). Larval encounter with different water temperatures can also “carry-over” to influence the composition of settling juveniles: in addition to being younger at settlement, *T. bifasciatum* settling in warmer temperatures were smaller and of higher condition at settlement, and grew faster as juveniles, compared to fish settling during cooler water temperatures (Grorud-Colvert & Sponaugle 2011).

In contrast, the skipjack tuna, *K. pelamis*, had a dome-shaped relationship with growth peaking at an optimal temperature, suggesting the existence of constraints at higher temperatures. Such temperature-related growth curves are common in poikilothermic (cold-blooded) organisms as there is typically an optimal thermal range that controls physiological processes (Fry 1971, Jobling 1981, Takasuka et al. 2007). Further, there may also be a food-related constraint on growth at the highest temperatures. Although their appendicularian prey are plentiful in the SOF, and prior gut content analyses have revealed high gut fullness (Llopiz et al. 2010), *K. pelamis* rapidly transition to piscivory at ~7 mm (Llopiz et al. 2010) and may experience elevated energetic demands to successfully make this transition. Fast development of *K. pelamis* larvae in this study (3.4-6.6 mm) is required to prepare for piscivory (e.g., digestive tract, eyes, mouth). Larvae in the warmest temperatures may not be able to sustain these increased metabolic demands with a planktivorous diet, and if not developmentally ready to switch to piscivory, would likely experience reduced growth (and survival). This switch to piscivory is a critical period for larval Atlantic bluefin tuna in the Mediterranean Sea, and in warmer temperatures, a faster shift in diet is accompanied with higher mortality rates (Reglero et al. 2011). An earlier transition to piscivory is generally beneficial for growth and survival and delays in this switch can result in reduced growth (Reglero et al. 2014). Compared to bluefin tuna, *K. pelamis* has a faster growth rate (Muhling

et al. 2017) and more trophic specialization (Llopiz & Hobday 2015), therefore a rapid reduction in larval growth at the highest temperatures is not surprising.

Optimal temperatures for larval tuna growth has been shown for yellowfin tuna in both the laboratory (26-31 °C; Wexler et al. 2011) and natural conditions in the Gulf of Mexico (29°C; Lang et al. 1994). *K. pelamis* larvae analyzed in our study were collected in waters ranging from 26.5-29 °C, with growth peaking at an optimum of 28 °C. Skipjack tunas generally spawn in 26-30 °C water, and larvae have been observed in 24-31 °C (Muhling et al. 2017, and references therein). The SOF is at the warmer end of this range (Llopiz & Hobday 2015) with temperatures up to 31°C in the warmest months (Shulzitski et al. 2016). Mortality of larval tunas can rapidly increase above optimal temperatures (Kimura et al. 2010), and larvae in marginal temperature conditions may become more vulnerable to predation due to decreases in swimming, escape, and foraging ability (Blaxter 1991). If *K. pelamis* larvae experience reduced growth above ~28°C, it appears that the warmest conditions they currently experience in the SOF are at their edge of their thermal limits.

Future warming is predicted to increase sea surface temperatures in the SOF by 3-4°C over the next century (Alexander et al. 2018). This will impact subtropical marine environments through enhanced thermal stratification; reducing productivity in an already oligotrophic environment (Brown et al. 2010). While the appendicularian prey of tunas are specialized to feed in this environment and benefit from these conditions (Landry et al. 2018), warming ocean temperatures are expected to increase mortality in subtropical larval fishes (Llopiz et al. 2014). Based on the optimal temperature for *K. pelamis* growth, we hypothesize that predicted warming will be detrimental to their larval growth and development needed for a shift to piscivory. These growth and survival implications should be included in future population models of this commercially important species (Lehodey et al. 2013). While the wrasses appear to be more resilient to temperature variability than the thermally-constrained tunas, *T. bifasciatum* larvae previously collected in the SOF during higher temperatures (29-31°C) experienced selective loss of fast growers (compared to no evidence of selective mortality in lower temperatures (26-28°C); Shulzitski et al. 2016). This difference was hypothesized to be due to prey conditions that could not support the high metabolic demands of fast-growing larvae in the hot conditions; lower selective loss was evident for larvae collected simultaneously from prey-rich recirculating eddies. While future

changes for the copepod prey of the wrasses is unclear (Landry et al. 2018), decreased abundance or availability of high-density patches of prey could significantly constrain their larval growth. If this is compounded with warmer temperatures that increase growth rates, prey availability for the wrasses may not be enough to meet energetic demands.

Conclusions

The integration of fine-scale in situ imaging and biological samples of larval fishes demonstrated that fine-scale variability in prey and predator concentrations have important implications for larval growth. For slow-growing species such as wrasses, prey patchiness can be as important as average prey density in determining larval growth. While larvae of both wrasse species are well-adapted to feed on a rare and patchy copepod prey, their growth is constrained at low average prey densities if high-density prey patches do not occur sufficiently frequently. In contrast, fast-growing species such as skipjack tuna rely on consistently abundant prey such as appendicularians, and are less dependent on prey patchiness. The distribution of predators also influences the composition of larval fish survivors, with the contrasting patterns of growth-selective predation likely related to larval fish size: selection against fast growers for the larger *X. novacula*, and selection against slow growers for the smaller *T. bifasciatum* and *K. pelamis*. Interestingly, the strength of growth-selective predation on the wrasses increased with the frequency of high-density patches of predators. Higher temperatures promoted growth for all larvae, but an optimal growth temperature for *K. pelamis* suggests that there may be metabolic constraints at high temperatures. Early onset of piscivory in this species places a premium on fast growth and development that may be hard to sustain at the highest temperatures. The balance between water temperatures and food availability is likely to play an increasingly important role in determining the survival of larval fishes under future climate change scenarios.

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Table 2.1. Generalized additive models (GAM) used to examine the influence of prey and predator distributions on recent larval growth patterns of *Thalassoma bifasciatum*, *Xyrichtys novacula*, and *Katsuwonus pelamis* in the Straits of Florida. Due to collinearity *K. pelamis* has separate prey and predator (background density only) GAMs; a predator interactive GAM could not be performed.

GAM formulations	
<i>T. bifasciatum</i> , <i>X. novacula</i>	$G = \text{PreyBD} + \text{PreyFE} + \text{PredBD} + \text{PredFE} + \text{Depth} + T + \text{EarlyGrowth}$
<i>K. pelamis</i> (prey)	$G = \text{PreyBD} + \text{PreyFE} + \text{Depth} + T$
<i>K. pelamis</i> (predator)	$G = \text{PredBD} + \text{Depth} + T$
Interactive GAM formulations	
<i>T. bifasciatum</i> , <i>X. novacula</i>	$G = \text{PreyBD} \times \text{PreyFE} + \text{PredBD} \times \text{PredFE} + \text{Depth} + T + \text{EarlyGrowth}$
<i>K. pelamis</i> (prey)	$G = \text{PreyBD} \times \text{PreyFE} + \text{Depth} + T$

G = recent growth (mean of last 3 full otolith increment widths as a detrended growth index)

PreyBD = prey background density ($\log_{10}$ transformed)

PreyFE = prey frequency elevated

PredBD = predator background density ($\log_{10}$ transformed)

PredFE = predator frequency elevated

T = temperature

EarlyGrowth = mean of otolith increment widths 5-10

Table 2.2 Summary of background densities (*BD*) and frequency elevated (*FE*) of prey and predator groups from *ISIIS* transects associated with larval fish growth data from the Straits of Florida. *Background density (BD)* is the average density of 1-m horizontal bin densities (ind. m⁻³) in each *ISIIS* half-transect. *Frequency elevated (FE)* is the percentage of 1-m horizontal bins in an *ISIIS* half-transect where the density is >2 standard deviations (SD) above the *BD*. Number of *ISIIS* half-transects = 30 (copepods), 14 (appendicularians), 34 (predators). *Elevated density minimum* is the density threshold for 1-m horizontal *ISIIS* bins to be considered elevated: mean *BD* + 2SD of 1m bins in each transect. *Elevated density* is the density of 1-m horizontal bins above the elevated density minimum; 1-m bins included in *FE*. Number of 1-m bins per transect = 3,341 – 11,217 (mean = 6,272)

	Mean (range)			
	Background density (ind. m ⁻³)	Frequency elevated (%)	Elevated density minimum (ind. m ⁻³)	Elevated density (ind. m ⁻³)
Prey: copepods (cyclopoid & harpacticoid)	7.4 (2.0 - 19.7)	4.9 (2.0 - 13.7)	29.5 (12.9 - 59.6)	41.5 (14.4 -192.4)
Prey: appendicularians	67.7 (30.0 - 111.4)	3.6 (2.3 - 5.3)	140.0 (79.1 - 207.3)	161.8 (85.3 - 365.7)
Predators: chaetognaths + hydromedusae	27.5 (6.2 - 72.9)	4.3 (3.0 - 5.7)	74.9 (31.4 -155.9)	92.8 (32.2 - 335.0)

Table 2.3. Summary of the best generalized additive models (GAM) and interactive GAMs explaining the influence of prey and predator distributions on recent larval growth patterns of *Thalassoma bifasciatum*, *Xyrichtys novacula*, and *Katsuwonus pelamis* in the Straits of Florida. Estimated degrees of freedom (or linear coefficient in the case of parametric terms) and statistical significance are shown for each term, as well as deviance explained (Dev. exp; %), generalized cross validation (GCV), and Akaike information criterion (AIC) scores for each model. Variables are defined in Table 2.1 and described in Methods. NS (not significant) denotes predictor variables removed in backward selection. Dashes denote predictor variables not included in the model. · $p \leq 0.1$, * $p \leq 0.05$, ** $p \leq 0.01$, *** $p \leq 0.001$

GAMs	Predictor Variables								Dev. exp	GCV	AIC
	PreyBD	PreyFE	PredBD	PredFE	PreyBD× PreyFE	PredBD× PredFE	Depth	T			
<i>T. bifasciatum</i>	2.11***	1.00**	NS	NS	-	-	0.44**	1.00**	26.3	0.62	348.44
<i>X. novacula</i>	1.00***	1.11*	2.96**	2.90**	-	-	0.67**	1.98·	19.6	0.57	354.85
<i>K. pelamis</i> (prey)	1.00***	2.28*	-	-	-	-	NS	2.78***	32.4	0.54	300.74
<i>K. pelamis</i> (predator)	-	-	1.00***	-	-	-	NS	2.89***	31.3	0.55	298.66
Interactive GAMs											
<i>T. bifasciatum</i>	-	-	-	-	3.01***	7.26*	NS	1.00*	31.5	0.63	350.12
<i>X. novacula</i>	-	-	-	-	3.00·	5.89***	NS	1.00·	21.8	0.54	348.44
<i>K. pelamis</i> (prey)	-	-	-	-	4.19***	-	NS	2.67***	33.9	0.54	299.28

Figure 2.1. Map of locations in the Straits of Florida (SOF) sampled in (top) May-June 2014 and (bottom) June 2015. Multiple Opening/Closing Net and Environmental Sensing System (MOCNESS) replicate tows and *In Situ* Ichthyoplankton Imaging System (*ISIIS*) transects at each depth (15 m and 30 m) were centered on a drogue that drifted northeastward with the Florida Current. Distances between MOCNESS tows and *ISIIS* transects appear farther apart in the western SOF where the Florida Current is stronger, compared to east SOF, but in all regions the same water mass was sampled in a moving current. Map generated using ArcGIS version 10.6 (<http://www.esri.com/>).

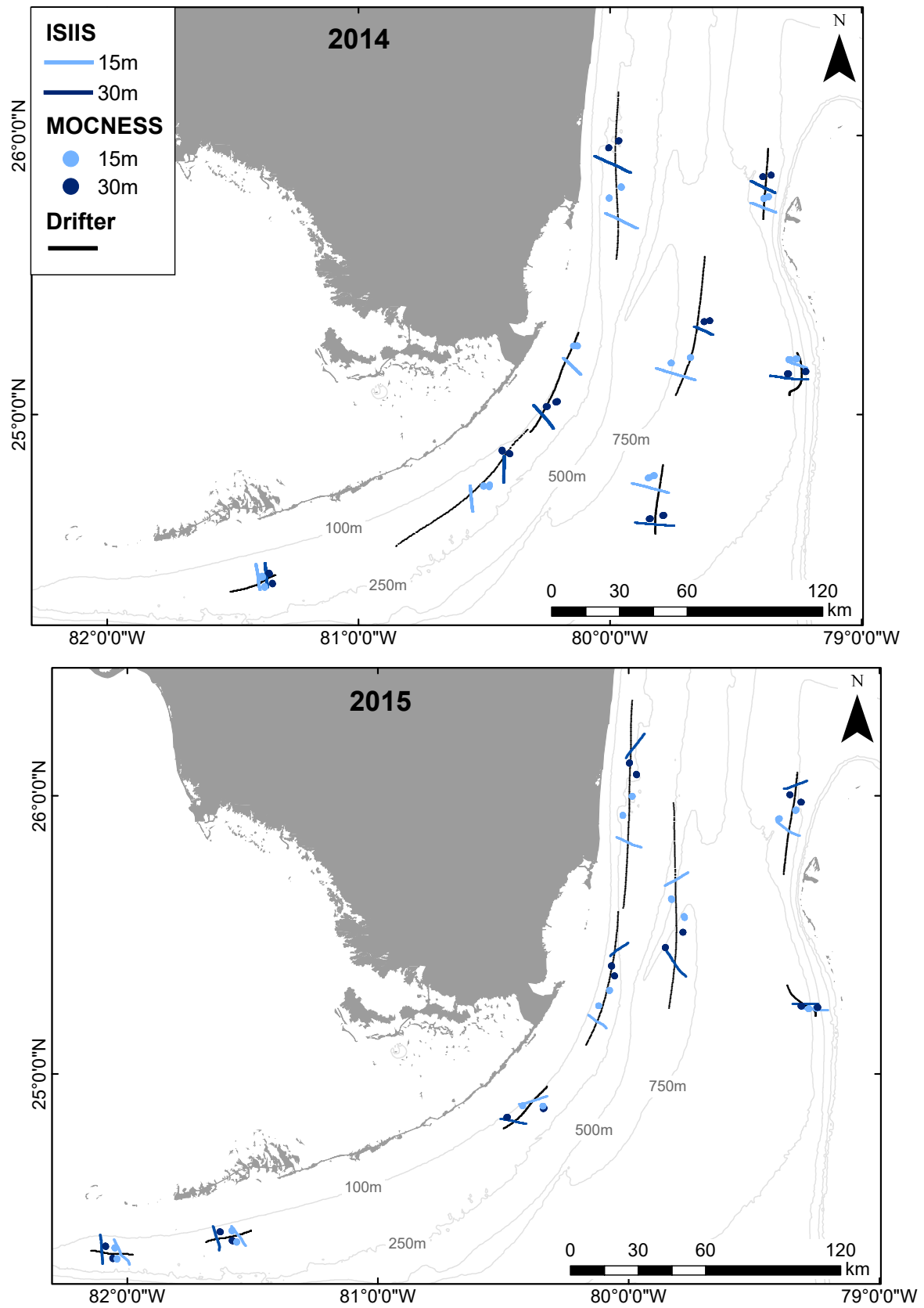


Figure 2.1

Figure 2.2. Size class frequency of larval (a) *Thalassoma bifasciatum*, (b) *Xyrichtys novacula*, and (c) *Katsuwonus pelamis* sampled from all tows (gray; n = 64 tows) and from larvae selected for otolith analysis (black). Number of larvae in all tows (gray) = 339 (*T. bifasciatum*), 479 (*X. novacula*), 295 (*K. pelamis*). Number of larvae in otolith analyses (black) = 147 (*T. bifasciatum*), 156 (*X. novacula*), 134 (*K. pelamis*).

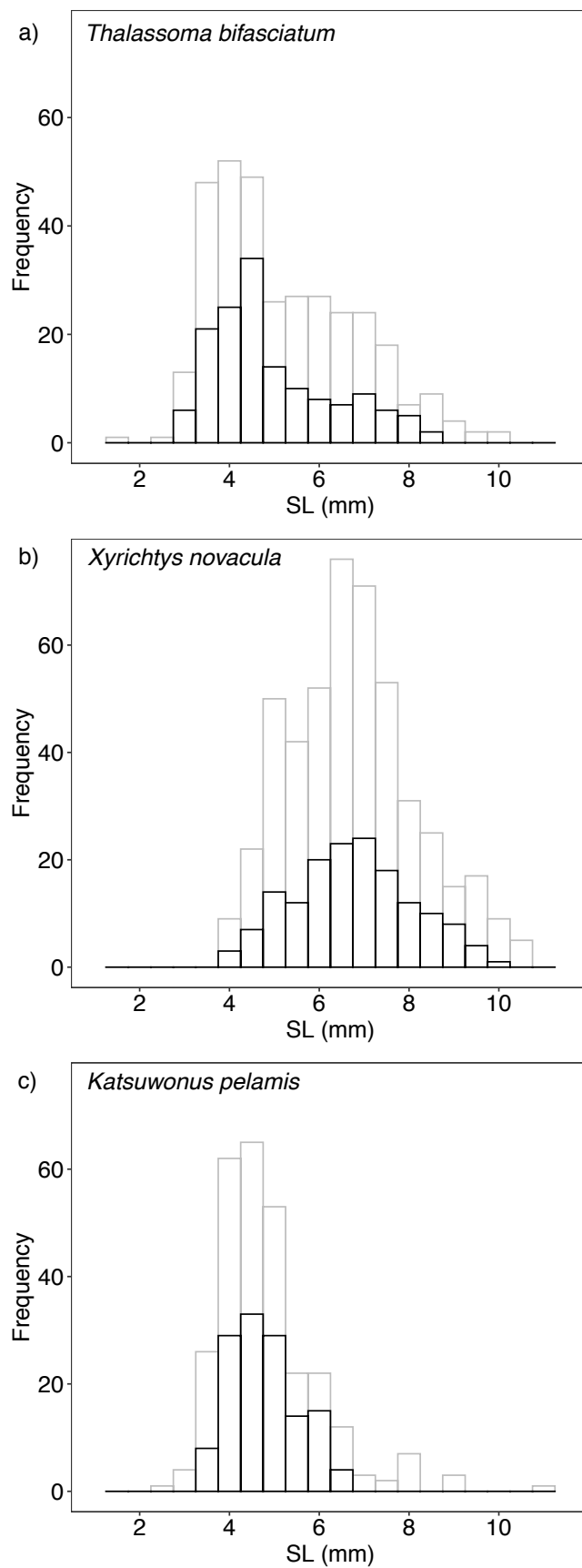
**Figure 2.2**

Figure 2.3. Model results of (a, d) the interactive effect of prey background density (*BD*) and frequency elevated (*FE*), (b, e) the interactive effect of predator *BD* and *FE*, and (c, f) temperature on recent growth of (a-c) *Thalassoma bifasciatum* and (d-f) *Xyrichtys novacula*. Predicted recent growth is expressed as a detrended growth index and shown with warmer colors for faster growth and cooler colors for slower growth. Please note that given *BD*, *FE*, and growth values vary by prey and predator groups as well as larval fishes, both axes and scales vary among plots. For interaction plots (a, b, d, e) black dots are field observations for each interactive covariate, thus where the modeled results can best be interpreted. For temperature (c, f) fitted lines, 95% confidence intervals (gray shaded areas) and partial residuals (dots) are shown; whiskers on x-axes are field observations for that covariate.

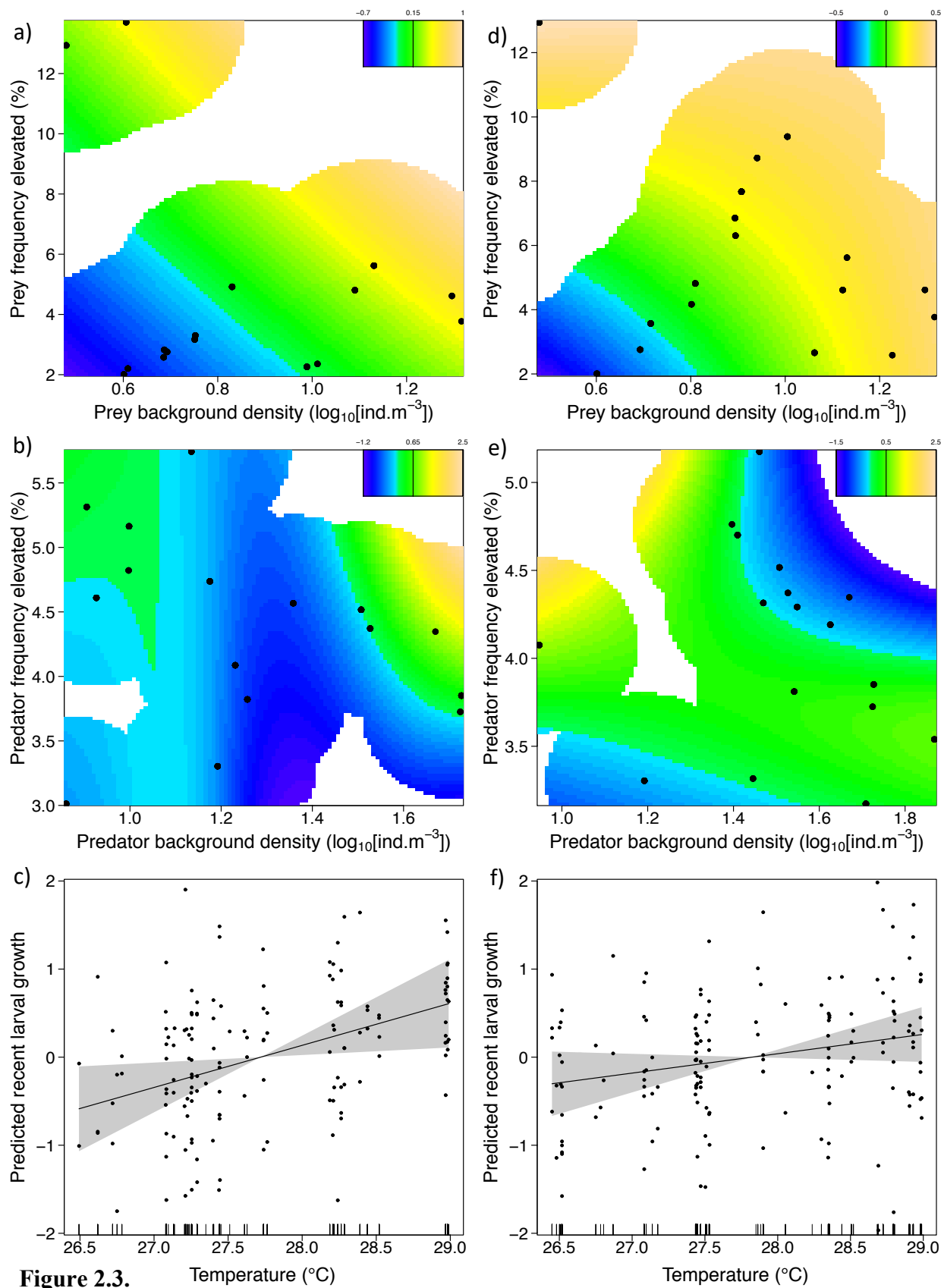
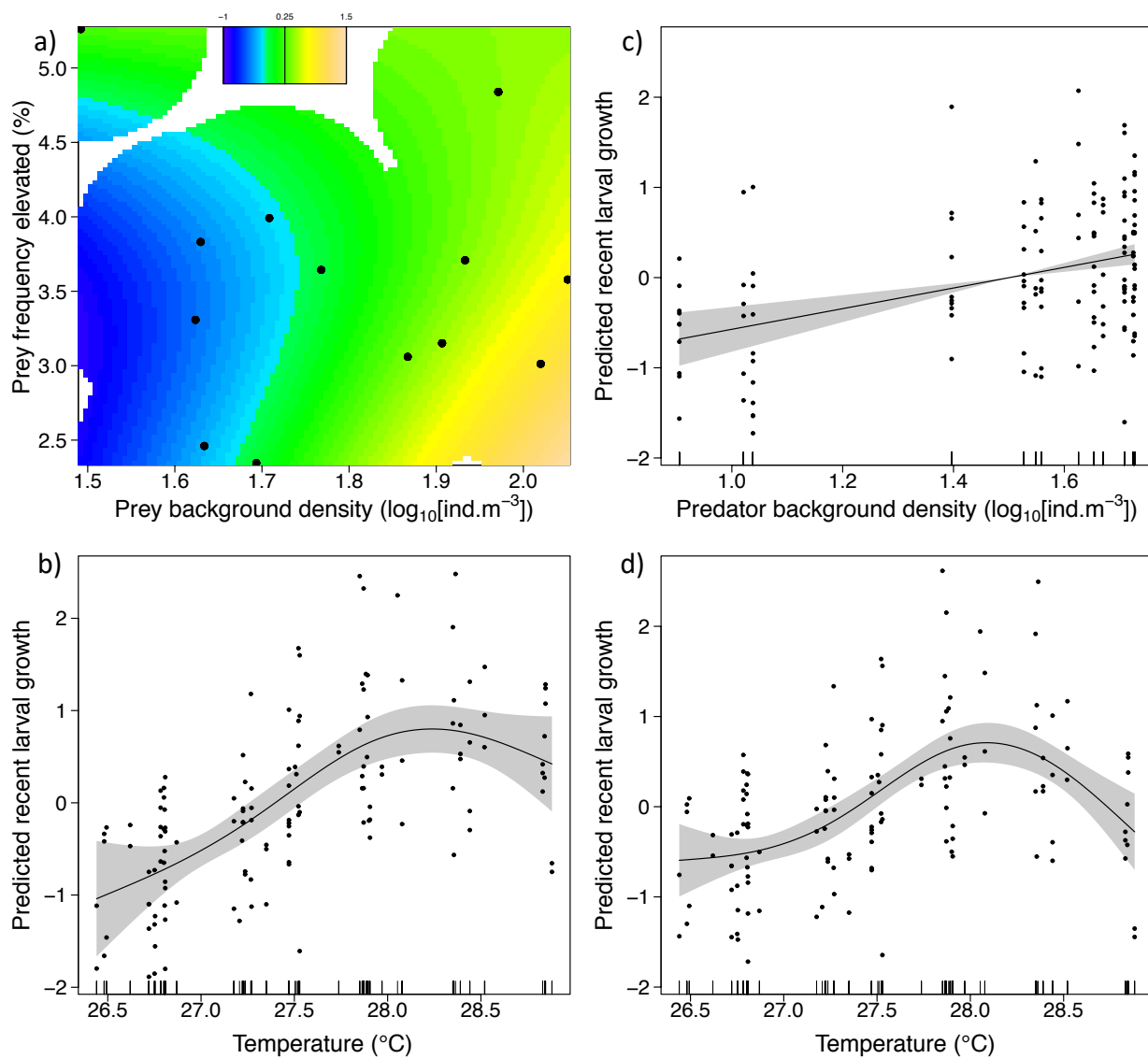


Figure 2.3. Temperature ($^{\circ}\text{C}$)

Figure 2.4. Model results of (a) the interactive effect of prey background density (*BD*) and frequency elevated (*FE*), (c) predator *BD*, and (b, d) temperature on recent growth of *Katsuwonus pelamis*. Results are from separate (a, b) prey and (c, d) predator models. Predicted recent growth is expressed as a detrended growth index. For the prey interaction plot (a) warmer colors are faster growth, cooler colors are slower growth, and black dots are field observations for each interactive covariate, thus where the modeled results can best be interpreted. For predators and temperature (b-d) fitted lines, 95% confidence intervals (grey shaded areas) and partial residuals (dots) are shown; whiskers on x-axes are field observations for that covariate.

**Figure 2.4**

**CHAPTER 3: SOME LIKE IT HOT, HUNGRY TUNAS DO NOT!
IMPLICATIONS OF TEMPERATURE AND PLANKTON FOOD WEB
DYNAMICS ON LARVAL BLACKFIN TUNA (*THUNNUS ATLANTICUS*)
GROWTH AND DIET**

Abstract

Restricted to low-productivity environments near their thermal maxima, larval tunas may be threatened by warming global temperatures, yet our understanding of how they are constrained is limited. We examined blackfin tuna (*Thunnus atlanticus*) diet and growth in the context of their prey and predators in the Straits of Florida in two years with contrasting summer conditions: low temperature (26.7–28.3°C)-high prey in 2014 and high temperature (28.4–29.0°C)-low prey in 2015. In the cooler, high prey conditions, larvae had 30% faster growth (0.45 mm d⁻¹), fuller guts from predominantly feeding on calanoid copepods, and were 10x more abundant, dominating the larval fish assemblage. In contrast, in warm, low prey conditions fewer, younger, and slower-growing (0.35 mm d⁻¹) *T. atlanticus* fed predominantly on nauplii, and had less full guts. Modeling individual growth across years revealed that growth peaked at an optimum of 28.5°C (5°C below their known thermal maximum) and high densities of predators selectively consumed slower-growing larvae. Low prey availability may reduce the thermal optima of larvae, as growth and survival are especially diminished when low prey and high temperature coincide. Our results illustrate the importance of considering food web dynamics together with temperature when predicting the response of organisms to ecosystem variability, particularly ongoing climate change.

3.1 Introduction

Understanding the ecology of larval fishes has never been more important to the future of our pelagic ecosystems and fisheries. Increasing global temperatures are affecting ocean ecosystems (Hoegh-Guldberg *et al.*, 2018), driving changes in productivity (Behrenfeld *et al.*, 2006) and restructuring planktonic food webs (Richardson, 2008), with consequences for higher trophic levels (Beaugrand *et al.*, 2003; Pörtner and Peck, 2010). Long-term monitoring has revealed changes in plankton communities with northward shifts in species distributions, timing of biomass peaks, and changes in biomass (Richardson, 2008), resulting in asynchrony of food availability for fish populations and dramatic regime shifts (Peterson and Schwing, 2003; Alheit and Niquen, 2004). Over the last two decades, such changes have occurred over shorter time scales as frequent marine heat waves (Frölicher and Laufkötter, 2018) exacerbate the effects of warming on marine fish populations (Mills *et al.*, 2013; Cavole *et al.*, 2016).

Marine fishes in subtropical and tropical regions are particularly sensitive to temperature increases as they are adapted to a narrow and relatively stable thermal regime (Tewksbury *et al.*, 2008), and frequently exist near their upper thermal limit (Rummer *et al.*, 2014). The metabolic rate of these ectotherms increases exponentially with temperature (Gillooly *et al.*, 2001), requiring increased food intake to support basic functions (e.g., growth) at higher metabolic rates (Houde, 1989; McLeod *et al.*, 2013). Yet in warm, oligotrophic oceans, projected increases in stratification with global warming will further reduce delivery of deep water nutrients to surface waters, favoring water column nutrient recycling via food webs with smaller-sized organisms (e.g., bacteria, protists, flagellates), more trophic levels, and less efficient energy transfer (Behrenfeld *et al.*, 2006; Fu *et al.*, 2016). Recent studies document some of these changes, but system-specific responses are highly variable (Ivory *et al.*, 2019), with documented decreases (Lavaniegos and Ohman, 2007) and increases (Sheridan and Landry, 2004; Steinberg *et al.*, 2012) in primary and secondary production. Given that subtropical fishes already exist near their thermal limits in low-productivity systems, measuring the combined effects of changes in temperature and food web dynamics is critical to our understanding of how climate change is influencing marine fish populations.

The pelagic larval phase is a critical period in the life of most marine fishes when survival depends on the ability of larvae to find food, grow quickly, and avoid predation (Houde, 1987), with success impacting cohort strength (Castonguay *et al.*, 2008). For larvae in warm-water systems, successfully locating ample prey is especially important since their relatively short pelagic larval duration (~1 month) necessitates generally fast growth. Fast larval growth not only increases the probability of survival (by reducing vulnerability to predation; Satoh *et al.*, 2013) but also influences juvenile survival through higher condition at metamorphosis and/or settlement (Searcy and Sponaugle, 2001; Sponaugle and Grorud-Colvert, 2006). Growth is inherently linked to feeding success (Houde, 1989; Sponaugle *et al.*, 2009; Reglero *et al.*, 2014a), with the specialized diets and feeding strategies of tropical larvae adapted for planktonic food webs in low-productivity systems (Llopiz and Cowen, 2009; Llopiz and Hobday, 2015). Temperature also has a strong impact on tropical fish larvae, despite seemingly little seasonal temperature variation, with higher temperatures generally resulting in faster growth and shorter pelagic larval durations (Sponaugle *et al.*, 2006). However, where food supply is low and insufficient for sustaining such high growth rates, growth under high temperatures may be reduced (Houde, 1987; Buckley *et al.*, 2004; McLeod *et al.*, 2013). Challenges associated with measuring all of these variables *in situ* have resulted in relatively few studies that have examined larval growth and diet in the context of prey availability, predation pressure, and temperature variability (Wexler *et al.*, 2007; Satoh *et al.*, 2013).

Larval tunas have some of the fastest growth and often occur in high abundance in warm-water spawning regions; however, they are constrained by temperature and feeding conditions. Recent studies on larval tuna distributions (Reglero *et al.*, 2014b; Cornic and Rooker, 2018) have generally supported hypotheses that spawning grounds are restricted to regions >24 °C, where mesoscale oceanographic features (e.g., eddies, upwelling) both enhance food supply in an otherwise oligotrophic region and retain larvae in this favorable habitat (Schaefer, 2001; Bakun and Broad, 2003). Larval tuna diets reflect adaptations to such oligotrophic environments and change with ontogeny, from consuming small nauplii to larger copepods or appendicularians before a shift to piscivory (Llopiz *et al.*, 2010; Catalán *et al.*, 2011; Tilley *et al.*, 2016). However our understanding of how larval growth or diet is

connected to environmental conditions in the wild is limited, with only a few studies linking patterns over broad spatial or temporal scales (García *et al.*, 2013).

Considering that tuna larvae are restricted to regions that are both warm and have low productivity, understanding how larval traits are connected to diet, prey availability, and temperature is essential to predicting their vulnerability to changes in the environment with increasing temperatures. In the Intra-Americas Sea (Gulf of Mexico, Caribbean Sea, Straits of Florida), recent sustained elevated temperatures (+1 °C from 2010-2015; Domingues *et al.*, 2018) have focused attention on longevity of spawning regions. Temperature increases projected under future climate scenarios predict that suitable larval habitat for Atlantic bluefin tuna (*Thunnus thynnus*) will dramatically decrease by 93-96% in the next 80 years (Muhling *et al.*, 2011, 2015). In contrast, habitat suitability may increase for skipjack (*Katsuwonus pelamis*) larvae (Muhling *et al.*, 2015), a more warm-tolerant species. However, a recent study modeling the effects of local prey availability, predators, and temperature on larval growth for *K. pelamis* identified an optimal temperature for growth (28 °C; Gleiber *et al.*, 2020) well below physical conditions considered suitable for survival (up to 30-32 °C; Muhling *et al.*, 2015). This suggests that other aspects of the environment should be considered in evaluating how larval tunas respond to change. Examining predator-prey interactions on a fine scale (individual level), over a range of conditions is necessary to realistically predict the interactive effects of warming on larval survival and eventual recruitment (Hunsicker *et al.*, 2011; Llopiz *et al.*, 2014).

In addition to changes in suitable habitat with warming, tuna populations are threatened by overfishing (Collette *et al.*, 2011). With the decline of large pelagic tuna species, fishing pressures are increasing on smaller tunas (e.g., blackfin, bullet, frigate), yet formal stock assessments and management plans for these species have not been conducted (Spencer *et al.*, 2016; Restrepo *et al.*, 2017). Blackfin tuna (*Thunnus atlanticus*) have a similar ecology to many of the larger pelagic tunas, with larvae highly abundant in the plankton, following summer spawning (Richardson *et al.*, 2010; Cornic and Rooker, 2018). While they are a more warm-temperature tolerant species, *T. atlanticus* larval diets are similar to other temperature-sensitive *Thunnus* species (e.g., bluefin; Llopiz *et al.*, 2010), and are therefore a good model for examining food web constraints on larval tunas. *T. atlanticus* larvae are known to occur in waters >29 °C and associate with mesoscale eddy activity

(Rooker *et al.*, 2013; Cornic and Rooker, 2018), but little else is known about their larval ecology. Understanding how *T. atlanticus* feeding and growth may be influenced by variability in predator-prey dynamics with food web changes is key in predicting their survival with future temperature-driven changes in the region.

This study coupled *in situ* imaging with biological sampling to examine how local prey, predator, and temperature conditions influenced larval diet and growth of *T. atlanticus* in the Straits of Florida (SOF). The SOF is a region characterized by a high abundance and diversity of larval fishes, including *T. atlanticus*, imbedded within a major western boundary current, the Florida Current. Regional physical processes (cyclonic mesoscale eddies and upwelling) can elevate prey, likely making the region ideal habitat for *T. atlanticus* larvae. Elevated prey associated with these physical processes have been linked to higher gut fullness and growth rates for abundant larval reef fishes (Sponaugle *et al.*, 2009; Shulzitski *et al.*, 2015), billfishes (Sponaugle *et al.*, 2010), and tunas (Llopiz *et al.*, 2010). If prey availability similarly influences larval condition of *T. atlanticus*, we expected high prey conditions to enhance gut fullness and growth rates. Temperature can also be important for larval growth in this region (Sponaugle *et al.*, 2006; Gleiber *et al.*, 2020). While our understanding of the effect of predator densities on larval growth is limited, selective mortality has been documented in larval coral reef fishes and *K. pelamis* (Sponaugle *et al.*, 2011; Shulzitski *et al.*, 2016; Gleiber *et al.*, 2020), with the strength of selection against particular traits increasing with predator densities. The overall goal of this study is to examine how variability in temperature and predator-prey interactions influence larval *T. atlanticus* diet and growth, information that will enable us better model population replenishment of tunas in light of climate change.

3.2 Methods

3.2.1. Study area and field sampling

Thunnus atlanticus larvae and their planktonic prey and predators were sampled in the Straits of Florida (SOF; Figure 3.1), a region bordered by the Florida Keys to the west and Bahamas to the east. The region is dominated by the rapid north-eastward flowing Florida Current (average speed = 160 cm s⁻¹; Lee *et al.*, 1991), which links the waters of the Gulf of Mexico and Caribbean to the Gulf Stream in the North Atlantic. *T. atlanticus* are

known to spawn in the SOF from May to November with high abundances throughout the region from May through September (Richardson et al. 2010). Sampling was conducted on two cruises aboard the R/V *FG Walton Smith* from 28 May - 6 June, 2014, and 18 - 26 June, 2015. Each year, we sampled eight stations encompassing north-south and cross-strait variability in the SOF using biological net sampling for *T. atlanticus* together with *in situ* plankton imagery of their prey and predators. Larval fishes were collected at each station using a Multiple Opening/Closing Net and Environmental Sensing System (MOCNESS) with a 4 m² opening, four 1-mm mesh nets, and sensors that simultaneously measured conductivity, temperature, and depth. To sample larval fishes on a fine horizontal spatial scale, we sequentially fired each of the four MOCNESS nets every ~125 m along the transect, at a depth of either 15 m or 30 m. Traveling at a speed of 1 m s⁻¹, each MOCNESS net sampled ~500 m³. At every station, this net sampling was repeated with two complete MOCNESS tows at each depth (randomized order), yielding eight replicate nets per depth. We used the *In Situ* Ichthyoplankton Imaging System (ISIIS; Cowen & Guigand 2008) to measure zooplankton distributions along two 8-16 km transects at discrete depths of 15 m and 30 m (Gleiber et al., 2020). Towed at a speed of 2.5 m s⁻¹, the ISIIS sampled the water column at ~140 L s⁻¹, imaging particles from ~200 µm to 13 cm. See figure 1 in Gleiber et al. (2020) for detailed sampling design.

To ensure all ISIIS and MOCNESS transects sampled the same water mass, transects and net tows at each depth were centered on a GPS-tracked Lagrangian drifter drogued at 10 m depth and moving with the Florida Current. Each replicate MOCNESS tow (four nets) per depth at each station corresponded with one half of the ISIIS transects (half-transects = 4-8 km). All sampling occurred during daylight hours, approx. 0600 – 1800, to minimize diel effects, and because larval tunas in the SOF typically feed during daylight hours (Llopiz et al., 2010). Biological samples were preserved in 95% ethanol; to reduce degradation of otoliths, ethanol was changed after 24-48 h, and again after 2-3 months for high biomass samples. All larval fishes were separated out of the samples in the laboratory, and identified to the lowest possible taxonomic grouping following Richards (2005). *Thunnus* spp. were identified to genus, since external morphological characteristics are not diagnostic to species level (Richards et al., 1990). Prior molecular analysis of *Thunnus* spp. in the SOF (n > 1000) indicated that 95% of larvae were *T. atlanticus* (blackfin tuna; Richardson et al., 2010),

therefore for purposes of the present study, we assumed all *Thunnus* spp. were *T. atlanticus*. Since 97% of all *T. atlanticus* collected were from 15 m depth ($n = 1672$ at 15 m, 54 at 30 m), we included only 15 m depth samples in our study. Density (ind. 1000 m^{-3}) of *T. atlanticus* was calculated by dividing counts from each net by the volume of water filtered through the net. The proportion of *T. atlanticus* of all larval fishes sampled was also calculated for each net.

3.2.2. Otolith analysis

We used otolith microstructure analysis to estimate larval age for individual larvae and growth rates across populations. This is the first study to examine the otoliths of larval *T. atlanticus*, but daily increment deposition has been confirmed for similar *Thunnus* larvae (*T. thynnus*: Itoh *et al.*, 2000, *T. maccoyii*: Jenkins and Davis, 1990, *T. albacares*: Wexler *et al.*, 2001). Further, daily increment formation has been documented for juvenile *T. atlanticus* in the SOF (Adams and Kerstetter, 2014). Given uncertainties with when otolith increment deposition begins in *Thunnus* spp. (Itoh *et al.*, 2000; Wexler *et al.*, 2001; Malca *et al.*, 2017), we used the most parsimonious assumption: that the first increment represents the first day of life. All larvae collected ($n = 1672$) were measured for standard length (SL) and body depth using a Leica dissecting microscope with camera and image analysis software (Image-Pro Plus 7.0 and Premier 9.3). We analyzed the sagittal otolith microstructure on a subset of larvae ($n = 4-18$) from a subset of replicate tows at different stations ($n = 26$) with different prey and predator densities. Since *T. atlanticus* are known to rapidly switch to piscivory at ~ 7 mm standard length (SL), which potentially greatly changes growth rates, we focused our analyses on < 7 mm SL larvae. The size distribution of the subset of larvae used for otolith analysis ($n = 286$) was proportional to the size distribution of all < 7 mm *T. atlanticus* larvae in each tow. While we examined the otoliths of all > 7 mm larvae collected ($n = 26$) and report SL and age information in the Figure 3.2, further otolith data analyses excluded these larvae.

Sagittal otoliths were extracted and stored in immersion oil on a glass slide to facilitate reading (Sponaugle, 2009). Prepared otoliths were read along the longest axis at 1000x (oil immersion) magnification using a Leica compound microscope with an attached camera and Image-Pro Premier 9.3. Otoliths were read 2-3 times by the same reader. If reads

did not differ, one read was randomly chosen for analysis; otoliths where all three reads differed were removed from further analysis ($n = 9$; Sponaugle 2009). Any larvae revealed to be precociously piscivorous through gut contents analysis (below) were removed ($n = 18$) from otolith-derived growth analyses so as not to bias results (i.e., with fast growth rates following piscivory).

Sampling in each year encompassed different temperature regimes as measured from MOCNESS tows at 15 m depth: generally cooler in 2014 (26.7 – 28.3 °C), compared to 2015 (28.4 – 29.0 °C). To test whether otolith deposition rates were consistent between years, we initially examined the relationship between least-squares regressions of otolith radius-at-age residuals vs. SL-at-age residuals (Hare and Cowen, 1995). Positive otolith radius-at-age residuals indicate larvae with large otoliths for their age; positive SL-at-age residuals indicate larvae with larger lengths (SL) for their age. The relationships were not consistent between years, demonstrating that otolith increment widths could not be used to directly compare growth between years. Instead, we used overall somatic and otolith growth to compare the variation in larval growth of *T. atlanticus* in the cooler (2014) vs. warmer (2015) years. Growth rates were calculated as the slope from least-squares regressions of SL-at-age (overall somatic growth), otolith radius-at-age (overall otolith growth), as well as body depth-at-age and body depth:SL-at-age (proxy for condition; Ferron and Leggett, 1994). We compared each growth parameter between years using analysis of covariance (ANCOVA), conducted both with and without temperature included as a covariate to explore the influence of temperature on variation in growth between years. A significant interaction between age and year (or SL-on-age residuals and year) indicates a difference growth (e.g. slopes) between year, while a significant intercept indicates a difference in initial size. The full structural model is:

$$Y = \beta_0 + \beta_1 x_1 + \beta_2 x_2 + \beta_3 x_3 + \beta_4 (x_1 \cdot x_2) + e$$

where Y is the response variable, x_1 through x_3 are explanatory variables, β_0 is the intercept, the other β s are all slopes, and e is the error. Response and explanatory variables are detailed in Table 3.3 and Supplementary Table B4. To obtain an individual value of somatic growth for use in the modeling approach (below), we computing the residuals of the SL-at-age regression ($p < 0.001$, $r^2 = 0.66$) to account for the increase in growth with age.

3.2.3. Gut contents analysis

We examined the gut contents of all *T. atlanticus* larvae used in the otolith analyses (including >7 mm larvae; total n = 310). Gut contents were examined under a Leica dissecting microscope by removing the entire alimentary canal, and then teasing out prey with minuten pins (Llopiz and Cowen, 2009) in a few drops of glycerol on a microscope slide. Prey were identified to the lowest taxonomic level possible for comparison with environmental prey availability and enumerated. We note that copepods were not differentiated between copepodites and adults. Prey lengths (i.e., prosome length for copepods, carapace length for other crustaceans, longest dimension otherwise) were measured using a Leica dissecting microscope with camera and image analysis software (Image-Pro Plus 7.0 and Premier 9.3). To estimate the biomass of prey at the time of ingestion, prey lengths were converted to dry weight using published length:dry weight conversions (Chisholm and Roff, 1990; Clarke and Roff, 1990; Webber and Roff, 1995; Hopcroft *et al.*, 1998). The dry weight of copepods that could not be identified to order, and unknown crustacean remains were estimated with the mean of all length:dry weight conversions used for copepod prey groups or all crustacean prey groups, respectively. Since appendicularians in the gut could not be accurately measured for length, we used mean dry weight estimates for distinctly large (*Oikopleura*, 1.0 µg) and small (*Fritillaria*, 0.2 µg) appendicularians, following Llopiz *et al.*, 2010. Larval fish prey in the guts of piscivorous larvae (n = 30), could not be estimated for length due to distortion and degradation, thus piscivorous larvae were excluded in biomass analyses. For simplification, some prey groups of a similar type were combined (e.g., different types of nauplii).

Total ingested prey biomass was calculated as the sum of individual prey dry weights within each larva and the ingested biomass by prey type was calculated as the sum of dry weights of a specific prey type within each larvae. A standardized ingested prey biomass was calculated separately for total ingested prey biomass and ingested biomass of each prey type by dividing each biomass value by SL^3 (proxy for larval biomass) to account for the increase in gut capacity with growth. Quantitative estimates of gut fullness were calculated as the residuals of the linear relationship between total ingested prey biomass and larval SL (Dower *et al.*, 1998). Mean standardized ingested prey biomass (total and by prey type) and gut fullness were calculated for all larvae in each year and separately by prey type for small (3-5

mm) and larger (5-7 mm) larvae. Mean ingested prey length for each prey type was also calculated for all larvae in each year. Interannual differences were compared with Wilcoxon rank sum tests, as data were non-parametric.

Feeding incidence was calculated as the proportion of larvae with prey present in the gut; larvae with empty guts ($n = 5$) were excluded from all other analyses. Prey composition data also included the frequency of occurrence of prey types (%FO; proportion of larvae with the prey type present in gut), numerical percentage (%N; proportion of each prey type from all prey extracted), and relative biomass (%B; proportion of each prey type in total ingested prey biomass). We calculated %FO, %N, and %B of all prey types at each cross-strait region (West, Central, East) within a sampling year, and for each sampling year (all regions combined). To examine the relative biomass (%B) of prey types for small (3-5 mm) compared to larger (5-7 mm SL) *T. atlanticus*, these values were also calculated by size class within each sampling year. We note that %FO and %N calculations include piscivorous larvae, while %B excludes piscivorous and >7 mm SL larvae (see above). Since %FO and %N can be biased by the size of the ingested prey, we primarily focused on biomass, but provide values of %FO and %N in Supplementary Table B1. For simplicity, we focus on %B for combined prey groups, but provide values for %B to the lowest taxonomic level in Supplementary Table B2.

3.2.4. Prey/predator availability

Environmental prey/predator availability was calculated using biological counts from ISIIS imagery and described in Gleiber *et al.* (*in progress*) (Chapter 4). An automated algorithm classified zooplankton taxa into image classes based on taxonomy and morphology. Methodology associated with raw image analysis, image classification, training sets, and confusion matrices are detailed in Luo *et al.*, 2018 and Schmid *et al.*, 2020. Mean densities of prey and predator groups were calculated for each ISIIS half-transect, as the mean densities in each of 1-m horizontal distance bins (ind. m^{-3} ; $n = 3891 - 11467$). The dominant prey groups of *T. atlanticus* in this study, calanoid copepods and appendicularians, were determined from the analysis of larval gut contents. The ‘calanoid copepods’, and ‘appendicularian’ ISIIS groups were comprised of 10 and 4, respectively, morphological classifications of different taxa imaged from various angles. While crustacean nauplii are an

important part of *T. atlanticus* diet (Llopiz *et al.*, 2010), this group was not imaged effectively due to camera resolution limitations. *ISIIS* densities of potential gelatinous predators of larval fishes were combined in 1-m horizontal bins, thus mean half-transect predator densities represent the total abundance of the predator field. *ISIIS* groups included in the combined predator variable were based on known larval fish predators (Bailey and Houde, 1989; Purcell and Arai, 2001 and references therein): ‘hydromedusae’, ‘narcomedusae’, ‘cestid ctenophore’, ‘cydippid ctenophore’, ‘lobate ctenophore’, ‘calycophoran siphonophore’, ‘physonect siphonophore’, ‘chaetognaths’, and ‘other jellyfish’.

3.2.5. Multivariate diet analysis

We used non-metric multidimensional scaling (NMDS) to visualize differences in the multivariate *T. atlanticus* consumed prey composition structure across sampling years and how it was related to variables in the environment. NMDS was performed on a Bray-Curtis dissimilarity matrix from the ingested biomass of each prey type for individual larvae, standardized by larval size ($\mu\text{g dry weight mm}^{-3}$), and $\log(x + 1)$ transformed to reduce skewness. Prey types used in the analyses were those present in $\geq 5\%$ of larvae analyzed, and excluded unidentifiable prey. This resulted in six prey categories and 238 individual *T. atlanticus*; piscivorous and >7 mm larvae were also excluded. To examine the potential drivers or effects of prey composition, the final ordination (lowest stress solution) was overlaid with explanatory and response variables using a biplot to show linear relationships with ordination axes. Explanatory variables included temperature and local densities of prey (calanoid copepod, appendicularians), predators (all combined), and phytoplankton (diatom, protist, trichodesmium); response variables included individual somatic growth (residual SL-at-age), standardized total ingested prey biomass, and gut fullness. Temperature was calculated as the mean of the respective net(s) sampled by the MOCNESS. Environmental prey, predator, and phytoplankton groups were sampled by *ISIIS*, and values used were mean densities from half-transects (see above). The minimum correlation coefficient for an explanatory variable to be included in the ordination axes was $r^2 = 0.1$. To test whether differences in consumed prey composition were greater across years with different temperature regimes or spatially across the SOF, we conducted separate analysis of

similarities (ANOSIM) using random permutations of the data to assess significance (i.e. whether distances between groups are greater than within groups). We performed all multivariate analyses in R software (Version 3.6.0; R Core Team, 2019) using the *vegan* package (Oksanen *et al.*, 2013).

3.2.6. Modeling approach

We examined the effect of temperature, gut fullness, and local prey and predator availability on individual somatic growth of *T. atlanticus* using generalized additive models (GAMs) with a Gaussian distribution. These non-parametric regression techniques allow for non-linear relationships between dependent and independent covariates (Wood, 2006). GAMs are modeled using smoothing functions with additive techniques where all covariates are independent, allowing for easy inference, as the effect of each covariate is the same regardless of the values of the remaining covariates. The model included individual somatic growth (SL-at-age residuals) from 251 *T. atlanticus* larvae as the dependent variable, excluding piscivorous and >7 mm SL larvae. Fixed covariates were *gut fullness* (continuous), *temperature* (continuous), *prey density* (continuous), and *predator density* (continuous). Gut fullness was the residual gut content biomass from the linear relationship between total ingested prey biomass and larval SL. Temperature was from MOCNESS environmental data, averaged across individual nets in each tow. Prey (calanoid copepods) and predator (all gelatinous predators combined) densities from ISIIS half-transects corresponded to each MOCNESS tow (n = 26). We included only calanoid copepods as prey in the model since they were the dominant prey group that could be imaged by ISIIS. While larval density could potentially influence growth due to competition for resources, preliminary analyses revealed an increasing linear relationship between individual somatic growth and *T. atlanticus* density ($p < 0.001$, $r^2 = 0.08$), indicating increased larval density is unlikely limited by available resources. Additionally, calanoid copepod prey are ~85-34,000 (mean = 2,300) times more abundant than their *T. atlanticus* predator, therefore, density dependence was not considered in the model.

Prior to the GAMs, we used variance inflation factor (VIF) analysis to detect collinear variables and removed those variables above a VIF cut-off of 3. Gut fullness was log-transformed to reduce the influence of the highest and lowest values, and increase the spread

of the data. Smoothing functions were applied to continuous variables and to avoid model overfitting, the number of knots used in the smoothers was restricted to 4. Model selection was performed using a backward stepwise approach. Full and reduced versions of the models were compared using Akaike Information Criterion (AIC) as a measure of goodness of fit, and Generalized Cross Validation (GCV) as a measure of the model's predictive performance. The best model was identified by minimizing both AIC and GCV. We incorporated the dependency of growth on larvae collected from the same MOCNESS tow by including a random intercept in the fixed model, but AIC indicated that models without a random effect were best. Model diagnostics and residuals were checked for potential deviations from normality, homogeneity of variance, and other anomalies. All calculations and models were coded in R software (Version 3.6.0; R Core Team 2019) using the *mgcv* library.

3.3 Results

3.3.1. Water Temperature

Water temperatures measured at 15 m depth during net tows varied significantly between years, with temperatures in 2015 on average 1.2 °C warmer than in 2014 ($p < 0.001$; Table 3.1). Temperature ranges did not overlap between years: 26.7 – 28.3 °C in 2014, and 28.4 – 29.0 °C in 2015, and were consistent in all cross-strait regions ($p < 0.001$; Table 3.1).

3.3.2. Larval abundance, size, and age distribution

Density of larval *T. atlanticus* was almost an order of magnitude greater in 2014 than in 2015 (Wilcoxon, $p = 0.03$, Table 3.1, Figure 3.1). This trend was the strongest in the western SOF where *T. atlanticus* densities were 17x greater in 2014 than in 2015 (Wilcoxon, $p < 0.001$). *T. atlanticus* was the most abundant larval fish sampled at 15 m in 2014, comprising 19% of the larval fish assemblage (Table 3.1). In 2015, they comprised 12% of the larval fish assemblage, behind the following families: Carangidae, Nomeidae, Gonostomatidae, and Myctophidae (Gleiber *et al.*, *in progress*, Chapter 4).

T. atlanticus <7 mm SL (non-piscivorous) in 2014 ranged from 5-12d and were, on average, 0.5 mm larger (SL; Wilcoxon, $p < 0.001$) and 1 d older (Wilcoxon, $p < 0.001$) than those in 2015 (4-12d; Figure 3.2). This pattern held for all *T. atlanticus* sampled (including

>7 mm and piscivorous larvae) but the overall age range was similar between years (5-16 d in 2014, 4-15 d in 2015). The maximum size of larvae was similarly larger in 2014 (10.7 mm SL) than in 2015 (8.8 mm SL) (Figure 3.2).

3.3.3. Growth rates

Overall *T. atlanticus* somatic growth rate was faster in 2014 (0.45 mm day⁻¹) compared to 2015 (0.35 mm day⁻¹; $p = <0.01$, homogeneity of slopes test, Table 3.2-3, Figure 3.3a). Body depth, and body depth:SL growth rates and initial size (intercept) followed a similar pattern (Supplementary Table B3-4, Supplementary Figure B1). Otolith growth rate did not differ between years ($p = 0.36$, homogeneity of slopes test), however initial otolith size was larger in 2015 ($p = <0.01$; homogeneity of intercepts test, Table 3.2-3, Figure 3.3b). The relative difference in somatic and otolith growth rates between years is reflected in the relationship of otolith size-at-age residuals vs. SL-at-age residuals, with 1.6x faster otolith growth relative to somatic growth rate in 2015 compared to 2014 ($p < 0.001$; Tables 3.2-3, Figure 3.3c). These patterns held for all variables when temperature was included as a covariate in the ANCOVA (Table 3.3), suggesting that more than temperature is influencing the relationship between somatic and otolith growth between years.

3.3.4. Consumed prey biomass, gut fullness, and diet variability

Larval *T. atlanticus* consumed more prey in 2014 than in 2015, with an average of twice the total standardized consumed prey biomass and gut fullness as in 2015 (Wilcoxon, $p < 0.001$; Figure 3.4a,b). The pattern was similar between years for both 3-5 mm and 5-7 mm SL larvae (Figure 3.4c,d). Diet composition also varied across years with differences in diet greater between years than among cross-strait regions (Figure 3.5a, b). In 2014, *T. atlanticus* larvae consumed predominantly calanoid copepods, followed by *Farranula* spp. copepods (Figure 3.5a, 3.6, Supplementary Table B2). In contrast, in 2015, the dominant prey, by biomass, was nauplii (copepod, euphausiid, barnacle), with *Farranula* spp. and appendicularians also important in the west and central SOF (Figure 3.5b, 3.6, Supplementary Table B2). On average, individual *T. atlanticus* consumed a 6x higher standardized biomass of calanoid copepods in 2014 compared to 2015 (Wilcoxon, $p < 0.001$; Figure 3.6). Calanoid copepods consumed in 2014 were also significantly larger (0.45 ± 0.01

mm prosome length, $n = 254$; Wilcoxon, $p < 0.001$), compared to 2015 (0.36 ± 0.02 mm, $n = 60$). Additionally, larvae in 2014 consumed more *Farranula* spp. (Wilcoxon, $p < 0.001$) and other copepods (i.e., harpacticoid, *Oithona*, *Oncaea*, and unknown; $p < 0.01$) while larvae in 2015 consumed significantly more nauplii and appendicularians ($p < 0.01$; Figure 3.6).

Interannual differences in diet composition also tended to be greater than ontogenetic differences, with calanoid copepods dominating the diet of both 3-5 mm SL and 5-7 mm SL larvae in 2014 (Figure 3.5c,d). In 2015, 3-5 mm SL *T. atlanticus* consumed predominantly nauplii (Figure 3.5c), while for 5-7 mm SL larvae *Farranula* spp. and appendicularians were also important (Figure 3.5d).

3.3.5. Prey/predator availability

Calanoid copepod density differed more between years than among cross-strait regions, with double the density of calanoid copepods in 2014 compared to 2015 (Welch's t-test, $p < 0.001$; Table 3.1). This interannual difference was also similar within the western and eastern regions (t-test, $p < 0.001$ and 0.02 , respectively; Table 3.1), but not the central region (Welch's t-test, $p = 0.08$). Within each year, there were no significant cross-strait differences in calanoid copepod density (Welch's ANOVA, Table 3.1). Predators followed a similar pattern, with 1.5x higher densities in 2014 than in 2015 (t-test: $p < 0.011$), but with cross-strait differences within years. In both 2014 and 2015, predators were more abundant in the west compared to central and eastern SOF (Welch's t-test, $p < 0.01$; Table 3.1).

3.3.6. Multivariate diet composition

Multivariate analysis of consumed prey data revealed that the diet composition of *T. atlanticus* was similar among regions ($p = 0.27$) but differed significantly between years (ANOSIM: $p = 0.001$, based on 999 random permutations of the data; Figure 3.7). In 2014, the larval *T. atlanticus* diet was characterized by calanoid and other copepods, whereas in 2015 larva predominately consumed nauplii (Figure 3.7). Explanatory and response variables that were significantly correlated with ordination axes included: calanoid copepod density ($r^2 = 0.24$), gut biomass (0.24), temperature (0.22), gut fullness (0.16), and diatom density (0.15). Temperature was the only variable that correlated positively with the nauplii-dominated diet composition in 2015 (Figure 3.7). All other variables strongly correlated with

the diet composition in 2014, suggesting that the calanoid copepod-dominant diet was related to a higher environmental abundance of calanoid copepods (Figure 3.7). Additionally, *T. atlanticus* larvae consuming more calanoid and other copepods had a higher gut biomass and gut fullness. Univariate analysis across years is consistent with this, as consumed calanoid biomass was significantly related to calanoid copepod environmental densities and biomass ($p < 0.001$, $r^2 = 0.58$; Figure 3.8). This calanoid-dominant diet and higher environmental availability in 2014 was also positively related to diatom density (Figure 3.7), and univariate analysis revealed that environmental densities of calanoid copepods were positively related to diatom densities across years ($r^2 = 0.45$, $p < 0.001$).

3.3.6. Modeled relative somatic growth

Generalized additive modeling revealed the influence of temperature, predators, and gut fullness on somatic growth of *T. atlanticus* (Figure 3.9). Growth was strongly affected by temperature ($p < 0.001$), increasing to a peak at 28 - 28.5 °C before decreasing at the higher temperatures experienced in 2015 (Figure 3.9a). Predators significantly affected larval growth as well ($p < 0.001$), with the slowest growth occurring at lowest predator densities ($<30 \text{ ind. m}^{-3}$), and fastest growth at highest predator densities ($>60 \text{ ind. m}^{-3}$; Figure 3.9b). Larval growth was also related to gut fullness ($p < 0.001$), with lowest growth associated with mid-range values of gut fullness (Figure 3.9c). However, we note that interpretation of predicted growth at the highest and lowest gut fullness values is challenged by low sample sizes.

3.4 Discussion

The two years of sampling in this study captured significant differences in early-summer conditions in a sub-tropical, oligotrophic system, allowing for a valuable examination of how the pelagic environment influences larval tuna feeding and growth. *Thunnus atlanticus* (blackfin tuna) larvae had contrasting patterns of gut fullness, diet composition, somatic growth and abundances in two years with different temperature regimes, prey availability, and predator abundances. In 2014, when water temperatures were lower (26.7 – 28.3 °C), *T. atlanticus* in the SOF consumed primarily calanoid copepods, had guts that were twice as full, and had 30% faster growth rates than larvae in 2015.

Consequently, they were 10x more abundant and the dominant larval fish in the region in 2014, with larvae on average both larger and older than in 2015. In contrast, the 1.2°C warmer waters of 2015 had fewer, smaller, younger, and slower-growing *T. atlanticus* whose guts were less full and dominated by nauplii. Modeling individual larval growth across years further revealed that temperature, predator densities, and gut fullness had a significant effect on growth.

Water temperature and prey availability were both important bottom-up mechanisms affecting *T. atlanticus* growth and diet. Larvae in the warmer waters of 2015 had a slower overall growth rate (0.35 mm d⁻¹), despite temperatures (28.4 – 29.0 °C) being well within the range previously reported for this species' distribution (23 - 33 °C ; Rooker *et al.*, 2013; Muhling *et al.*, 2017; Cornic and Rooker, 2018). In contrast, larvae in the cooler water of 2014 had an overall higher growth rate (0.45 mm d⁻¹), consistent with other tuna species (bluefin, yellowfin, and skipjack) in the region (0.44 – 0.47 mm d⁻¹; Lang *et al.*, 1994; Malca *et al.*, 2017; Gleiber *et al.*, 2020). Environmental prey availability (both composition and biomass) appears to be limiting any growth advantages from increased metabolic rates in warmer temperatures. The lower gut biomass and fullness of *T. atlanticus* in 2015 (warmer) compared to 2014 (cooler) is directly related to fewer calanoid copepods in the environment. In 2014, when environmental calanoid copepod densities ranged from 10 - 103 ind. m⁻³ (mean = 31 ind. m⁻³), calanoids comprised 41% of larval *T. atlanticus* gut biomass. In comparison, in 2015, calanoid copepod densities were only 5 - 21 ind. m⁻³ (mean = 13 ind. m⁻³) and calanoids comprised only 11% of larval gut biomass. Instead, a much smaller prey, crustacean nauplii, were the dominant prey by biomass (25%), followed by appendicularians (13%).

Growth of larval *T. atlanticus* has not been examined previously but in similar tuna species growth has been shown to increase with temperature (Wexler *et al.*, 2011; García *et al.*, 2013; Satoh *et al.*, 2013), peaking at an optimum near the edge of their thermal limits (Kimura *et al.*, 2010; Gleiber *et al.*, 2020). However, sufficient prey availability is necessary to sustain faster growth in warmer temperatures, especially for such fast-growing species (Houde, 1989; Peck *et al.*, 2012). Prey availability generally has a positive effect on larval tuna growth in the wild (Wexler *et al.*, 2007; Satoh *et al.*, 2013; Gleiber *et al.*, 2020), and higher growth has been documented where warmer temperatures and higher prey abundances

(Lang *et al.*, 1994; Malca *et al.*, 2017) or higher quality prey (García *et al.*, 2013) co-occur. Our results build upon these findings to demonstrate that despite warmer water temperatures growth of *T. atlanticus* was significantly reduced in larvae with lower gut fullness, due to less favorable feeding conditions.

Environmental variability and larval growth patterns

Individual larval *T. atlanticus* growth rates across the two years were strongly affected by temperature. Modeling revealed a dome-shaped relationship with growth peaking at an optimal temperature of 28 - 28.5 °C, then decreasing over the warmer temperature range that occurred in 2015, suggesting the existence of constraints at higher temperatures. While the shape of this relationship matches theoretical growth rate-temperature curves (Jobling, 1997), the temperature of peak growth is surprising since both larvae and adult *T. atlanticus* are considered to be relatively tolerant of high temperatures (Muhling *et al.*, 2017). In contrast, *T. thynnus* (Atlantic bluefin tuna) is sensitive to high temperatures occurring in the Gulf of Mexico (GOM) in waters of 24 - 29 °C (Muhling *et al.*, 2010, 2015), at the edge of their upper thermal threshold for survival. *T. atlanticus* larval distributions range from 24 - 33 °C in both the GOM and Straits of Florida (SOF; Richardson *et al.*, 2010; Rooker *et al.*, 2013; Cornic and Rooker, 2018).

Despite the wide temperature range of known larval *T. atlanticus* distributions, the narrow thermal optima for growth we observed, coupled with lower growth and densities during warm temperatures in 2015, suggests that the poor feeding conditions larval *T. atlanticus* experienced could not support higher temperature-induced growth. A similar thermal optima for growth was recently shown for larval *K. pelamis* which feed predominantly on appendicularians (Gleiber *et al.*, 2020). Environmental abundances of this preferred prey in the SOF were also significantly lower in 2015 than in 2014 (Gleiber *et al.*, *in progress*, Chapter 4). Together, these results suggest that for fast growing larvae near their metabolic limits, the thermal optima for growth may be shifted when poor feeding conditions are unable to support growth in warmer conditions. These patterns reflect theoretical models suggesting growth in fishes is influenced not only by temperature, but also food availability (Jobling, 1997), with lower food availability reducing the temperature for optimal growth (Brandt, 1993). The combined negative effects of lower food in elevated temperature

conditions have been demonstrated in experimental studies as reef fish larvae took longer to settle (McLeod *et al.*, 2013) and adults experienced reduced growth rates with lower reproductive success (Donelson *et al.*, 2010). While most studies of tuna larvae have found growth to increase with temperature (Lang *et al.*, 1994; Kimura *et al.*, 2010; Wexler *et al.*, 2011; García *et al.*, 2013; Satoh *et al.*, 2013), temperatures near the edge of thermal limits or conditions of low prey availability were not included. Our results point to the importance of considering the synergistic effects of multiple stressors, and not just temperature or prey availability alone.

The interacting negative effects of poor prey in warmer water temperatures for *T. atlanticus* larvae are further evident by the relative rates of otolith and somatic growth. While overall somatic growth of larvae was significantly lower in 2015 (0.35 mm d⁻¹) compared to 2014 (0.45 mm d⁻¹), overall otolith growth rates were similar. Thus, the apparent relative rate of otolith to somatic growth was actually 1.6x greater in 2015, when poor feeding conditions in warmer temperatures limited somatic growth. Additionally, the slower growth in body depth and body depth:length of 2015 larvae suggests that this otolith scaling discrepancy is due to differences in larval condition (Ferron and Leggett, 1994). Somatic and otolith growth are often assumed to be proportional (i.e. coupled), but temperature and feeding can affect this relationship. In extreme situations (e.g., starvation), somatic growth and otolith growth can be decoupled, since the otolith incrementally grows even during periods of little to no somatic growth (Secor *et al.*, 1989). The resulting pattern of larger otoliths and relatively faster otolith growth rates in individuals with low somatic growth rates has been documented in suboptimal, warm temperature conditions (Mosegaard *et al.*, 1988), or poor feeding regimes (Secor and Dean, 1992; Strelcheck *et al.*, 2003). Since the contrasting temperature and prey regimes between the years sampled in our study appeared to have affected the proportionality of otolith and somatic growth for *T. atlanticus*, we were unable to examine variability in daily growth using otolith increment widths. This potential proxy issue (see also Hare and Cowen, 1995) is especially critical to consider when examining growth of fast growing larvae such as tunas and as environmental parameters increasingly exceed normal conditions.

Prey variability and larval tuna diet

Similar to prior studies on *Thunnus* spp. (Llopiz *et al.*, 2010, 2015; Tilley *et al.*, 2016), *T. atlanticus* larvae in both years consumed a mixed diet of nauplii (copepod, euphausiid, barnacle), copepods (calanoid and *Farranula* copepodites and adults), appendicularians, and smaller larval fishes. However, the proportion of each prey consumed varied between years according to their abundance in the environment. Variability in the plankton community had an effect on the diet of *T. atlanticus* larvae, as evident in the relative composition, magnitude, and size of prey consumed. In particular the abundance of calanoid copepods in the environment had the largest effect on the larval tuna diet. The biomass of calanoid copepods in the diet was significantly related to calanoids in the environment, demonstrating that tuna larvae fed opportunistically, consuming more calanoids as more were available in 2014. Larvae were not only consuming more calanoids, but the calanoids in their guts were 25% larger in 2014 than in 2015. As a result, *T. atlanticus* larvae had a 6x greater biomass of calanoid copepods in their gut in 2014 compared to 2015. Interestingly, this is the strongest reliance on calanoid copepods documented in the diet of *Thunnus* spp. larvae. Calanoid copepods are usually a more rare component of the larval tuna diet (Llopiz and Hobday, 2015) and typically occur in lower proportions in the gut than would be suggested by the environmental prey community (Young and Davis, 1990; Llopiz *et al.*, 2015). In 2015, when calanoid copepods were less abundant in the environment, larvae consumed a higher biomass of nauplii and appendicularians. This 2015 diet is more similar to diets previously described for *T. atlanticus* in the SOF (Llopiz *et al.*, 2010) and other Atlantic *Thunnus* species (Catalán *et al.*, 2011; Llopiz *et al.*, 2015; Tilley *et al.*, 2016). A high reliance on calanoid copepod prey appears to be beneficial for *T. atlanticus* growth and survival. Meanwhile, the typical nauplii/appendicularian diet combined with high temperatures in 2015 resulted in 30% lower growth, well below any previously documented growth rates for *Thunnus* spp. The mixed-prey diet consumed by the *Thunnus* tunas has been hypothesized to allow flexibility in feeding (Llopiz *et al.*, 2010, 2014), on a variable zooplankton community. Our results suggest that *T. atlanticus* are able to respond to a more productive food web by exploiting available prey.

T. atlanticus and *T. thynnus* in the SOF and GOM have a distinctive shift in diet with ontogeny from smaller, less mobile prey (nauplii), to increasingly larger, faster prey as they develop (copepodites, adult copepods ; Llopiz *et al.*, 2010, 2015; Tilley *et al.*, 2016). This

ontogenetic shift was evident in 2015 where small larvae (3-5 mm SL) consumed predominantly nauplii while larger (5-7 mm SL) larvae consumed similar proportions of *Farranula*, appendicularians, and nauplii. However this ontogenetic shift was less evident in 2014. Instead, calanoid copepods dominated the diet of all size classes, with ontogenetic shifts only in the size of calanoid copepods they consumed. As a result, 5-7 mm SL larvae in 2014 had double the gut biomass/fullness of the same size larvae in 2015.

Thunnus larvae also tend to incorporate more appendicularians in their diet prior to piscivory (Llopiz *et al.*, 2010, 2015; Catalán *et al.*, 2011). Llopiz *et al.* (2010) found appendicularians in the gut of ~50% of 5 - 7 mm SL and 80% of 7 - 11 mm SL *T. atlanticus* in the SOF. Our results reflect this pattern in 2015, but less so in 2014. *T. atlanticus* diets in 2015 included appendicularians in 53% of 5 - 7 mm SL larvae and 77% of 7 - 9 mm larvae, in contrast to only 18% (5 - 7 mm SL larvae) and 31% (7 - 9 mm larvae) in 2014. These findings suggest that where calanoid copepods are abundant and incorporated into the diet, a shift to feeding on appendicularians is not necessary prior to a transition to piscivory. Such robust feeding on calanoid copepods may facilitate the transition to piscivory: from the few >7 mm larvae sampled, there is a higher prevalence (75%) of piscivory in larvae in 2014 compared to 2015 (15%). Thus, the dietary composition of young larvae not only influences their immediate growth, but by influencing ontogenetic shifts in diet may ‘carry over’ to affect growth and survival of later stages.

Gut fullness was an important predictor of individual larval growth, although the modeled relationship suggests that prey composition is also a key aspect of the growth response. Individuals with higher gut fullness had faster growth, yet fast growth was also predicted at low levels of gut fullness. While this lower end of gut fullness was represented by relatively few data points, such a non-linear relationship suggests that there are more aspects of the diet than gut fullness influencing growth (e.g., composition, nutritional quality). The range of prey types consumed by individuals likely decouples this relationship between gut fullness and growth. Surprisingly, calanoid copepod density was not a significant predictor of *T. atlanticus* growth. We hypothesize that the disproportionate importance of calanoids in 2014 diets and lack thereof in 2015 rendered this variable not useful for predicting growth across feeding regimes.

Larval tunas in a high predator environment

Predators (chaetognaths, gelatinous zooplankton) were abundant in the SOF plankton community in both years. Predators had a significant effect on individual larval *T. atlanticus* growth, with predicted growth increasing over the range of predator densities across both years. This pattern suggests that predators are selectively consuming smaller, slower-growing larvae such that with increased predation pressure, apparent growth of survivors is faster. This pattern of selective mortality has been frequently hypothesized and documented in larval fishes (i.e. Growth-Survival Paradigm; Houde, 1987; Anderson, 1988), and is consistent with other scombrid larvae (Atlantic mackerel; Robert *et al.*, 2007), including a recent study examining growth of *K. pelamis* in the SOF (Gleiber *et al.*, 2020). Coupled with high water temperatures and poor feeding conditions, such selection against slower-growers likely exacerbates larval mortality rates. Additionally, while there were higher predator densities in 2014, the relatively lower abundances of their potential prey in 2015 (e.g., calanoids, larval fishes; Gleiber *et al.*, *in progress*, Chapter 4) resulted in a higher relative predation pressure and reduced larval survival of *T. atlanticus* larvae in 2015.

The prevalence of predators in the SOF environment, and the strong selective effect they have on larval growth contradicts prior assumptions about larval tuna habitats. Oligotrophic environments are hypothesized to be evolutionarily beneficial for larval tuna survival, offering low predation pressure (thus reduced predation mortality), with the tradeoff of potentially poor feeding conditions (Bakun and Broad, 2003; Ciannelli *et al.*, 2015). Yet, high feeding incidences in the SOF documented here and by others (Llopiz and Cowen, 2009; Llopiz *et al.*, 2010) suggests mortality from predation may be higher than starvation mortality in the region. Quantification of predators has previously been difficult since small (mm to cm) gelatinous zooplankton that are potential predators of larval fishes (Bailey and Houde, 1989; Purcell and Arai, 2001) are too small and fragile to effectively sample with conventional net sampling. *In situ* imaging now enables a comprehensive enumeration of the entire gelatinous zooplankton predator field a larval fish may experience, and recent studies suggest that small gelatinous predators maybe be more abundant in oligotrophic systems than previously thought (Luo *et al.*, 2014) and function as important selective predators of larval fishes (Sponaugle *et al.*, 2009; Gleiber *et al.*, 2020). Our results demonstrate that predation is a key aspect of the pelagic environment that tuna larvae experience, and should be

considered in predicting future larval success.

Implications with future changes

The simultaneous examination of larval growth and diet in the context of *in situ* environmental conditions revealed the central importance of temperature and the planktonic food web. Our sampling captured snapshots of contrasting food web and temperature regimes that likely reflect some of the environmental variability that will occur under future conditions in the Intra-Americas Sea (SOF/GOM) and other subtropical/tropical environments. Higher temperatures and decreased current flow/eddy activity are key regional climate-driven pressures on tunas, with implications such as metabolic stress and reduced productivity in spawning regions (Dell'Apa *et al.*, 2018). Offshore surface sea temperatures in the GOM have increased over the past 30 years (Karnauskas *et al.*, 2013), with unprecedented warming of 1 °C from 2010-2015 in the Florida Current (Domingues *et al.*, 2018). Future sea surface warming (2 - 3 °C by 2100) is predicted to also decrease current strength (Domingues *et al.*, 2018), reducing eddy activity in the region (Liu *et al.*, 2015) a key source of productivity (Lee *et al.*, 1991; Hitchcock *et al.*, 2005). Our findings suggest that with this predicted warming alone, thermally tolerant tuna larvae may be in water up to 5 °C above optimal growth conditions during the summer months when they are most abundant (Richardson *et al.*, 2010). However, the predicted reduction in current strength combined with increased stratification due to warming will likely further decrease productivity in an already nutrient deficient region (Behrenfeld *et al.*, 2006), resulting in changes in prey composition and biomass. It is difficult to predict specifically how the oligotrophic food web will change (Landry *et al.*, 2019), but shifts to a less efficient, microbial-dominated planktonic food web have been documented with increased temperature and stratification in other subtropical regions (Sheridan and Landry, 2004; Lavaniegos and Ohman, 2007; Steinberg *et al.*, 2012), and are predicted with future warming (Fu *et al.*, 2016). While larval tunas are adapted to feed in such oligotrophic environments (Llopiz and Hobday, 2015), our findings suggest that these prey conditions, combined with the higher mean temperatures, may be unable to support increased metabolic activity due to higher temperatures, resulting in decreased growth beyond the thermal optima, with serious implications for development and survival (Pörtner and Peck, 2010).

Top-down pressures on larvae are also important to consider, as any changes in the planktonic food web will cause variability in predator composition and biomass, including their abundance relative to potential prey. Little is known about how zooplankton predators of larval fishes (e.g., gelatinous zooplankton, chaetognaths; Bailey and Houde, 1989) will change in complex, oligotrophic food webs. Gelatinous zooplankton may be increasing in some regions (Brotz *et al.*, 2012), but global populations tend to fluctuate with decadal oscillations (Condon *et al.*, 2013), and complex food-web dynamics further complicate population dynamics (Stone *et al.*, 2019). We found faster growth among *T. atlanticus* larvae in higher predator densities (i.e. increased selective loss of slow-growing individuals), suggesting that larvae experiencing low growth in high temperature/low prey conditions might also experience heightened predation mortality. The direction of selective mortality in subtropical larval fishes can be variable, with evidence of selection both for and against slow growers (Sponaugle *et al.*, 2011; Shulzitski *et al.*, 2016; Gleiber *et al.*, 2020). Even if future directional changes in selective mortality and predator abundances are uncertain, relative predation pressure is likely to increase as lower-productivity food webs will also have reduced potential prey for predators.

Our study captured dramatic variability in environmental conditions and the associated effects on individual larval fish traits and trophic ecology, indicating food web dynamics are critical in fully understanding the implications of increased temperature for larval tuna survival. Current population models use physical characteristics of larval habitat to predict how changes in oceanographic conditions will influence tuna larvae (Rooker *et al.*, 2013; Muhling *et al.*, 2015; Cornic and Rooker, 2018). Yet, hypothesized changes in food web dynamics necessitate the inclusion of variable predator-prey interactions together with such changes to temperature and other physical variables (Hunsicker *et al.*, 2011; Landry *et al.*, 2019). Ecosystem-based approaches to fisheries management (Levin and Lubchenco, 2008) provide an opportunity to integrate biological data and predator-prey relationships of larvae (Sponaugle, 2010) with food web dynamics to build comprehensive understanding of how fish populations are replenished and will survive under future environmental conditions. Further understanding how larvae respond to multiple aspects of environmental variability is essential in exploring new fisheries and sustainably managing current populations in a changing ocean.

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Table 3.1. Mean temperature, *Thunnus atlanticus* density and % of larval fish assemblage, and environmental densities of prey (calanoid copepods) and predators (gelatinous zooplankton) sampled at 15 m in the Straits of Florida 2014 and 2015. Data given for all regions combined and individual cross-strait regions. Temperature and *T. atlanticus* were sampled with a MOCNESS net system, and prey/predators were sampled with the *In Situ* Ichthyoplankton Imaging System (ISIIS), thus sample sizes differ. Mean and range are reported for temperature. Mean and standard error reported for density variables. 2014 vs. 2015 all regions: Temperature ($p < 0.001$), *T. atlanticus* density ($p = 0.03$), *T. atlanticus* % larval fish assemblage ($p = 0.06$), calanoid copepod density ($p < 0.001$), predator density (<0.01). Wilcoxon rank sum test for temperature and *T. atlanticus*. Welch's 2-sample t-test for calanoids and predators.

Nets	2014				2015			
	All	West	Central	East	All	West	Central	East
Temperature (°C)	27.5 (26.7-28.3)	27.4 (26.7-28.3)	27.6 (27.4-27.8)	27.4 (27.2-27.6)	28.7 (28.4-29.0)	28.7 (28.5-28.9)	28.9 (28.8-29.0)	28.5 (28.4-28.7)
<i>Thunnus atlanticus</i> (ind. 1000m ⁻³)	56 (±11)	103 (±18)	15 (±4)	4 (±2)	6 (±<1)	6 (±1)	4 (±1)	8 (±2)
<i>Thunnus atlanticus</i> (% of all larval fishs)	19 (±2)	25 (±3)	22 (±4)	3 (±2)	12 (±1)	7 (±1)	12 (±3)	23 (±4)
n	64	32	16	16	64	40	8	16
ISIIS								
Prey (ind. m ⁻³) Calanoid copepods	31 (±3)	29 (±2)	39 (±10)	28 (±6)	13 (±1)	14 (±1)	13 (±<1)	10 (±2)
Predators (ind. m ⁻³) Gelatinous zooplankton	60 (±7)	81 (±7)	39 (±3)	38 (±9)	38 (±4)	48 (±4)	32 (±2)	16 (±2)
n	16	8	4	4	16	10	2	4

Table 3.2. Summary of linear regressions between *Thunnus atlanticus* standard length (SL; mm) vs. age (days), otolith radius (μm) vs. age, and otolith size-at-age residuals vs. SL-at-age residuals. N = 139 (2014) and 122 (2015). Excludes piscivorous and >7 mm SL larvae.

Relationship	Year	Slope	Intercept	r^2	p
SL vs. Age	2014	0.45	1.31	0.61	<0.001
	2015	0.35	1.93	0.67	<0.001
Radius vs. Age	2014	4.62	-9.63	0.75	<0.001
	2015	4.32	-5.85	0.75	<0.001
Otolith size-at-age residuals vs. SL-at-age residuals	2014	5.71	0	0.58	<0.001
	2015	8.88	0	0.73	<0.001

Table 3.3. Summary of ANCOVA (Type 1 SS ANOVA table) for *Thunnus atlanticus* standard length (SL) vs. age (days), otolith radius (μm) vs. age, otolith size-at-age residuals vs. SL-at-age residuals with/without temperature as a covariate. Full structural model is: $Y = \beta_0 + \beta_1 x_1 + \beta_2 x_2 + \beta_3 x_3 + \beta_4 (x_1 \cdot x_2) + e$, where Y is the response variable, x_1 through x_3 are explanatory variables, β_0 is the intercept, the other β s are all slopes, and e is the error. $N = 139$ (2014), 122 (2015). Excludes piscivorous and >7 mm SL larvae.

Response variables (Y)	Explanatory variables (x)	df	Mean square	F	p
Standard Length	Age (x_1)	1	121.7	534.05	<0.001
	Year (x_2)	1	1.1	4.86	0.028
	Age * Year ($x_1 \cdot x_2$)	1	1.7	7.30	0.007
	Error	257	0.2		
Standard Length	Age (x_1)	1	121.7	570.80	<0.001
	Year (x_2)	1	1.1	5.20	0.023
	Temp (covariate; x_3)	1	4.4	20.44	<0.001
	Age * Year ($x_1 \cdot x_2$)	1	1.3	6.06	0.015
	Error	256	0.2		
Otolith Radius	Age (x_1)	1	13945.1	794.47	<0.001
	Year (x_2)	1	132.9	7.57	0.006
	Age * Year ($x_1 \cdot x_2$)	1	15.0	0.85	0.357
	Error	257	17.6		
Otolith Radius	Age (x_1)	1	13945.1	828.79	<0.001
	Year (x_2)	1	132.9	7.90	0.005
	Temp (covariate; x_3)	1	210.8	12.53	<0.001
	Age * Year ($x_1 \cdot x_2$)	1	7.7	0.46	0.498
	Error	256	16.8		
Radius-at-age residuals	SL-at-age residuals (x_1)	1	2871.80	493.09	<0.001
	Year (x_2)	1	0.00	0.00	1
	SL-at-age residuals * Year ($x_1 \cdot x_2$)	1	142.46	24.46	<0.001
	Error	257	5.82		
Radius-at-age residuals	SL-at-age residuals (x_1)	1	2871.8	491.97	<0.001
	Year (x_2)	1	0.0	0.00	1
	Temp (covariate; x_3)	1	0.1	0.01	0.903
	SL-at-age residuals * Year ($x_1 \cdot x_2$)	1	144.8	24.81	<0.001
	Error	256	16.8		

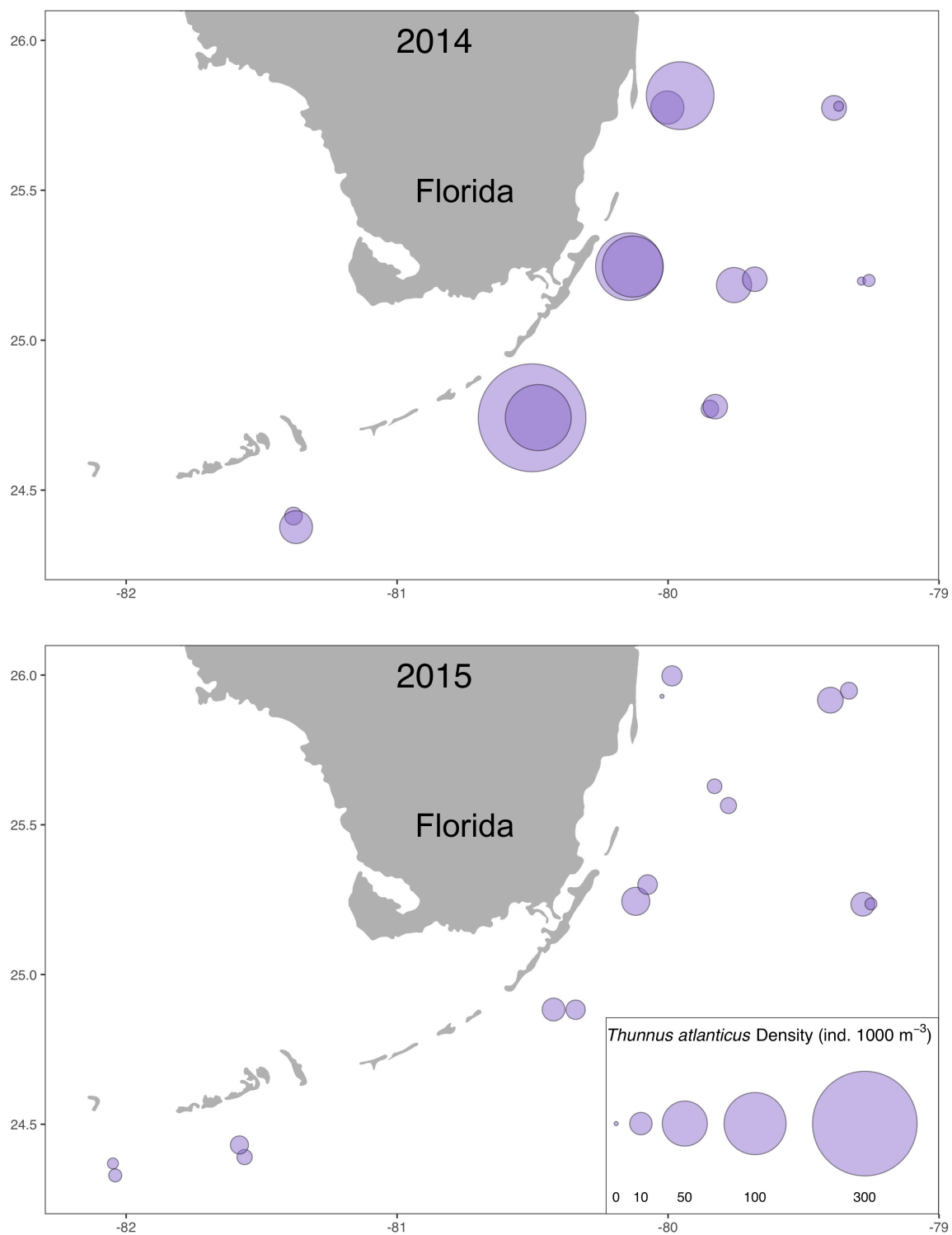


Figure 3.1. Mean densities of *Thunnus atlanticus* (individuals 1000m⁻³) sampled at stations in the Straits of Florida with a 4 m² MOCNESS in (top) May-June 2014 and (bottom) June 2015. Densities are means from nets in a tow (n = 4).

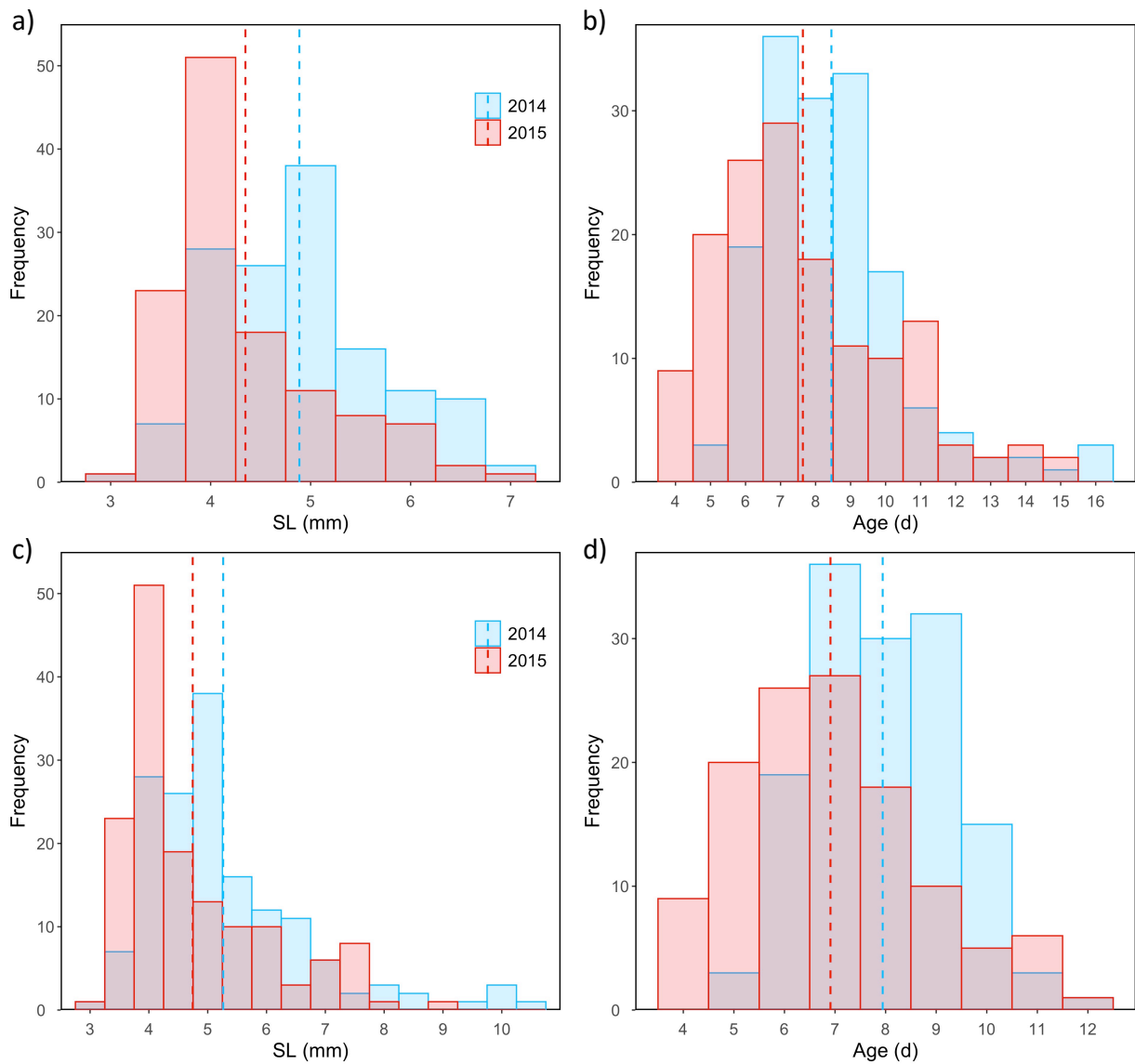
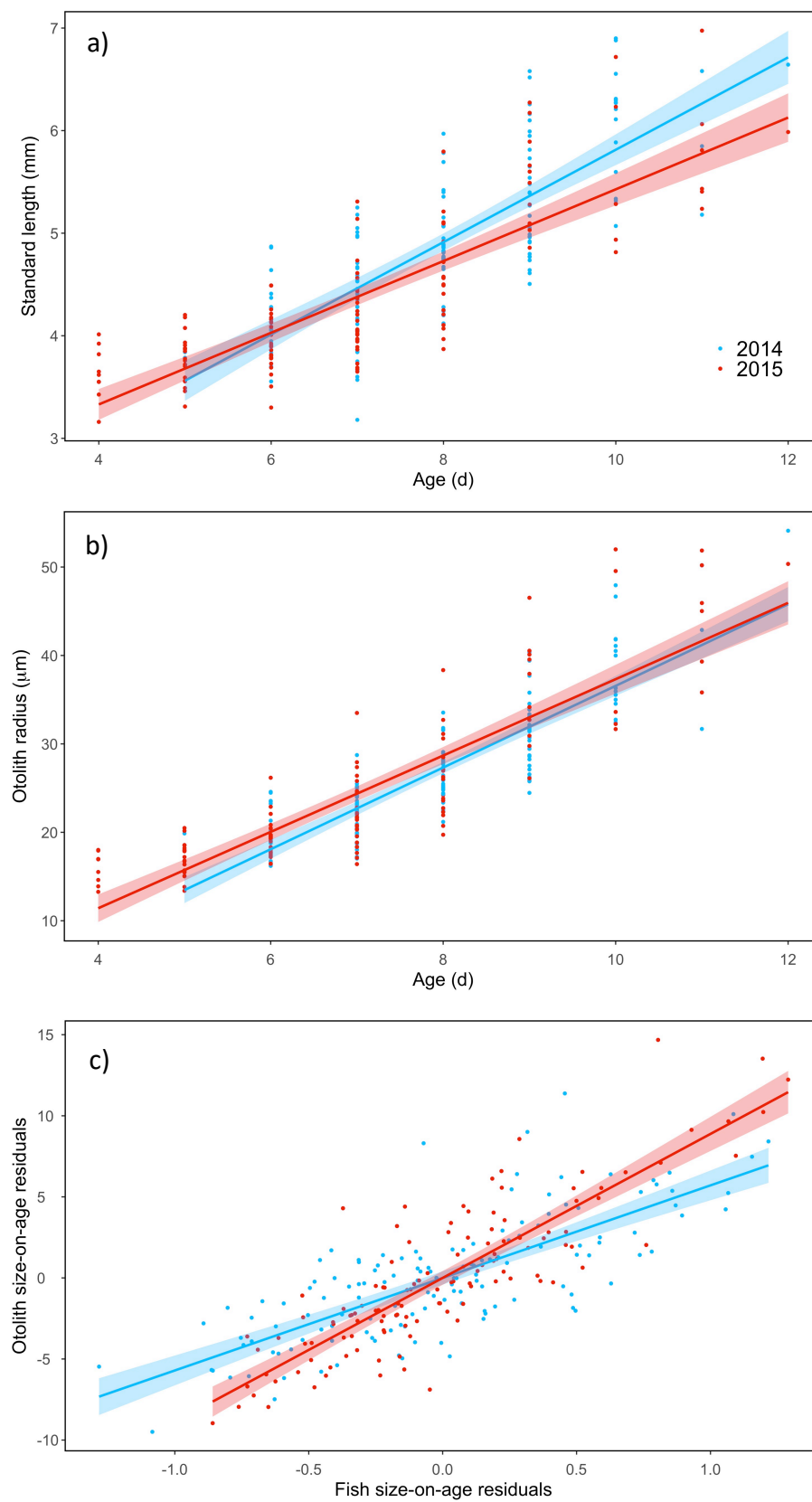


Figure 3.2. (a,c) Size (standard length; SL) class frequency, and (b,d) age class frequency of all *Thunnus atlanticus* larvae examined for otolith and gut content analyses. (a,b) Excludes piscivorous and >7 mm SL larvae; n = 139 (2014) and 122 (2015). (c,d) Includes piscivorous and >7 mm SL larvae; n = 157 (2014) and 146 (2015).

Figure. 3.3. *Thunnus atlanticus* standard length (SL; mm) vs. age (days), otolith radius (μm) vs. age, and otolith size-at-age residuals vs. SL-at-age residuals. N = 139 (2014) and 122 (2015). Excludes piscivorous and >7 mm SL larvae.

**Figure 3.3**

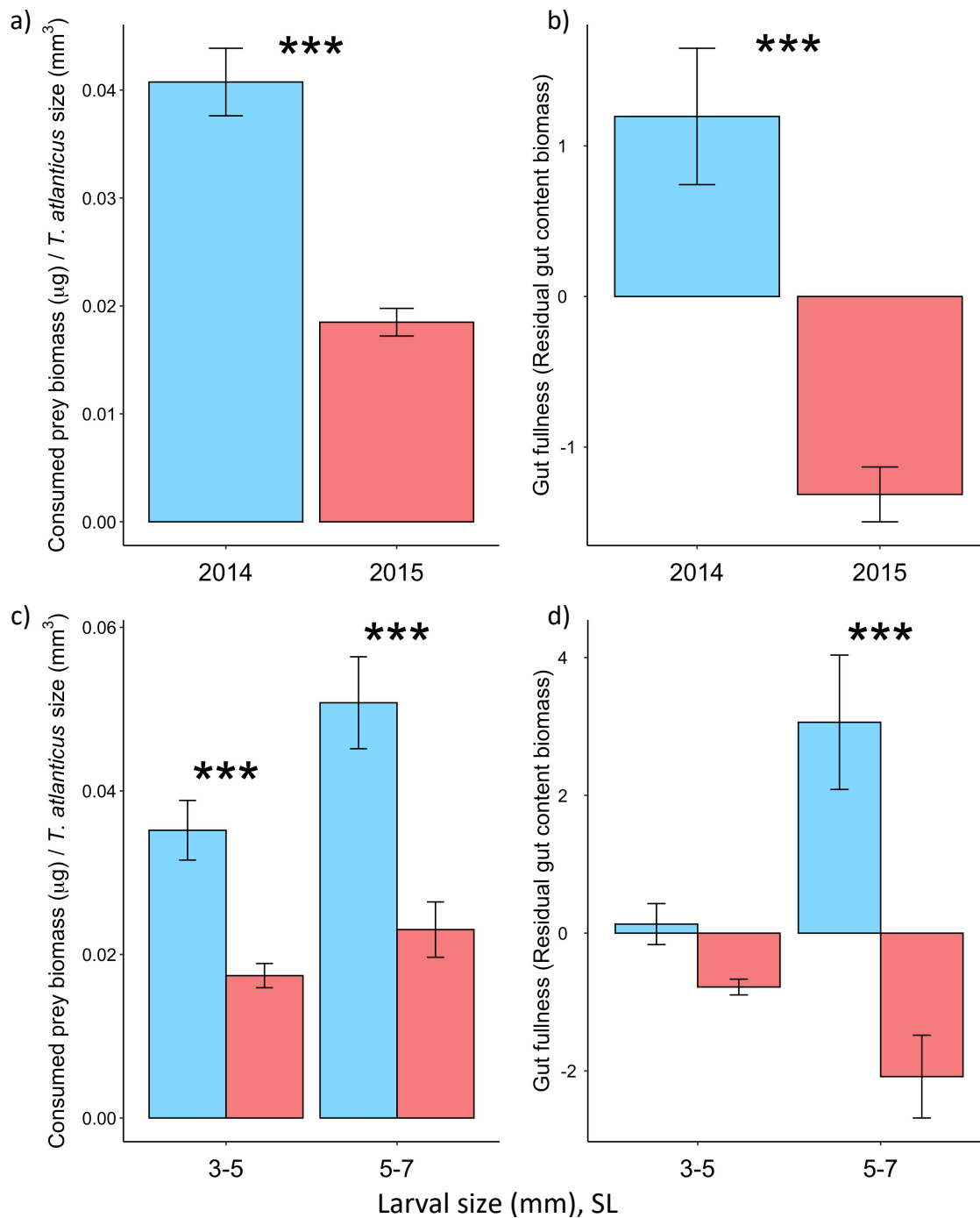


Figure 3.4. *Thunnus atlanticus* (a,c) mean standardized total consumed prey biomass (μg dry weight/*T. atlanticus* standard length [mm³]), and (b,d) mean gut fullness as residual gut content biomass (residuals of total consumed prey biomass vs. standard length) for (a,b) all larvae and (c, d) larvae by size class. 2014 (blue) vs. 2015 (red): Wilcoxon rank sum tests, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$. (a,b) All larvae: $n = 144$ (2014) and 131 (2015). (c,d) 3-5 mm SL larvae: $n = 84$ (2014) and 93 (2015). 5-7 mm SL larvae: $n = 56$ (2014) and 27 (2015). Excludes piscivorous larvae.

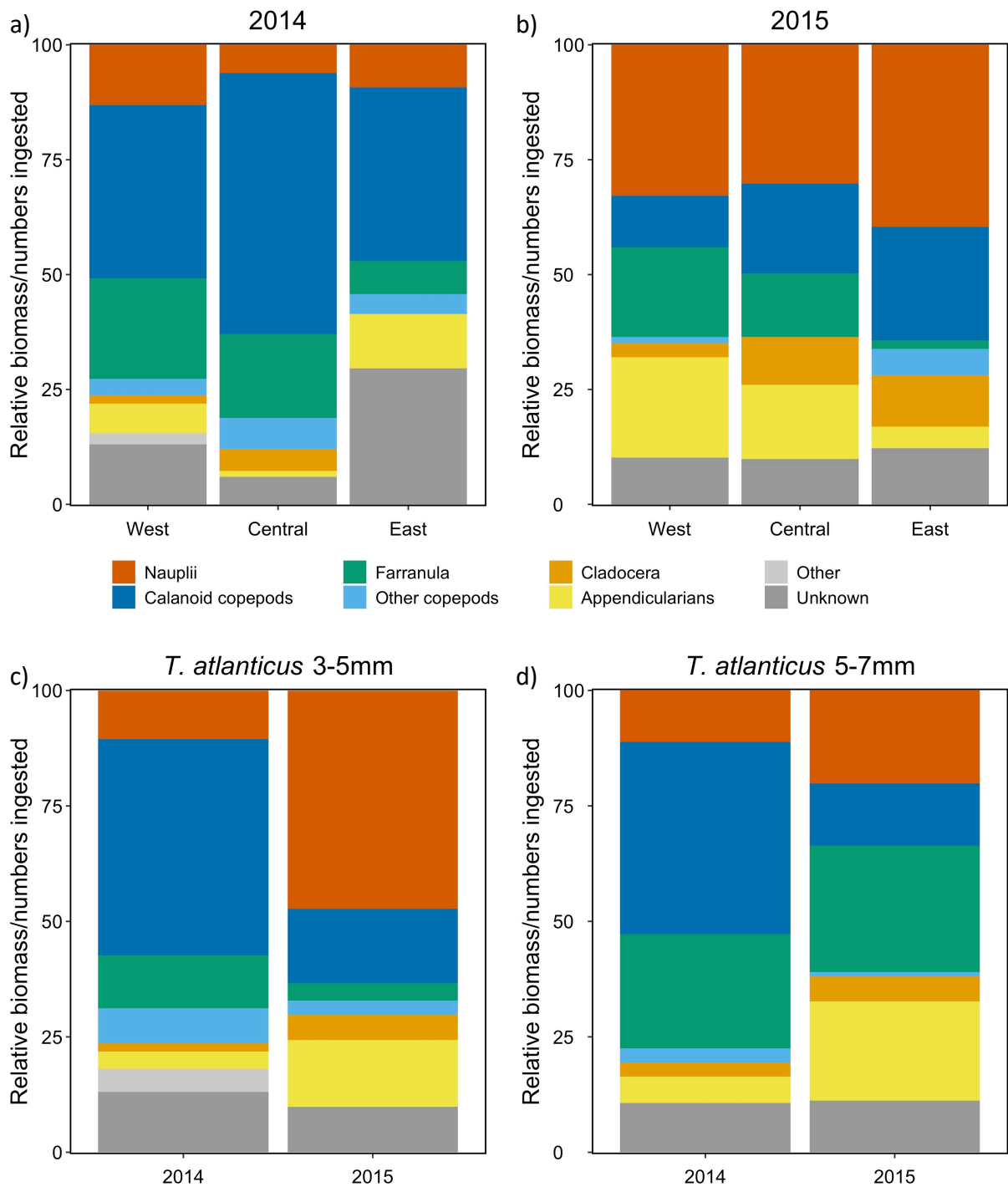


Figure 3.5. *Thunnus atlanticus* ingested biomass (μg dry weight) of prey groups, presented as proportion of all gut contents for (a, b) all larvae in Straits of Florida cross-strait regions in 2014 and 2015, (c) 3-5 mm SL larvae in 2014 vs. 2015, and (d) 5-7 mm SL larvae in 2014 vs. 2014. Excludes piscivorous and >7 mm SL larvae.

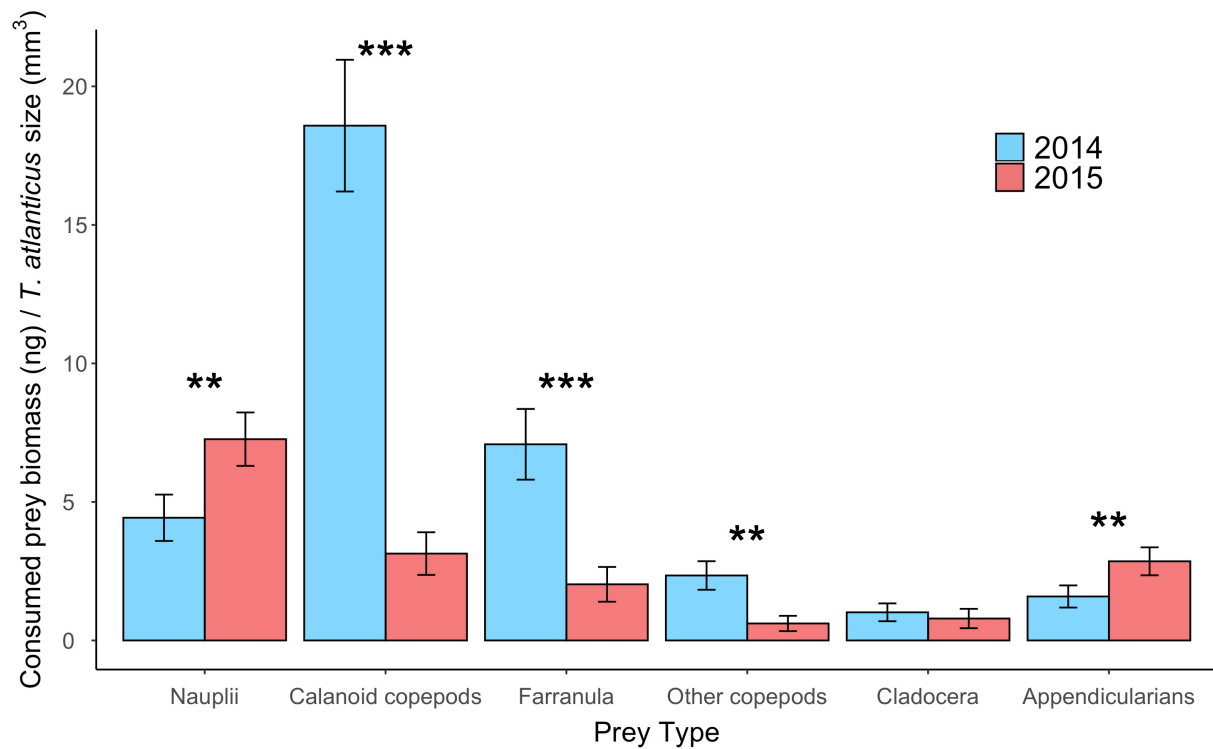


Figure 3.6. *Thunnus atlanticus* mean standardized consumed prey biomass (μg dry weight/*T. atlanticus* standard length [mm^3]) per individual prey group. 2014 vs. 2015: Wilcoxon rank sum, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$. $N = 836$ (2014), 601 (2015). Excludes piscivorous and >7 mm SL larvae.

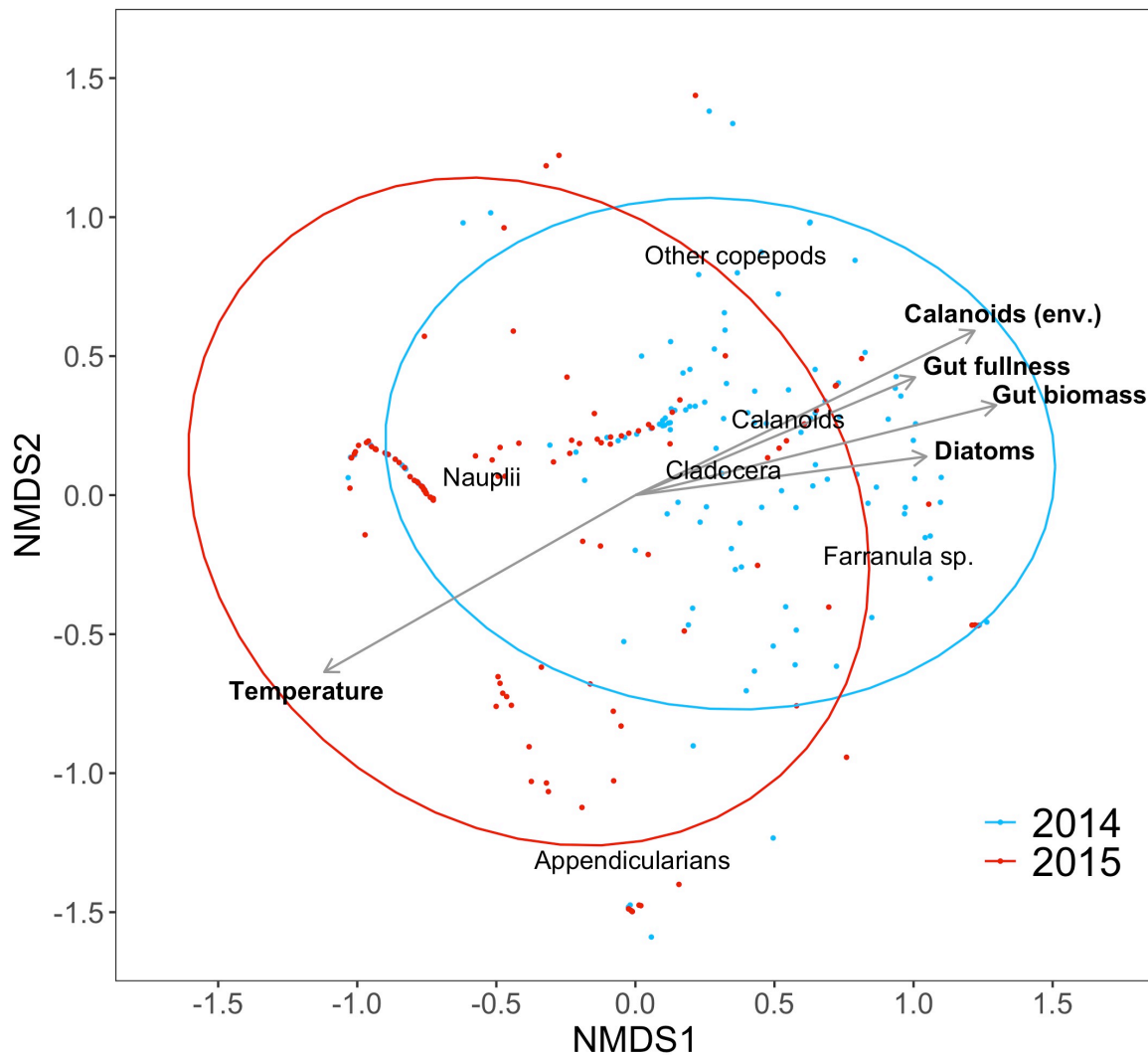


Figure 3.7. Non-metric multidimensional scaling of standardized consumed prey biomass (μg dry weight/*T. atlanticus* standard length [mm^3]) of prey groups in 2014 ($n = 124$) vs. 2015 ($n = 114$). Points represent individual larval fish. Regular text represents centroid for each prey group. Arrows represent correlations between ordination and explanatory/response variables (bold text), arrow direction is direction of correlation, and arrow length is magnitude of correlation. Only correlations $r^2 = >0.1$ shown. Calanoids (env.) = environmental calanoid copepod density. Stress = 0.11 – a measure of concordance between the multivariate data and this three-dimensional representation. Excludes piscivorous and >7 mm SL larvae.

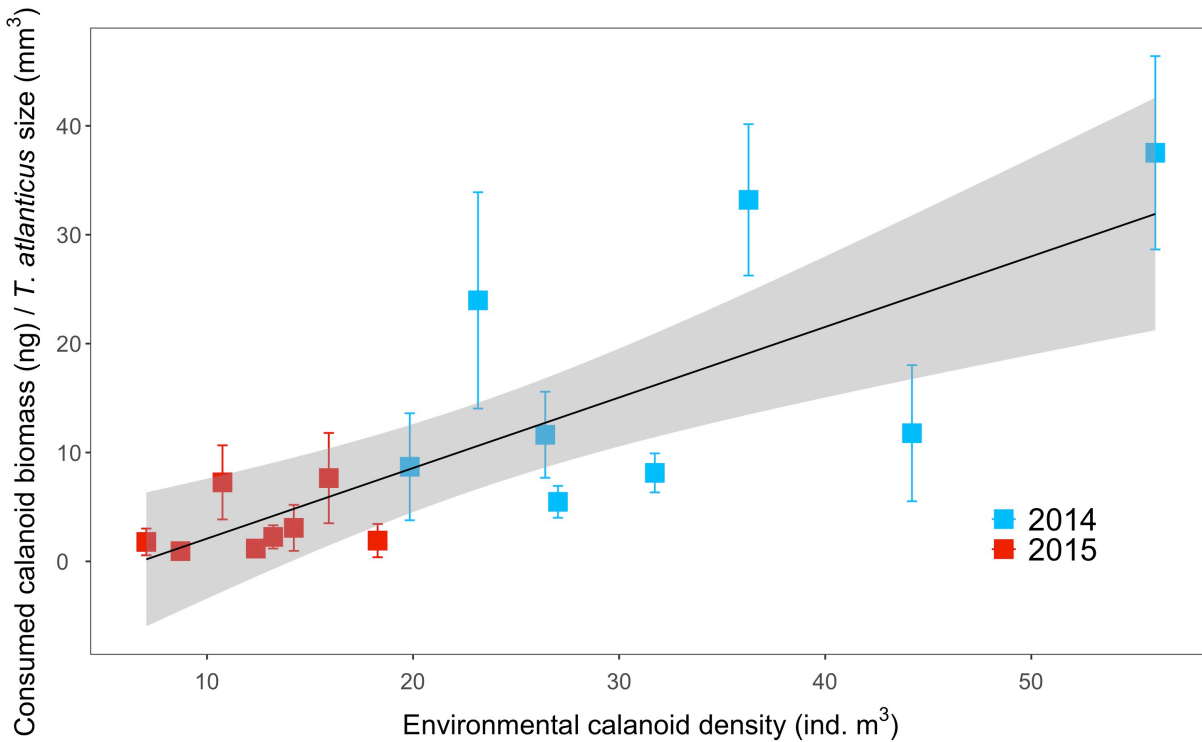


Figure 3.8. Linear relationship between *Thunnus atlanticus* mean standardized consumed calanoid copepods biomass (μg dry weight/*T. atlanticus* standard length [mm^3]) and environmental calanoid copepod density (ind. m^{-3}). Consumed calanoid copepods biomass is mean from *T. atlanticus* sampled in two replicate MOCNESS tows at each station ($n = 5 - 33$ individuals per station). Environmental calanoid copepod densities are mean of 1 m binned densities from both ISIIS half-transects ($n = 7782 - 22934$). $r^2 = 0.58$, $p < 0.001$, $n = 16$. Excludes piscivorous larvae.

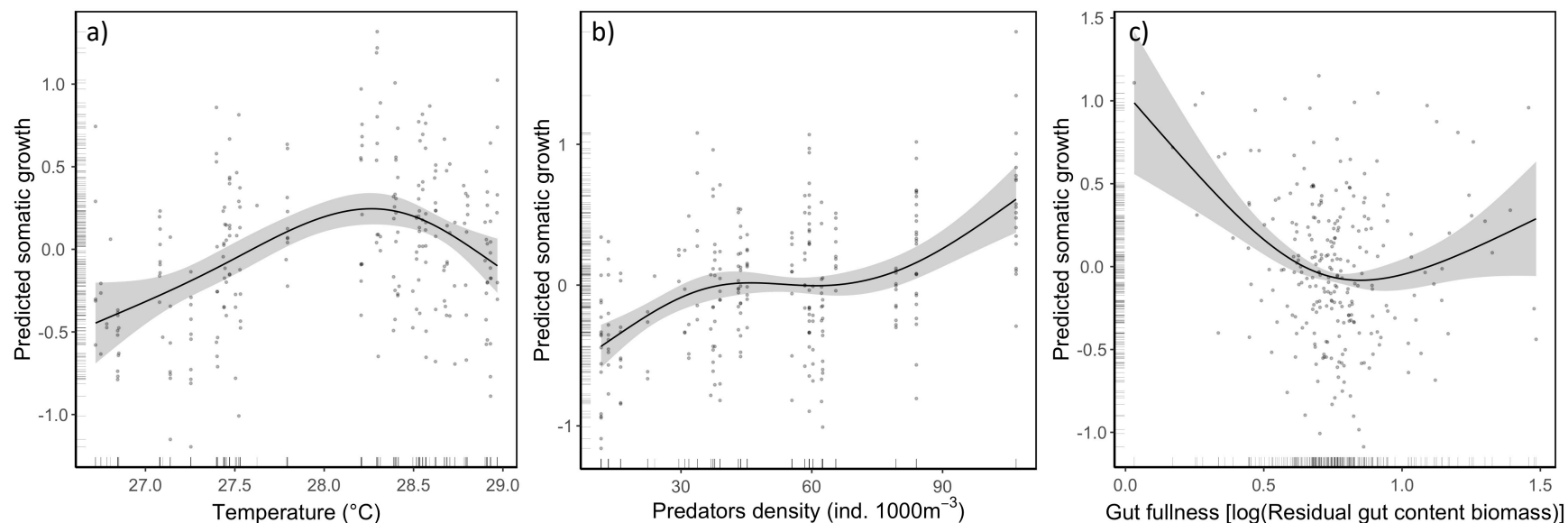


Figure 3.9. Model results of the partial effect of (a) temperature, (b) predator density, and (c) gut fullness (residual gut content biomass; log transformed) on individual somatic growth (standard length-at-age residuals) of *Thunnus atlanticus*. Model AIC = 292.09, deviance explained = 27.3%. Fitted lines, 95% confidence intervals (grey shaded areas) and partial residuals (dots) are shown; whiskers on axes are field observations for that covariate. N = 251. Excludes piscivorous and >7 mm SL larvae.

CHAPTER 4: SCOPE OF VARIABILITY IN MARINE LARVAL FISH ASSEMBLAGES AND FOOD WEBS OVER A CONTINENTAL TO OCEANIC GRADIENT

Survival of marine fishes during their early life history stage is tightly related to prey availability and predation pressure, both of which can vary over a range of spatial and temporal scales. As global climate change introduces increasingly frequent environmental changes there is uncertainty about how larval fish assemblages from near- to offshore in low-latitude systems respond to variability in planktonic food webs. We integrated *in situ* imaging with biological sampling to examine how interannual variability in the planktonic food web may influence larval fishes through predator-prey relationships in two oceanographic regions different in their proximity to a major land mass and nutrient enrichment: the upwelling influenced continental (western) versus more oligotrophic oceanic (offshore) regions associated with a major western boundary current (the Florida Current). Early-summer sampling in two years (June 2014, 2015) captured contrasting food web conditions, illustrating how larval fishes in continental compared to oceanic regions co-vary with prey conditions. The larval fish assemblage in the continental region was tightly linked to major interannual fluctuations in prey, especially for key fish species in the region (e.g., tunas, flatfishes, reef fishes). Overall, densities of larval fishes were 3.5x greater in high-prey relative to low-prey conditions. In contrast, the composition and abundance of fish larvae in the oligotrophic oceanic region were more consistent. Larvae abundant in these waters were species with more flexible growth-related traits suggesting adaptations to a poor prey environment. Strong predation pressure by gelatinous zooplankton in the continental region may compound the effects of variable prey, as larval fish in the poor-prey year experienced similar predation pressure as in high-prey conditions. We hypothesize that continental larval fishes require higher prey conditions to survive, making them sensitive to food web variability, while oceanic larvae are more resilient to low prey conditions. Considering climate change and human land-use are disproportionately impacting coastal marine systems, larvae in nearshore regions may be threatened by future changes.

4.1 Introduction

Climate change is increasing environmental variability on our planet, with implications for ecological interactions across systems. Marine fish populations are sensitive to changes in planktonic food webs due to tight trophic relationships that can have match and mismatch consequences (Beaugrand et al. 2002, Polovina 2005), especially for early life stages. In pelagic ecosystems, shifts in communities at all trophic levels (Beaugrand et al. 2003, Cavole et al. 2016) are associated with changes in the magnitude, timing, and composition of planktonic communities (Hays et al. 2005, Richardson 2008). Larval fish survival during the pelagic phase, which can last from weeks to months, depends on the ability of larvae to find food and avoid predation. Their success in doing so can directly impact patterns of recruitment and adult population dynamics (Ringuette et al. 2002, Castonguay et al. 2008, Huebert et al. 2018).

Larval fishes are connected to planktonic food webs through both their prey and predators. Enhanced prey availability has been consistently linked to greater larval feeding success which generally translates to faster growth rates and higher condition (Dower et al. 2009, Sponaugle et al. 2009, Pepin et al. 2014). Favorable larval growth and condition increases the probability of larval survival by reducing vulnerability to gape-limited predation through larger sizes and shorter larval stage durations (Miller et al. 1988, Hare & Cowen 1997, Satoh et al. 2013) and can influence juvenile survivorship through condition at metamorphosis/settlement (Searcy & Sponaugle 2001, Hamilton 2008). Yet favorable feeding conditions can be risky scenarios for larvae due to a high co-occurrence of predators (Purcell & Arai 2001, Garrison et al. 2002), as both are frequently concentrated by physical oceanographic processes that enhance biological productivity (Mann & Lazier 2013, McGillicuddy 2016). Predators influence larval survivorship via mortality that is often selective (Takasuka et al. 2003), with predators selectively consuming smaller, slower-growing individuals (Anderson 1988, Hare & Cowen 1997), although the opposite direction of selective mortality has also been documented (Sponaugle et al. 2011, Takasuka et al. 2017). Examining predation pressure on larval fishes has been difficult due to sampling limitations, but *in situ* imaging now enables the quantification of the mesozooplankton predator field revealing frequent fine-scale overlap of larval fishes, their prey, and predators with implications for larval survival (Axler 2019, Schmid et al. 2020). Considering the tight

relationship between zooplankton and larval fishes, understanding how variability in key prey and predators influences larval fishes is critical to predicting the demographic consequences of climate change for marine fish populations.

The response of planktonic food webs to climate change effects in warm, oligotrophic oceans is unknown. Models generally predict that global warming will enhance stratification, further reducing the delivery of deep-water nutrients to surface waters and favoring microbial loop processes via food webs with lower productivity and small-sized organisms (e.g., bacteria, protists, flagellates; Behrenfeld et al. 2006, Fu et al. 2016). However, the few long-term studies at low-latitudes suggest highly variable responses, with documented decreases (Roemmich & McGowan 1995, Lavaniegos & Ohman 2007) and increases (Sheridan & Landry 2004, Steinberg et al. 2012) in primary and secondary production. Additionally, dynamic physical oceanographic features (e.g., currents, upwelling, eddies) in coastal pelagic environments can introduce spatial heterogeneity with regionally or locally enhanced biological productivity (McGillicuddy et al. 1998, Hitchcock et al. 2005, Hernández-León et al. 2007). Thus, while warm-water, oligotrophic environments are often considered nutritionally constraining, nearshore regions can have elevated abundances of phytoplankton, zooplankton and ichthyoplankton (Fernández-Álamo & Färber-Lorda 2006, Ignacio Vilchis et al. 2009, Llopiz et al. 2010), leading to important fisheries production (Pauly & Christensen 1995).

In subtropical and tropical oceans, oceanographic processes in nearshore regions introduce nutrients that enrich prey conditions and fuel the food web. Larval fishes associated productive oceanographic features can experience faster growth, better biochemical condition (Nakata et al. 2000, Sponaugle et al. 2009, Shulzitski et al. 2015), and higher survival (Logerwell & Smith 2001, Shulzitski et al. 2016). Additionally, many of these physical processes (e.g., eddies, fronts) can serve as retention mechanisms by entraining coastal waters and associated larvae, or enhancing larval delivery to juvenile habitats (Richardson et al. 2009, Satoh 2010, Condie et al. 2011, Sponaugle et al. 2012). Most studies of larval fish assemblages in coastal oligotrophic systems have focused on patterns of proximity to adult spawning locations, larval transport, retention, and association with oceanographic structure (Leis & Miller 1976, Borges et al. 2007, Shulzitski et al. 2018). In comparison, we know relatively little about how larval fish assemblages distributed at different distances from

continental land masses may respond to variability in plankton food web productivity. Over broad (1000s km) spatial scales, distinct larval fish assemblages associated with coastal-upwelling versus offshore oligotrophic regions of the tropical eastern Pacific responded differently to long-term variability in productivity (and likely prey) associated with the El Niño-Southern Oscillation (Ignacio Vilchis et al. 2009). Strong variability in the upwelling assemblage in contrast to a more stable oligotrophic assemblage was hypothesized to be due to stronger resilience to warm water-low productivity conditions by larval fish in extremely oligotrophic waters. Considering the importance of high productivity coastal regions for larval fishes, and subsequently fisheries production, understanding how larvae respond to environmental variability through changes in prey availability or exposure to predators is critical to predicting the consequences of future climate change scenarios.

The Straits of Florida (SOF) is a model system for examining the response of continental to oceanic larval fish assemblages to low latitude environmental variability. The SOF is a largely oligotrophic region with dynamic nearshore processes that enhance productivity and contribute to a high abundance and diversity of larval coastal (coral reef), mesopelagic, and pelagic fishes (Limouzy-Paris et al. 1994, Richardson et al. 2010, Shulzitski et al. 2018). The major western boundary current, the Florida Current dominates flow through the region driving physical dynamics and enhancing delivery of larval fishes (Cowen et al. 2003, Sponaugle et al. 2005). The Florida Current is stronger along the continental (western) edge of the SOF and frontal meandering generates cyclonic eddies that move through the system (Lee et al. 1991, Hitchcock et al. 2005). Together with nearshore runoff and coastal upwelling, these recirculating features result in regional gradients in nutrients, primary productivity, zooplankton, and larval fishes, with generally higher values in western continental waters compared to eastern oceanic waters (Lee et al. 1991, Llopiz et al. 2010, Richardson et al. 2010). These elevated prey conditions typically enhance larval fish feeding, growth, and condition: larvae of coral reef and pelagic fishes have higher gut fullness and growth rates in the continental region (Sponaugle et al. 2009, 2010, Llopiz et al. 2010) and are associated with transient eddies (Shulzitski et al. 2015), likely due to higher prey availability (Schmid et al. 2020). Not only does this faster growth enhance settlement to the reef (Shulzitski et al. 2016), but it ‘carries over’ and leads to increased survival of recruited juveniles (Grorud-Colvert & Sponaugle 2011). While our understanding of

predation is limited, predator abundances are hypothesized to be greater in the productive continental region (Sponaugle et al. 2009). These predators prey selectively on larval reef fishes and tunas (Sponaugle et al. 2011, D'Alessandro et al. 2013, Shulzitski et al. 2016), with the strength of selection against particular traits increasing with predator densities (Gleiber et al. *in progress*, 2020, Chapter 2, Chapter 3). This accumulated wealth of knowledge on larval fishes in the SOF sets the stage for an examination of how prey and predator conditions may influence larval fish assemblages.

We coupled *in situ* imaging with biological sampling to examine how variability in the planktonic food web influences continental versus oceanic larval fishes through predator-prey relationships. Our sampling captured a snapshot of contrasting conditions during the peak recruitment season of two years (2014, 2015) in this oligotrophic system. Low calanoid copepod abundances coinciding with high temperatures in 2015 had significant feeding, growth, and survival consequences for an abundant larval tuna in the region, *Thunnus atlanticus* (blackfin tuna; Gleiber et al. *in progress*, Chapter 3). We hypothesized that since other fish species would have experienced similar conditions during our sampling efforts, there may have been major changes in larval fish assemblage structures. Further, due to the known SOF cross-strait gradient in productivity and prey availability, as well as potential predator abundances, we hypothesized that larval fish assemblages in continental and oceanic regions may differ in their response to environmental variability. Nearshore marine systems, including the SOF, are experiencing more frequent fluctuations in environmental conditions due to anthropogenic climate change (e.g., currents, temperature, storms; Wu et al. 2012, Liu et al. 2015, Domingues et al. 2018) and proximity to human land-use impacts (e.g., nutrient loading, Halpern et al. 2008, Rabalais et al. 2009). Gaining a better understanding of how different larval fish assemblages are affected by environmental changes is key to understanding how low-latitude marine fish populations will be influenced by future changes in marine systems.

4.2 Methods

4.2.1. Plankton and larval fish sampling

To examine how larval fish assemblages are related to variability in the plankton community, we collected *in situ* plankton (zooplankton and ichthyoplankton) imagery

together with biological samples of larval fishes. Sampling was conducted on two cruises in the SOF aboard the R/V *FG Walton Smith* from 28 May - 6 June, 2014 and 18 - 26 June, 2015. Each year, we sampled eight stations encompassing the cross-strait (continental, oceanic) variability in the SOF (Fig. 4.1). Continental station sampling was <30 kilometers offshore of the Florida/Florida Keys coastline, within the Florida Current; oceanic sampling was >30 kilometers offshore of mainland United States. At each station we used the *In Situ* Ichthyoplankton Imaging System (*ISIIS*; Cowen & Guigand 2008) to measure plankton distributions and physical environmental conditions. The *ISIIS* imaged the water column at $\sim 140 \text{ L s}^{-1}$ with a pixel resolution of 55-68 μm , imaging particles and plankton from $\sim 200 \mu\text{m}$ to 13 cm. Sensors on *ISIIS* simultaneously measured conductivity, temperature, depth, and chlorophyll *a* (chl *a*). The large image frame, with a 50 cm depth of field, allows for imaging of a variety of plankton types including fragile gelatinous zooplankton that can be important predators of larval fishes [e.g., siphonophores, medusae, ctenophores; Purcell & Arai (2001) and references therein]. We imaged plankton at each station along two 8-16 km transects at depths of 15 m and 30 m (Fig. 4.1). We additionally characterized the local physical environmental conditions of the water column with transects where the *ISIIS* was undulated from 0 – 100 m in 2014, and 0 – 40 m in 2015.

Larval fishes were collected at each station using a Multiple Opening/Closing Net and Environmental Sensing System (MOCNESS) with a 4 m² opening and 1-mm mesh nets. The MOCNESS is equipped with sensors that simultaneously measured conductivity, temperature, and depth. To capture larval fishes on a fine horizontal spatial scale, we sequentially fired each MOCNESS net every $\sim 125 \text{ m}$ along single depth (15 m and 30 m) transects. Traveling at a speed of 1 m s^{-1} each MOCNESS net sampled $\sim 500 \text{ m}^3$. We fired a total of five nets per tow; one net was open from the surface to depth (net zero; not included in analysis), and the four remaining nets sampled sequentially at the same depth. At every station, this fine-scale net sampling was repeated with two complete MOCNESS tows (depth determined in randomized order), yielding eight replicate nets per depth (Fig. 4.1). Once onboard, the nets were rinsed with seawater and the contents of each cod end preserved in 95% ethanol. In the laboratory, all larval fishes were separated out of the samples and identified to the lowest possible taxonomic grouping following Richards (2005), and further grouped based on adult habitat (Shulzitski et al. 2018). Densities (ind. 1000 m^{-3}) of larval fish

species (or lowest taxonomic grouping) were calculated by dividing counts from each net by the volume of water filtered through the net. All larvae of select abundant species and families were measured for standard length using a Leica dissecting microscope with camera and image analysis software (Image-Pro Plus 7.0 and Premier 9.3).

To ensure all *ISIIS* and MOCNESS transects sampled the same water mass, transects and tows at each depth were centered on a GPS Lagrangian drifter at 10 m depth that moved with the Florida Current (Fig. 4.1). Each replicate MOCNESS tow (four nets) per depth at each station corresponded with one half of the *ISIIS* transects (half-transects = 4-8 km). All sampling occurred during daylight hours, approx. 0600 – 1800 to minimize diel effects.

4.2.2. *ISIIS* image analysis

An automated algorithm was used to sort zooplankton taxa into image classes based on taxonomy and morphology. *ISIIS* raw image files were flat-fielded and segmented images classified using a Sparse Convolutional Neural Network (Graham 2014), following methods in Luo et al. (2018). The algorithm was implemented with training sets comprised of 124 classes representing 40 broader groups (e.g., classes of different shapes or orientations of chaetognaths combined into a single ‘chaetognath’ group; Schmid et al. 2020). Automated image classifications were corrected for mis-classifications with scaling factors determined by confusion matrices which consisted of a random subset of images from each year (0.005% of all ~ 100 million classified images) that were manually classified (Luo et al. 2018, Schmid et al. 2020). Physical data and biological counts from image analyses were synchronized using the sample time stamp and quantified by 1-m horizontal distance bins. Corrected counts (see above) of organisms in each classification group were used to estimate plankton densities (ind. m⁻³) based on the volume of water sampled by *ISIIS* in each 1-m horizontal bin. Mean plankton densities for each classified group were calculated for each half-transect as the mean of densities in 1-m horizontal distance bins (ind. m⁻³; n = 3341 - 12579). *ISIIS* densities of some taxonomically similar classification groups were further combined (e.g., calyphoran and physonect siphonophores combined as ‘siphonophores’), and non-organismal groups (‘detritus’, ‘fecal pellet’, ‘artifact’) excluded. Copepod groups were not further combined, since larval fishes in the SOF are known to specifically feed on different copepod orders (Llopiz & Cowen 2009, Llopiz et al. 2010, D’Alessandro et al. 2011).

Copepod groups were ‘calanoid copepods’, ‘oithona copepods’ and ‘other copepods’ (a morphological classification including copepods without visible antennae, e.g. Corycaeidae; Gleiber et al. 2020). *ISIIS* image resolution is capable of sampling larger-sized phytoplankton; therefore diatom, trichodesmium, and protist densities were included in our analysis, although we recognize they do not include smaller individuals that comprise the majority of the assemblage in oligotrophic environments (Azam et al. 1983).

Water column profiles from *ISIIS* undulation tows were used to examine variability in regional vertical structure of physical environmental variables. *ISIIS*-derived environmental data for each undulation transect were kriged (R package ‘gstat’; Gräler & Heuvelink 2016) onto a grid spanning the length of each transect, at 1-m vertical and 500-m horizontal resolution (Schmid et al. 2020). *ISIIS* undulation data were used to calculate mixed layer depth (Kara et al. 2000) in both years from 0 - 40 m, as sampling in 2015 was restricted to 40 m depth.

4.2.3. Plankton and larval fish multivariate analyses

We used non-metric multidimensional scaling (NMDS) to visualize differences in the multivariate structure of the plankton and larval fish assemblages and how they were related to environmental variables. Separate analyses were conducted for plankton groups sampled by *ISIIS* and larval fish groups sampled by MOCNESS. Biological samples were used for fishes because they enabled a higher taxonomic resolution for this group than *ISIIS*. Each NMDS was performed on a Bray-Curtis dissimilarity matrix from the mean density of plankton groups (ind. m⁻³) in *ISIIS* half-transects or larval fish groups (ind. 1000 m⁻³) in replicate net tows. Larval fish densities were log(x + 1) transformed to reduce skewness; transformation was not necessary for plankton densities. Larval fishes used were those present in ≥25% of replicate tows. Mantel tests were used to confirm that the ordination did not significantly change with the removal of rare taxa. Plankton groups were present in all half-transects; therefore no rare taxa removal was necessary for plankton NMDS analyses. To examine the potential physical drivers of assemblage structure, the final ordination (lowest stress solution) was overlaid with explanatory variables using a biplot to show linear relationships with ordination axes. Explanatory physical environmental variables included in each NMDS were temperature, salinity, mixed layer depth (see above), and chl *a*.

Temperature, salinity, and chl *a* were calculated as the mean of the respective half-transects (plankton) or replicate tows (larval fishes). Potential prey and predators of larval fishes, as well as phytoplankton groups, were also included as explanatory variables in the larval fish NMDS analyses. These were log ($x+1$) transformed mean densities of abundant groups of prey (calanoid copepods, *Oithona* copepods, other copepods, appendicularians, pteropods), predators (chaetognaths, ctenophores, hydromedusae, siphonophores, other cnidarians), and phytoplankton (diatoms, trichodesmium, protists) from half-transects associated with each replicate tow. The minimum correlation coefficient for an explanatory variable to be included was $r^2 = 0.2$.

To test whether differences in the plankton or larval fish assemblage were greater among regions (continental vs. oceanic) or years (2014 vs. 2015), we conducted separate permutational multivariate analysis of variance (perMANOVA; Anderson 2001). perMANOVA used Bray-Curtis dissimilarity matrices and significance was tested using permutation. Since perMANOVA revealed that regional assemblage differences were greater than interannual differences for both plankton and larval fishes (Table 4.1), we also performed separate NMDS within each region, as described above. Plankton NMDS included 19 groups from 64 (all regions), 36 (continental), or 28 (oceanic) half-transects. Larval fish NMDS included 43 (all regions), 45 (continental), or 35 (oceanic) larval fish taxa from replicate tows corresponding to each half-transect ($n = 64, 36, \text{ or } 28$, respectively). We performed all multivariate analyses in R software (Version 3.6.0; R Core Team, 2019) using the *vegan* package (Oksanen et al. 2013). We note that assemblage differences based on depth were not included as prior analyses revealed similarities among larvae sampled at these shallower depths (Shulzitski et al. 2018).

We examined the regional and interannual variability of abundant groups of zooplankton prey and predators of larval fishes (see above) and phytoplankton with multiple linear regressions. Separate regression analyses were conducted for each group, with group densities from *ISIIS* half-transects ($n = 64$) as the response variable and *year* (2014, 2015) and *region* (continental, oceanic) as fixed categorical covariates. We included a *year x region* interaction to account for the possibility of regional effect depending on year (or vice versa). Full (interactive) and reduced models were compared using an extra sum of squares F-test (Chambers 1992), and the reduced model was used if the interaction was not significant.

Densities were $\log(x + 1)$ transformed to deal with zero-inflated distributions and model diagnostics were examined for outliers. Suspected influential observations were omitted; if results of the analysis changed when outliers were removed both results are noted.

To further examine the response of the larval fish assemblage to interannual variability within region, we compared densities of individual larval fish taxa between years within each region using Wilcoxon rank tests as larval fish densities were positively skewed. Analyses were conducted on larval fish taxa that comprised $>1\%$ of the larval fish assemblage.

4.2.4. Trophic relationships

Taxon-specific larval fish-prey relationships

We used linear regressions to examine how larval fish taxa densities (from replicate MOCNESS tows) were related to their potential prey (from respective *ISIIS* half-transects). All densities were $\log(x + 1)$ transformed to deal with zero-inflated distributions. Separate analyses were conducted for each oceanographic region (continental, oceanic), as well as within each year (2014, 2015) in each region. Larval fish taxa included were based on three criteria: presence in $>50\%$ of replicate tows, variability in density (variance >5), and prey known from prior diet analyses in the SOF (Llopiz & Cowen 2009, Llopiz et al. 2010, Gleiber et al. *in progress*, Chapter 3) or other tropical/subtropical regions (Sampey et al. 2007 and references therein). Planktonic prey groups from *ISIIS* included calanoid copepods, *Oithona* copepods, other copepods, and appendicularians. While crustacean nauplii are an important part of the diet of many larval fishes, *ISIIS* camera resolution limitations precluded the analysis of this small sized taxon. Any larval fish taxa known to include multiple types of prey in their diet were compared to each prey type with separate linear regressions, with appropriate Bonferroni correction.

Relative prey availability and predation pressure

We estimated interannual differences in the relative prey availability for and predation pressure on larval fishes in both regions by comparing larval fish densities to total potential prey and predator densities sampled by *ISIIS*. Mean prey:predator ratios were calculated for the relative abundance of i) larval fish prey to larval fishes, ii) larval fishes to

their predators, and iii) alternate prey for larval fish predators to those predators. Densities are means from *ISIIS* half-transects ($n = 12 - 20$ per year/region combination). Prey densities are the sum of all potential prey groups of larval fishes (calanoid copepods, *Oithona* copepods, other copepods, appendicularians, pteropods), predator densities the sum of all potential predator groups of larval fishes (chaetognaths, ctenophores, hydromedusae, siphonophores, other cnidarians), and larval fishes are solely comprised of the ‘larval fish’ group. Alternative prey for predators of larval fishes include all larval fish prey, as above. We note that alternate prey for the predators of larval fishes may also include other zooplankton (*ISIIS* groups: ‘decapod’, ‘euphausiid’, ‘polychaete’), but these groups are all more rare than larval fishes (Supplementary Table C1) and thus comprise a negligible proportion of the alternate prey available. We use larval fish densities from *ISIIS* as sampling included individuals similar in size to those sampled by nets, but also included pre-flexion larvae that were not as well sampled by nets.

4.2.5. Local and regional influences on the oceanographic environment

To better understand potential drivers of interannual patterns of plankton community variability we compared local and regional influences on the physical oceanographic environment prior to our interannual sampling. South Florida (Miami) air temperature and precipitation daily time series data were obtained from the National Weather Service (NOAA). Daily air temperature and precipitation three months and two weeks prior to sampling were separately compared between years with pairwise comparisons, and tests of normality and homogeneity assumptions. The upstream location of the Gulf of Mexico (GOM) Loop Current (LC) can directly influence the SOF, delivering entrained waters from the Gulf (Otis et al. 2019) and influencing eddy activity in the region (Fratantoni et al. 1998). In its extended position, the LC can transport eutrophic water from the GOM to the SOF (Androulidakis et al. 2019), whereas when retracted, waters flow more directly from the oligotrophic deep GOM waters. Time series daily LC latitudinal position was based on CMEMS (former AVISO) data using the 17-cm sea surface height anomaly criterion (Leben 2005; M. Le Henaff, RSMAS, pers. comm.). Daily latitudinal position six months and three months prior to sampling were separately compared between years with Wilcoxon rank tests, as data were non-parametric. We also calculated the proportion of days in each time period

prior to sampling that the LC latitude was $>27^{\circ}\text{N}$, indicating an extended phase with deep penetration into the GOM (Leben 2005).

4.3 Results

4.3.1. Physical environmental conditions

Water temperature and salinity from 15 m and 30 m depths, as well as chlorophyll *a* (chl *a*; 0 – 40 m) varied significantly between years, while mixed layer depth calculated from 0 - 40 m depth varied by regions (Figures 4.2-3, Supplementary Table C2). Temperatures in 2015 ranged from $27.7 - 29.0^{\circ}\text{C}$, on average 1.3°C warmer than in 2014 ($25.8 - 28.3^{\circ}\text{C}$). Salinity had the opposite trend, higher in 2014 ($36.2 - 36.5$) compared to 2015 ($35.9 - 36.2$). Temperature and salinity ranges had little overlap between years (Figure 4.2), and these interannual differences were consistent within both regions. Temperature and salinity patterns across regions varied between years. In 2014, the oceanic region had higher temperatures and lower salinity than the continental (Supplementary Table C2). However, in 2015, temperature and salinity were similar between regions. All differences described above were significant, based on pairwise comparisons ($p < 0.001$, Wilcoxon). Water temperature trends tracked local South Florida trends in air temperature prior to sampling. Mean air temperatures in 2015 were warmer than 2014 by 1.7°C three months prior and 1.6°C two weeks prior to sampling ($p < 0.001$, $p = 0.004$, respectively, Wilcoxon). Salinity may be influenced by recent precipitation (thus freshwater input). Three months prior to sampling daily precipitation was significantly higher in 2015 (22.6 cm) than in 2014 (17.8 cm; $p = 0.008$, Wilcoxon). However, two weeks prior to sampling daily precipitation was significantly higher in 2014 (6.7 cm) than in 2015 (4.5 cm; $p = 0.013$, Wilcoxon).

Mixed layer depth was significantly shallower in the continental region (24.9 ± 2.8 m) than in the oceanic region in 2014 (37.2 ± 1.5 m; $p = 0.003$, Welch's *t*-test), but not 2015 ($p = 0.71$; Figure 4.3, Supplementary Table C2). There was no interannual difference within either region. Chl *a* was significantly higher in 2015 ($0.1 \mu\text{g L}^{-1}$) than in 2014 ($0.05 \mu\text{g L}^{-1}$), and this pattern was consistent within each region ($p < 0.001$, Wilcoxon; Figure 4.5, Supplementary Table C2). There was no regional difference in 0 – 40 m chl *a* in either year. We note that chl *a* was at the low range of the instrument detection limit resulting in little variability in sampled values, thus these data must be interpreted cautiously. However,

surface ocean color from satellite imagery shows generally higher chl *a* in 2015 (M. Le Henaff, RSMAS, pers. comm.), corroborating the *ISIIS* data.

Vertical profiles from *ISIIS* undulation tows (0 – 100 m) in 2014 illustrate regional hydrographic differences due to upwelling in the continental region (Figure 4.3). Continental temperature profiles show a clear thermocline as cooler, upwelled water shoals and meets warm surface waters. In contrast, temperature is more constant with depth in the oceanic region. These trends are consistent with mixed layer depth differences between regions. Chl *a* depth profiles further demonstrate the influence of continental upwelling with enhanced chl *a* ($>0.1 \mu\text{g L}^{-1}$) extending from the deep chlorophyll maximum ($\sim 0.3 - 0.6 \mu\text{g L}^{-1}$; 60 - >100 m) to depths shallower than the mixed layer. While chl *a* (0 – 40 m) was similar between regions (see above), in 2014, chl *a* integrated from 0 – 100 m (deeper depths not sampled in 2015) was significantly higher in the continental region ($0.18 \mu\text{g L}^{-1}$) than oceanic ($0.14 \mu\text{g L}^{-1}$; $p = 0.02$).

The Gulf of Mexico Loop Current (LC) differed dramatically in latitudinal position prior to sampling: in 2014, it was recently extended from a retracted position (i.e., lower latitude) while in 2015, the LC remained mostly extended (higher latitude). Latitudinal position was significantly lower in 2014 compared to 2015, six months (2014: $26.0 \pm 1.0^\circ\text{N}$, 2015: $27.6 \pm 0.9^\circ\text{N}$) and three months (2014: $26.5 \pm 1.0^\circ\text{N}$, 2015: $27.8 \pm 0.6^\circ\text{N}$) prior to sampling ($p < 0.001$, Wilcoxon). This resulted in major difference in the proportion of time the LC was $>27^\circ\text{N}$ prior to sampling. In 2014, the LC was $>27^\circ\text{N}$ only 18% of time six months prior whereas in 2015 it was $>27^\circ\text{N}$ 84% of the time.

4.3.2. Plankton assemblage variability

Plankton assemblages varied significantly across years and regions (perMANOVA: $p = 0.001$; Table 4.1), with regional differences explaining more of the variance (Fig. 4.4a). Mixed layer depth was the only physical environmental variable characterizing the regional variability (axis 1; Figure 4.4a). Mixed layer depth was deeper in the oceanic region, consistent with patterns described above, and significantly correlated with the ordinations ($r^2 = 0.25$). The regional difference in plankton assemblage structure was driven by significantly higher densities of almost all key groups of prey, predators, and phytoplankton in the continental region, compared to oceanic (Table 4.2). Siphonophores and ctenophores were

the exception to this, as both had similar densities in both regions.

Within each region, interannual differences (2014 vs. 2015) accounted for significant variability in the plankton assemblage (perMANOVA: $p = 0.001$; Table 4.1, Figure 4.5a, b). In both regions, temperature (continental $r^2 = 0.71$, oceanic $r^2 = 0.77$), salinity ($r^2 = 0.54$, $r^2 = 0.79$), and chl a ($r^2 = 0.41$, $r^2 = 0.89$) were significantly correlated with the ordination. The 2014 plankton assemblage was correlated to high salinities while the 2015 plankton assemblage was positively correlated to warmer temperatures and higher chl a , consistent with patterns described above. Interannual assemblage variability was generally consistent in both regions, evident from the few significant interactions (year * region) in the multiple regressions (see below). Higher densities of calanoid copepods, appendicularians, gelatinous predators, and diatoms characterized the 2014 assemblage in both regions (Table 4.2). Calanoid copepods had some of the greatest interannual variability with $\sim 2.5\times$ greater densities in 2014, compared to 2015, in both the continental (2014: 41 ± 6 ind. m^{-3} , 2015: $15 \pm <1$) and oceanic regions (2014: 28 ± 3 , 2015: 11 ± 1). In contrast, higher densities of ‘copepod other’ (e.g., *Farranula*, Corycaeidae, and other poecilostomatoid copepods), protists, and *Trichodesmium* were more characteristic of 2015 (Table 4.2). We note that while a significant interaction term for protists indicates the interannual effect differs by region, this is due to differences in protist densities between years being especially large in the oceanic region. Protists were more abundant in 2015 than in 2014 in both regions, but with $\sim 3\times$ greater densities in the oceanic region versus $\sim 1.5\times$ greater densities in the continental region (Supplementary Table C1). In contrast to *Trichodesmium* and protists, the abundance of diatoms in the oceanic region was low in 2015, with only half the densities. Pteropods are the only other group with a significant interaction between year and region. Densities were similar between years in the continental region but higher in 2015 than in 2014 in the oceanic region. Densities of both *Oithona* copepods and chaetognaths were similar between years.

4.3.3. Larval fish assemblage variability

Regional

Overall patterns of larval fish assemblage structure were consistent with the plankton assemblage. Larval fish assemblages varied significantly across years and regions

(perMANOVA: $p = 0.001$; Table 4.2), with regional differences explaining more of the variance (Figure 4.4b). The key phytoplankton (diatoms, $r^2 = 0.45$, trichodesmium, $r^2 = 0.71$), prey (*Oithona* copepods, $r^2 = 0.49$, calanoid copepods, $r^2 = 0.25$, appendicularians, $r^2 = 0.24$), and predators (chaetognaths, $r^2 = 0.67$, hydromedusae, $r^2 = 0.58$) had strong positive correlations with the continental assemblage (Figure 4.4b). While higher densities of phytoplankton, prey, and predators were associated with the continental assemblage, deeper mixed layer depth ($r^2 = 0.30$) was the only explanatory variable associated with the oceanic assemblage.

Total larval fishes sampled by net tows were on average twice as abundant in the continental (172 ± 13 ind. 1000 m^{-3} , $n = 144$) than in the oceanic region (79 ± 2 ind. 1000 m^{-3} , $n = 112$). Larval fishes sampled by *ISIIS* had similar regional variability, with mean densities 1.7x greater in the continental (2645 ± 164 ind. 1000 m^{-3}) than oceanic region (1553 ± 136 ind. 1000 m^{-3}). Larval fish densities sampled by *ISIIS* were over an order of magnitude greater than those sampled by nets because the net mesh size (1 mm^2) restricts sampling to larger larvae, while *ISIIS* imaging includes a high abundance of smaller, pre-flexion larvae. However, net sampling is necessary for finer resolution taxonomic information.

Interannual variability within the regional larval fish assemblages

Interannual differences explained a significant proportion of variability in larval fish assemblages in the continental region (perMANOVA: $p = 0.001$; Table 4.1, Figure 4.5c). In contrast, interannual variability in the assemblage of larval fishes in the oceanic region was weak ($p = 0.045$; Figure 4.5d). Explanatory physical variables (temperature, salinity, chl *a*) were significantly correlated with the ordination axes in each year, with trends matching those previously described: higher salinities in 2014, warmer temperatures and higher chl *a* in 2015. These interannual correlations were stronger in the continental (temperature, $r^2 = 0.74$, salinity, $r^2 = 0.74$, chl *a*, $r^2 = 0.62$), compared to oceanic region (temperature, $r^2 = 0.53$, salinity, $r^2 = 0.30$, chl *a*, $r^2 = 0.29$). In the continental region, the 2014 larval fish assemblage was significantly correlated with higher densities of calanoid copepods ($r^2 = 0.66$), ctenophores ($r^2 = 0.64$), and siphonophores ($r^2 = 0.60$), while the 2015 larval fish assemblage was significantly correlated with higher densities of ‘copepod other’ (e.g., *Farranula*, Corycaeidae, and other poecilostomatoid copepods; $r^2 = 0.32$) and protists ($r^2 = 0.32$; Figure

4.5c). In the oceanic region, the 2014 assemblage was significantly correlated with higher densities of *Oithona* copepods ($r^2 = 0.41$), hydromedusae ($r^2 = 0.36$), and appendicularians ($r^2 = 0.21$), while the 2015 assemblage was significantly correlated with higher densities of *Trichodesmium* ($r^2 = 0.31$; Figure 4.5d).

Interannual variability in larval fish assemblages in the continental versus oceanic regions is further emphasized by the total density and composition of larval fishes. Larval fish densities sampled by net tows in the continental region were 3.5x greater in 2014 than in 2015 (Wilcoxon: $p < 0.001$; Figure 4.6). In comparison, larval fish densities in the oceanic region were only 1.5x greater in 2014 than in 2015 ($p < 0.001$). Larval fish densities in the continental region in 2015 were so low they were similar to the oceanic densities in 2014 ($p = 0.55$).

The high densities of larval fishes in the continental region in 2014 were due to significantly greater densities of many fish taxa (Figure 4.7a), with a distinct shift in some of the dominant larvae in the region. In 2014, the following taxa comprised over half of the continental larval fish assemblage: *Thunnus atlanticus* (blackfin tuna; 18.4%), Myctophidae (13.0%), Anthiinae (serranidae; 12.0%), Gonostomatidae (6.0%), and Paralichthyidae (5.3%; Supplementary Figure C1). While in 2015, densities of Anthiinae, *T. atlanticus*, and Paralichthyidae were substantially lower (Figure 4.7a), comprising only 0.2%, 4.4%, and 1.3% of the larval fish assemblage (Supplementary Figure C1). Instead, the dominant taxa in 2015 included: Carangidae (13.7%), Nomeidae (12.7%), Myctophidae (12.1%), Gonostomatidae (11.8%), and *Euthynnus alletteratus* (little tunny tuna, 8.3%).

The oceanic region had less dramatic shifts in the larval fish assemblage between years, with fewer taxa with significantly different densities (Figure 4.7b). While the three most abundant taxa in 2014 (Myctophidae: 13.4 %, Gonostomatidae: 9.3%, and *Sparisoma* spp.: 8.2%) had significantly lower densities and proportions of the assemblage in 2015 ($p < 0.01$), differences in other abundant groups were not significant. Instead, in 2015, the most abundant taxa were *Thalassoma bifasciatum* (bluehead wrasse; 10%), Myctophidae (9.7%), and Bothidae (9.6%; Supplementary Figure C1).

4.3.4. Larval fish size

Continental larval fish were generally larger in 2014 than in 2015 (Figure 4.8a). This

difference was significant for all scombrids (tunas; $p < 0.001$, Wilcoxon) *Katsuwonus pelamis* (skipjack), *E. alletteratus* (little tunny), *Auxis thazard* (frigate), *Auxis* spp., the scarid *Sparisoma* spp. (parrotfish; $p = 0.003$, Wilcoxon), and larvae in the family Nomeidae ($p < 0.001$). The labrid (wrasse) *Xyrichtys novacula* (razorfish) was the only group we measured in the continental region that was significantly larger in 2015 ($p < 0.001$, Wilcoxon).

The oceanic region had fewer larval fish taxa with larger sizes in 2014 (Figure 4.8b). Only the scombrid *T. atlanticus* ($p < 0.001$, Wilcoxon), and *Sparisoma* spp. ($p = 0.02$) were significantly larger in 2014. In contrast, *T. bifasciatum* ($p < 0.001$) and *K. pelamis* ($p = 0.02$) were significantly larger in 2015.

4.3.5. Larval fish-prey relationships

Overall, the only significant relationships between specific larval fish taxa and availability of their potential prey occurred in the continental region (Supplementary Tables C4 and C5), therefore only significant (and $r^2 > 0.2$) results from this region are presented here (Fig. 4.9). Calanoid copepods were the prey group that had the most significant correlations with their potential larval fish predators (Supplementary Table C1). The reef fishes (Callionymidae and Scorpaenidae), flatfishes (Paralichthyidae and Bothidae), and blackfin tuna (*T. atlanticus*) had strong positive correlations with their calanoid copepod prey (Figure 4.9a, b, c). Since 97% of all *T. atlanticus* collected were from 15 m depth, analysis was constrained to 15 m depth. Fish taxa that relied on appendicularians were significantly correlated to them. Scombrid predators (*Auxis* spp., *E. alletteratus*, *K. pelamis*) had the strongest relationships, but only in 2014 (Figure 4.9d). Interestingly, carangids in the continental region had strong negative relationships with their potential prey, across both years and within 2014 (Supplementary Tables C4, C5). There were no significant correlations between larval fishes and their prey in the oceanic region.

4.3.6. Relative prey availability and predation pressure

Per capita potential prey availability for larval fishes varied between years in the continental, but not the oceanic region (Figure 4.10). Overall, continental prey availability was higher in 2014 with a potential prey:larval fish ratio of 55:1 (Figure 4.10a), compared to 2015 with 44:1 (Figure 4.10b). In contrast, prey availability was similar between years in the

oceanic region with 49-50 potential prey per larval fish (Figure 4.10c,d). Predation pressure on larval fishes is influenced by both direct predation on larvae and the availability of alternate (zooplankton) prey, as larvae are rare in the environment and encounter rates between predators and zooplankton prey are likely orders of magnitude higher. Since larval fish:predator ratios were consistently low (0.04 – 0.06 larvae/predator) across years and regions, alternate prey:predator ratios are especially informative. In fact, alternate prey:predator ratios were consistently higher in the oceanic region (3:1; Figure 4.10c,d), compared to continental (2:1; Figure 4.10a,b). Fewer alternative prey per capita for predators in the continental region would result in higher overall predation pressure on alternate prey and larvae, compared to the oceanic region. This higher predation pressure (on larval fishes and alternate prey) in the continental region was consistent in both years, despite fewer prey for larval fishes in 2015.

4.4 Discussion

Predicting the response of larval fishes in oligotrophic systems to climate change is difficult due to the dynamic physical processes influencing the environment and complex planktonic food web interactions. Yet, examination of how present contrasting food web conditions influence larvae can provide clues as to how predator-prey relationships may drive future populations under increased variability or prolonged extreme conditions in the environment. Here we demonstrate that nearshore (continental) and offshore (oceanic) larval fish assemblages responded differently to strong interannual summer variability in the plankton food web in the oligotrophic, but coastally-productive, Straits of Florida (SOF). This difference in response was further evident in significant relationships between abundant larval fish taxa and their potential zooplankton prey in the continental, but not oceanic regions.

Overall, the continental region had a more productive, high biomass food web, with higher densities of phytoplankton, zooplankton, and larval fishes, compared to the oceanic region, consistent with previously described patterns in the region (Lee et al. 1991, Lane et al. 1994, Llopiz et al. 2010). Physical processes (e.g., upwelling, eddies) provide nutrient enrichment to the continental region, in an otherwise oligotrophic system, driving regional variability in the SOF (Olson et al. 1994 and references therein, Hitchcock et al. 2005). This

productivity quickly attenuates eastward, with the oceanic region being consistently oligotrophic. The strong vertical (0 – 100 m) gradients of temperature and density, along with elevated chl *a* with depth in the continental region demonstrate the influence of cool, dense water upwelling in this region, boosting productivity. Larval fish densities were up to three times greater in the continental region compared to the oceanic region, associated with significant differences in all zooplankton prey groups (e.g., calanoid copepods, appendicularians, *Oithona* copepods, other copepods, pteropods), and many abundant gelatinous predators. These contrasting pelagic regions set up an interesting comparison for how larval fish assemblages co-vary with prey and predator conditions.

Contrasting regional environments led to different patterns in plankton assemblage structure that translated to larval fish assemblages. In both regions, 2015 (compared to 2014) had lower densities of key prey groups, calanoid copepods and appendicularians, associated with fewer diatoms and elevated densities of protists and *Trichodesmium*. In the continental region, the larval fish assemblage reflected these changes in potential prey as 2015 total larval fish density (from net tows) was only 29% of 2014 values, significant changes in most of the abundant taxa, with many of the abundant fish larvae smaller in size. The lower larval fish densities in 2015 were not only substantially reduced from the prior year, but equivalent to densities sampled in 2014 in the low-productivity oceanic region. In contrast, the larval fish assemblage in the oceanic region was similar in both years. Few abundant taxa in the oceanic region had interannual density fluctuations, and overall larval fish densities in the oceanic region were 69% lower in 2015 than in 2014. This regional difference suggests continental larvae are sensitive to fluctuations in prey availability, while oceanic larvae are more tolerant of low prey scenarios.

Interestingly in the continental region, the density of larval fishes sampled by *in situ* imaging was more similar between years than indicated by net tows: only 1.2x greater in 2014. *ISIIS* images organisms as small as 200 μm , while nets sampled fish larvae >1 mm in length. Thus, *ISIIS* samples highly abundant, small, pre-flexion larval fishes in addition to the older, larger individuals sampled by the nets. This is evident in the order of magnitude greater *ISIIS*-derived fish densities than net sampled larvae. This discrepancy in interannual differences in larval fish density between sampling equipment suggests that more larger, older larvae were surviving in the high prey conditions in the continental region in 2014.

Among those larger fish larvae sampled by the nets, many continental taxa were larger in 2014 than in 2015. In comparison, in the oceanic region few larval fish taxa differed significantly in size between years.

Greater risk of mortality from higher predation pressure in the continental region may also compound the effects of prey variability. Potential zooplankton predators followed the patterns of their prey with 2 - 5x greater densities of chaetognaths, hydromedusae, and other cnidarians in the continental region. Not only were predators more abundant, but also relative densities of predators to available prey (zooplankton and larval fishes) were higher in the continental region (1:2), compared to oceanic (1:3). High relative predation pressure in the continental region was consistent among years, thus larvae in substantially reduced feeding conditions in the continental region in 2015 experienced the same predation pressure as larvae in 2014 with more favorable feeding conditions. Stronger predation pressure on larval fishes has been predicted in the more productive continental (western) region in the SOF (Sponaugle et al. 2009), but the application of *in situ* imaging in this study now enables a comprehensive quantification of this substantial predator field.

The contrasting interannual patterns in the plankton community had strong implications for larval fishes suggesting variability in nutrient-enrichment, thus food web productivity. Temperature could be a key driver of the variability, with 1.3 °C warmer water temperatures following local South Florida trends in air temperature, 1.7 °C warmer in the three months prior to sampling 2015, compared to 2014. Interannual environmental patterns were consistent with the general expectation that warmer temperatures increase stratification, thus reducing enrichment from deeper nutrients (e.g., upwelling) in oligotrophic oceans (Behrenfeld et al. 2006, Landry et al. 2019). Higher densities of protists and *Trichodesmium* occurred in these warmer temperatures (2015) compared with a productive planktonic food web in the cooler 2014 conditions with a high abundance of diatoms and calanoid copepods. The upstream location of the Gulf of Mexico (GOM) Loop Current can also directly influence the SOF. In 2015, the Loop Current was extended into the northeastern GOM for a protracted time period preceding sampling. The lower salinity and higher chl *a* sampled in this year suggests potential entrainment of riverine-influenced nutrient-rich coastal GOM shelf waters (Le Hénaff & Kourafalou 2016, Androulidakis et al. 2019). While enrichment from coastal and riverine processes can enhance productivity, nitrogen-rich nutrient loading

in the GOM has been associated with a decrease in diatoms and copepods, and an increase in flagellates due to silica limitation (Turner et al. 1998, Rabalais et al. 2009). In contrast, 2014 sampling followed the early stages of Loop Current extension (from previously retracted), entraining waters from the deep GOM. Thus, it is possible these different water masses contributed to the contrasting SOF conditions in 2014 and 2015. However, teasing apart the drivers of plankton community differences is difficult in the dynamic SOF system, where complex local and distant physical processes influence the oceanography. Identifying ultimate causes of the observed variability is beyond the scope of the present study.

The biological consequences of lower prey availability for larval fishes in 2015 may have been exacerbated by the warmer conditions. The combined effect of low prey and higher temperature conditions can be detrimental to larval fishes, if food supply is insufficient to support basic functions (e.g., growth) at higher metabolic rates (Houde 1989, Buckley et al. 2004, McLeod et al. 2013). While temperature differences between years was only 1.3 °C, subtropical larvae are adapted to a narrow and relatively stable thermal regime (Tewksbury et al. 2008), and frequently exist near their upper thermal limit (Rummer et al. 2014), thus they are particularly sensitive to temperature increases. The high temperature and low prey conditions in the SOF in 2015 resulted in reduced growth, size, and abundance of *T. atlanticus* (blackfin tuna) associated with lower prey consumption (Gleiber et al. *in progress*, Chapter 3). However, fast- and slow-growing larvae may respond differently to such conditions (Pepin et al. 2014). Larval growth in fast-growing tunas has been demonstrated to peak at an optimum, below thermal limits, while growth in slower-growing reef fish larvae can be enhanced at higher temperatures without peaking (McCormick & Moloney 1995, Sponaugle et al. 2006, Gleiber et al. 2020).

Success of continental larval fish linked to prey variability

The interannual difference in larval fish abundance in the continental region was due to major fluctuations in key fish species, while the oceanic larval fish assemblage was remarkably similar between years. In 2014, densities of 16 of the top 20 most abundant larval fish in the continental region were significantly lower in 2015, with shifts across taxa from a range of habitat groupings (e.g., pelagic, reef, mesopelagic, flatfish). This is illustrated with a dramatic change in the most abundant continental larval fish species in 2014, *T. atlanticus*

(blackfin tuna; 18% of the larval assemblage), with 15x higher abundances than in 2015 when they comprising only 4% of all larval fishes. Similarly, other larval tunas (*K. pelamis*, *Auxis* spp), flatfishes (Paralichthyidae, Bothidae), mesopelagic fishes (Myctophidae, Gonostomatidae), and numerous reef fish families (Anthiinae, Scorpaenidae, Lutjanidae, Callionymidae, Gobiidae) in the continental region were 2 – 14x more abundant, or present only in 2014. These fluctuations in the composition of larval fish assemblages may be due to variability in the timing of spawning upstream, known to vary seasonally and regionally in the SOF (Richardson et al. 2010). However, the rapid flow of the Florida Current can transport larvae from numerous upstream and local locations (Cowen et al. 2006) and many SOF fishes spawn frequently throughout the year. Although we cannot exclude this possibility, prior work in the SOF has consistently linked elevated prey availability to fuller guts and faster growth in fish larvae (Sponaugle et al. 2009, Llopiz et al. 2010, Gleiber et al. 2020), with faster growers having higher survival and condition that carry over to and beyond settlement (Sponaugle et al. 2006, Shulzitski et al. 2016).

Interannual differences in the abundance and composition of larval fishes in the continental region reflects larval fish-prey relationships as evident through co-occurrence of higher abundances of specific taxa with higher abundances of their prey. This tight connection between the prey field and their larval fish predators suggests continental larvae are sensitive to variability in the environment through changes in feeding conditions. Calanoid copepods (and copepodites) are a key prey for many larvae in the SOF and other warm-water regions (Young & Davis 1990, Sampey et al. 2007, Llopiz & Cowen 2009). The 2014 vs. 2015 difference in SOF calanoid copepods densities (and temperature conditions, see above) in the SOF were recently shown to directly influence larval *T. atlanticus* diet and growth (Gleiber et al. *in progress*, Chapter 3). Larval reliance on calanoid copepods increased with environmental prey densities, resulting in 2014 larvae with fuller guts and faster growth. These fuller guts and faster growth appear to have influenced *T. atlanticus* survival, as the present study revealed a tight correlation between *T. atlanticus* densities and calanoid copepod densities. The abundance of other fish larvae that feed on calanoid copepods were also closely associated with their prey in this region, including scorpaenids (scorpionfish), callyonymids (dragonets), bothids and paralichthyids (flounders), and myctophids (lanternfish), suggesting increased survival in the highest prey conditions.

Appendicularians are another important prey group for larval fishes and have been previously associated with enhanced growth and success for larval fish predators such as young non-*Thunnus* tunas. In the SOF, these larval tunas co-occur with high abundances of their appendicularian prey (Llopiz et al. 2010), and larval growth of *Katsuwonus pelamis* (skipjack tuna) increased across an environmental gradient of appendicularian densities (Gleiber et al. 2020). Similarly, in the present study, most of the appendicularian-reliant tuna larvae had higher (2 - 5x) abundances in 2014, when appendicularian densities were 1.5x greater than in 2015. In 2014, these tuna larvae were not only more abundant, but larger in size likely due to more larger, older larvae surviving in the region. While size differences could be due to the timing of upstream spawning by adults, previous studies have demonstrated robust relationships between tuna growth and their prey and predators (Gleiber et al. 2020, *in progress*, Chapter 2, Chapter 3). Further, *T. atlanticus* in 2014 that were faster growing and had fuller guts were also larger in size. The sensitivity of tuna larvae to prey fluctuations is further illustrated by positive relationships between larval densities of *K. pelamis*, *Auxis* spp. (frigate tunas), and *Euthynnus alletteratus* (little tunny) across the 2014 gradient of regional appendicularian densities. Since larval tunas are some of the fastest growing fish larvae and require consistently abundant prey to support this growth (Pepin et al. 2014, Robert et al. 2014), decreased prey availability appears to rapidly translate to reduced growth and survival.

The productive continental side of the Florida Current provides enhanced prey availability that directly benefits a range of abundant fish larvae in the region. However, larval fishes in this environment are in a “high risk, high reward” tradeoff scenario, with high predation pressure and potential rapid downstream advection (Hare & Cowen 1991, Huebert et al. 2011). The dramatic interannual variation captured by our sampling demonstrates both “winning” and “losing” outcomes for fish larvae in this region. When prey were abundant, larval fish survival was high, evident in both greater abundances and larger sizes of larvae. In contrast, during poor feeding conditions larval fish abundances were severely reduced, with fewer larvae surviving to larger sizes. Densities of predators of larval fishes in the continental region were lower in 2015, but lower densities of their larval fish and zooplankton prey in this year translated into a similar predation pressure on larval fish in both years. Thus, despite poor feeding (and higher temperature) conditions, fish larvae in 2015 were exposed to the

same high predation pressure as larvae in high prey conditions, likely compounding the survival disadvantage.

Oceanic larval fish tolerant to variable prey abundances

The oceanic larval fish assemblage was characterized by a high prevalence of reef fishes that appeared to be more tolerant of changing food web structure, as few taxa fluctuated significantly in abundance between years. This consistency in the larval fish assemblage is further illustrated by the absence of significant larval fish-prey relationships in the region, suggesting either reliance on a range of prey types or flexible growth, allows survival during low prey conditions. Two key reef (labrid) species in this region, *Thalassoma bifasciatum* (bluehead wrasse) and *Xyrichtys novacula* (razorfish), had similar densities between years, likely due to their diet of poeilotomatoid copepods (Corycaeidae, Farranula; Llopiz & Cowen 2009).

In contrast to the other prey and predator groups, poeilotomatoid copepods appeared to thrive in the low productivity conditions in 2015. Since Corycaeidae are carnivorous copepods, they may be less dependent on grazing food webs characterized by diatoms and calanoid copepods, enabling their survival in low-productivity, microbial food webs dominated by protists (Landry et al. 2019 and references therein). In both regions, densities of poeilotomatoid copepods and protists were higher in 2015, consistent with generally oligotrophic conditions throughout the SOF in 2015. This prey group is moderately abundant to rare and patchy in the SOF, with faster growth in larval *T. bifasciatum* and *X. novacula* associated with higher densities of prey, but also where prey were rare but patchy (Gleiber et al. 2020). Adaptations of these labrids to inconsistent prey availability is evident through plasticity in their pelagic larval phase with flexibility in their growth, pelagic larval duration (PLD), and size-at-settlement (Hare & Cowen 1991, Searcy & Sponaugle 2000, 2001, Sponaugle & Pinkard 2004). This adaptability to an oligotrophic environment is further reflected in the present study as larval labrid densities were stable between years in both regions, and larvae were either similar to or larger in size in 2015 when their copepod prey were also more abundant. Although growth rates of these larval labrids are directly related to ambient temperatures (Sponaugle et al. 2006), they are likely less sensitive to higher temperature conditions than faster-growing larvae (Shulzitski et al. 2018, Gleiber et al.

2020). While these and other species in the oceanic region may have similar strategies to survive food-limited, oligotrophic environments, lower densities of some taxa in 2015 (e.g., myctophids, gonosotmatids, and *Sparisoma* scarids) suggest reliance on the more abundant prey groups (e.g., calanoid copepods, appendicularians).

Similarity in the abundance and composition of the oceanic larval fish assemblage between years may also reflect lower overall mortality of larvae in this region. This lower predation pressure was due to both lower overall densities of most predator groups (chaetognaths, hydromedusae, larger cnidarians) and fewer predators per capita on larval fishes or other potential zooplankton prey. The oceanic region has been previously predicted to have lower predation pressure, compared to the continental region (Sponaugle et al. 2009) and oceanic larvae survival may also benefit from reduced vulnerability to downstream advection since the Florida Current is less influential in this region (Leaman et al. 1989, Richardson et al. 2010). In comparison to the continental region, oceanic larvae exist in a “low risk, low prey” environment enabling larvae with flexible feeding and growth strategies to be successful in oligotrophic environments despite low and variable prey availability.

Conclusions

The effects of climate change on oligotrophic pelagic environments may decrease productivity (Behrenfeld et al. 2006, Fu et al. 2016), thus feeding conditions important for the survival of early life stages of marine fish. However, dynamic sub to mesoscale physical processes that enrich coastal regions, enhancing fisheries production in low-latitude oceans, result in spatially variable productivity that fuels differences in planktonic communities including larval fish assemblages. The regional comparison across a major western boundary current revealed contrasting responses of larval fishes. Larval fish assemblages in the upwelling-influenced continental region were tightly linked to fluctuations in their prey. In contrast, larval fish assemblages in the oligotrophic oceanic region were more consistent there despite fluctuating environmental conditions. Many of these larvae have flexible life history traits suggesting adaptations to a prey poor environment. A similar contrast in larval fish assemblage variability has been described, across broad spatial scales (1000's km) in response to extreme El Niño variability (Ignacio Vilchis et al. 2009). While the authors hypothesized that sensitivity of upwelling-associated larvae was related to changes in

productivity and thus prey availability, data were not available to test this theory. Our findings revealed a direct link between larval fishes and fluctuations in their prey especially in nearshore regions that frequently support a high abundance and diversity of larval fishes. The strength of this larval fish-prey connection in continental regions may also be enhanced by strong predation pressure and sensitivity to high temperature conditions. Understanding such variability in resilience of ecological communities is key to identifying regions that are more sensitive to change, demonstrated by population fluctuations in responses to environmental (e.g., prey, temperature) changes (Holling 1973, Scheffer et al. 2009). Nearshore marine systems are currently experiencing more frequent and intense environmental variability with increasing anthropogenic warming (Trenberth 2005, Wu et al. 2012, Liu et al. 2015) and coastal water quality degradation (Rabalais et al. 2009, Lapointe et al. 2019). Our findings suggest that if future changes in planktonic food webs result in enhanced microbial loop processes with decreased prey availability for larvae, survival of key fish taxa in nearshore systems may be threatened. In contrast, fish larvae with more variable life histories and feeding strategies may be more tolerant to future subtropical ocean conditions.

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Table 4.1. Comparison of plankton and larval fish assemblages among regions, years, and years within each Straits of Florida region (continental, oceanic). Results are from permutational multivariate analysis of variance (PerMANOVA) based on Bray-Curtis distances. Significance values based on 999 permutations.

Plankton assemblages					
Region	Source of variation	F.Model	df	r²	p
All	Region	44.07	2	0.415	0.001
All	Year	14.74	2	0.192	0.001
Continental	Year	15.60	2	0.315	0.001
Oceanic	Year	14.82	2	0.363	0.001
Larval fish assemblages					
Region	Source of variation	F.Model	df	r²	p
All	Region	5.76	3	0.159	0.001
All	Year	5.87	2	0.087	0.001
Continental	Year	11.08	2	0.246	0.001
Oceanic	Year	2.146	2	0.076	0.045

Table 4.2. Comparison of plankton densities among regions and years based on multiple linear regression results with region and year as categorical covariates. Prey, predator, phytoplankton, and larval fish densities (log transformed) are from *ISIIS* half-transects ($n = 64$). Dash denotes interaction not significant and reduced model results are provided. Estimate comparisons summarize significant differences in intercepts of categorical covariates. Model adjusted R^2 and p-value are provided (***) < 0.001). Mean densities ($\pm$ standard error) supplied to provide reference for relative abundances of each group. * denotes a single influential outlier was removed.

Type	Group	Density (ind. m ⁻³)	Source of p-value			Estimate comparisons		Model fit	
			Region	Year	Interaction	Region	Year	Adj. R ²	p-value
Prey	Appendicularian	52 $\pm$ 3	<0.001	0.003	-	C > O	14 > 15	0.31	***
	Calanoid copepod	24 $\pm$ 2	0.001	<0.001	-	C > O	14 > 15	0.55	***
	Oithona copepod	22 $\pm$ 2	<0.001	0.40	-	C > O	ns	0.43	***
	Copepod other	6 $\pm$ <1	0.004	0.03	-	C > O	15 > 14	0.18	***
	Pteropod*	4 $\pm$ <1	<0.001	0.005	0.01	C > O	15 > 14	0.76	***
Predator	Chaetognath	18 $\pm$ 2	<0.001	0.09	-	C > O	ns	0.78	***
	Siphonophore	15 $\pm$ 1	0.06	<0.001	-	ns	14 > 15	0.58	***
	Hydromedusae	7 $\pm$ <1	<0.001	<0.001	-	C > O	14 > 15	0.62	***
	Cnidaria other	2 $\pm$ <1	<0.001	<0.001	-	C > O	14 > 15	0.47	***
	Ctenophore*	1 $\pm$ <1	0.73	<0.001	-	ns	14 > 15	0.71	***
Phyto	Diatom*	189 $\pm$ 16	<0.001	<0.001	-	C > O	14 > 15	0.66	***
	Trichodesmium	129 $\pm$ 18	<0.001	0.006	-	C > O	15 > 14	0.61	***
	Protist	114 $\pm$ 9	<0.001	<0.001	0.006	C > O	15 > 14	0.52	***
Fish	Larval fish	2 $\pm$ <1	<0.001	0.004	-	C > O	14 > 15	0.47	***

Figure 4.1. Map of locations in the Straits of Florida (SOF) sampled in (top) May-June 2014 and (bottom) June 2015. Multiple Opening/Closing Net and Environmental Sensing System (MOCNESS) replicate tows (points) and *In Situ* Ichthyoplankton Imaging System (*ISIIS*; solid lines) transects at each depth (15 m and 30 m), and undulated from 0-100 m (thick shaded lines) were centered on a drogue (dashed line) that drifted northeastward with the Florida Current. Distances between MOCNESS tows and *ISIIS* transects appear farther apart in the western SOF where the Florida Current is stronger, compared to east SOF, but in all regions the same water mass was sampled in a moving current. Map generated using R software (Version 3.6.0; R Core Team 2019).

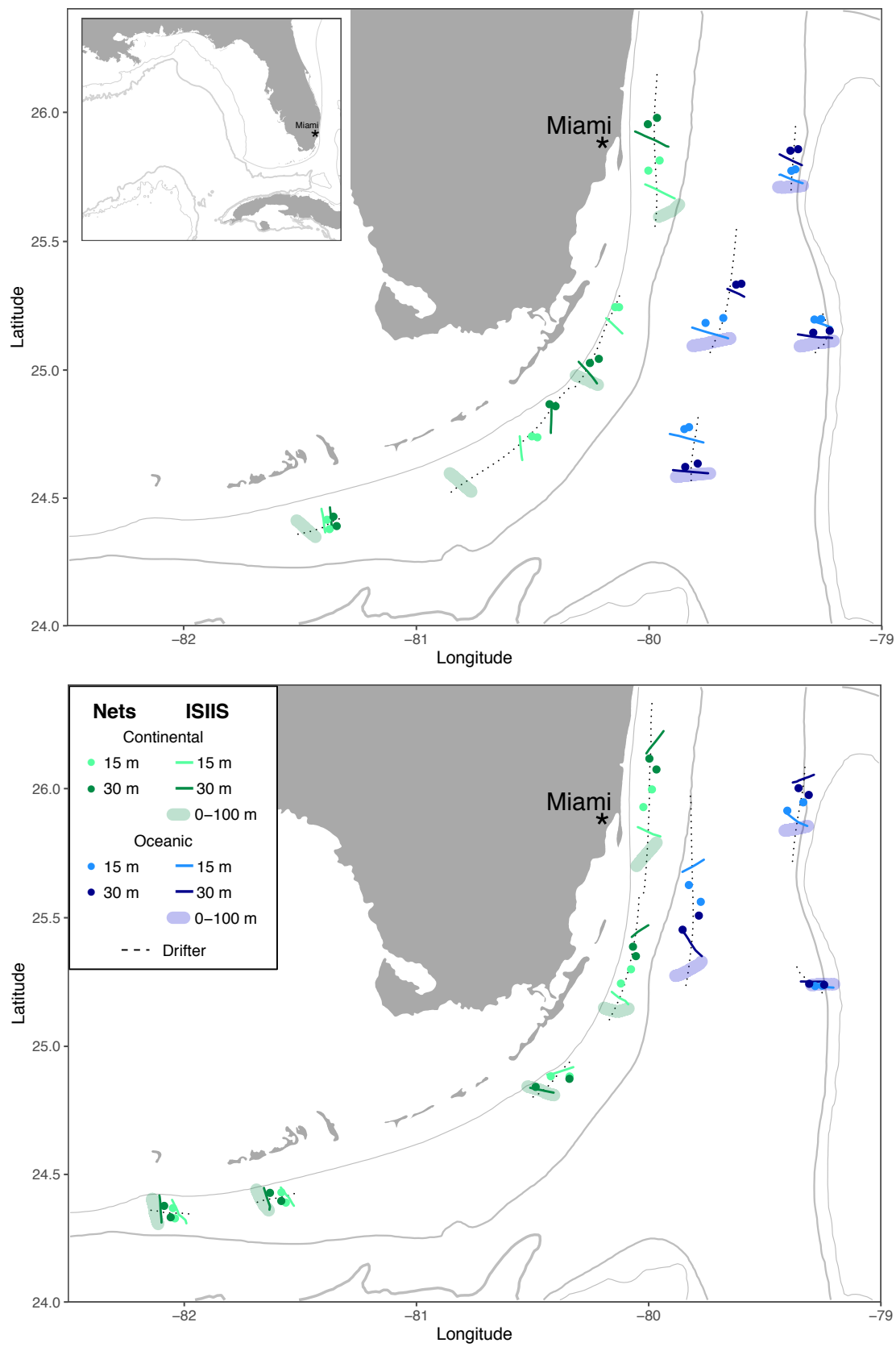


Figure 4.1

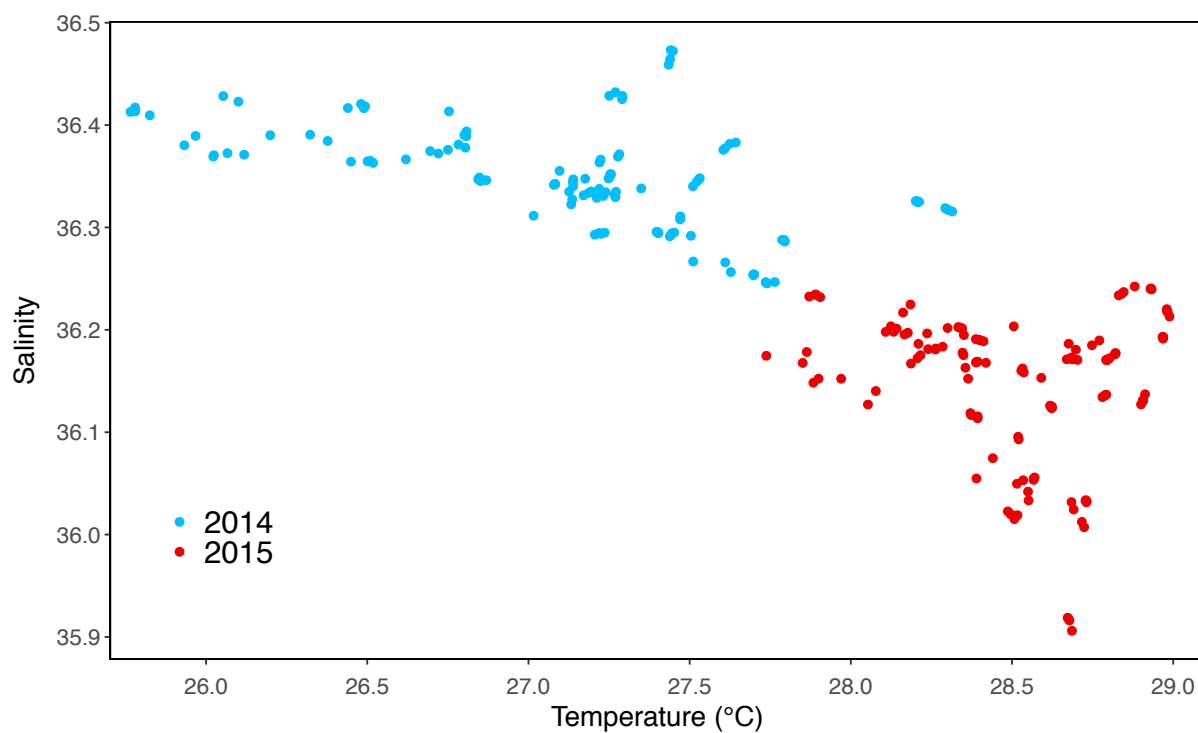


Figure 4.2. Temperature and salinity values sampled by MOCNESS at depths of 15 m and 30 m in the Straits of Florida in May-June 2014 (n = 128) and June 2015 (n = 128).

Figure 4.3. Representative environmental data recorded by *ISIS* for undulation transects in 2014 at stations characteristic of continental and oceanic regions. Continental transect start location: 24.412 °N, 81.513 °W; oceanic transect start location: 25.093 °N, 79.351 °W. Dashed line represents mixed layer depth.

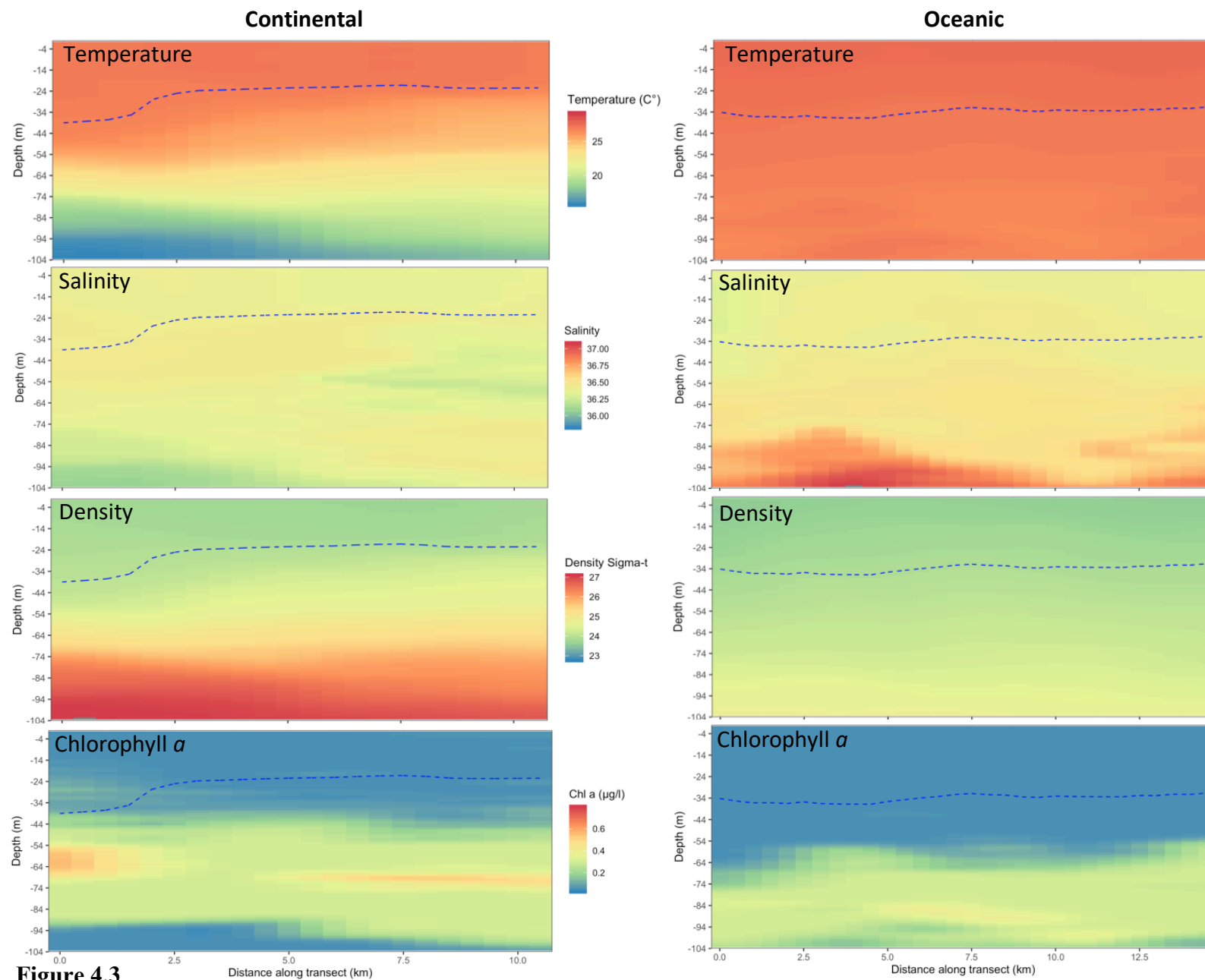


Figure 4.3

Figure 4.4. Non-metric multidimensional scaling (NMDS) showing regional (a) plankton and (b) larval fish assemblage structure in the Straits of Florida. Both years (2014, 2015) combined. NMDS conducted on log-transformed densities of (a) plankton groups from *ISIIS* half-transects (ind. m⁻³), and (b) larval fish taxa from replicate net tows (ind. 1000 m⁻³, mean of four individual nets per tow; see Methods). Points represent individual *ISIIS* half-transects (a) or replicate net tows (b). Arrows represent correlations between ordination and environmental variables, arrow direction is direction of correlation, and arrow length is magnitude of correlation (scaled separately in each plot). Physical environmental variables (black) included for both plankton and larval fish NMDS; prey, predator, and phytoplankton environmental variables (grey; log-transformed) included for larval fish NMDS. Only correlations with $r^2 > 0.2$ shown. Stress = 0.1 for two-dimensional solution (plankton), 0.15 for three-dimensional solution (larval fish). Stress is a measure of concordance between the multivariate data and the multi-dimensional representation. N = 36 (continental), 28 (oceanic).

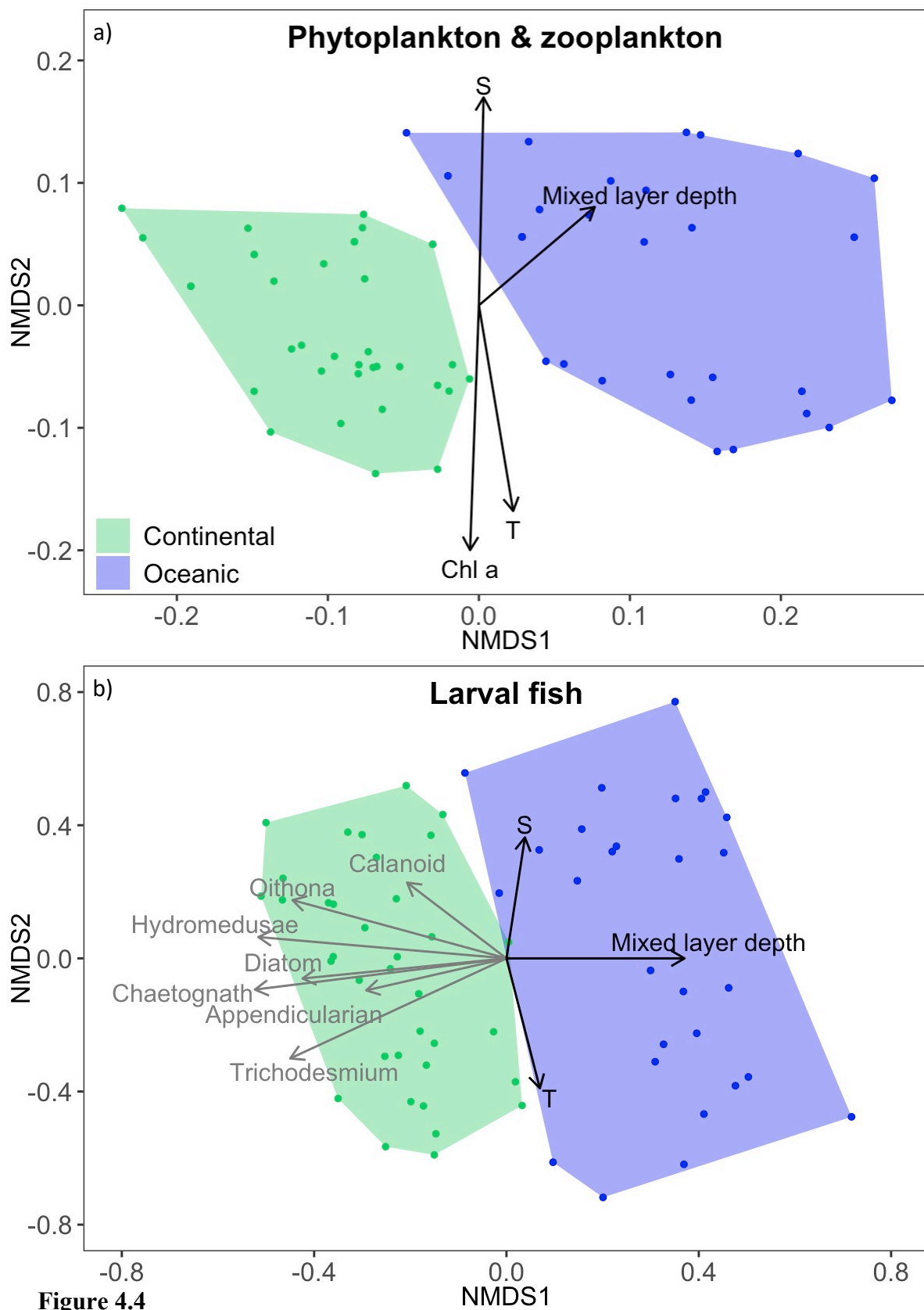


Figure 4.5. Non-metric multidimensional scaling (NMDS) showing interannual (a,b) plankton and (c,d) larval fish assemblage structure within the (a,c) continental and (b, d) oceanic regions in the SOF. NMDS conducted on log-transformed densities of (a,b) plankton groups from *ISIIS* half-transects (ind. m⁻³), and (c,d) larval fish taxa from replicate net tows (ind. 1000 m⁻³, mean of four individual nets per tow; see Methods). Points represent individual *ISIIS* half-transects (a,b) or replicate net tows (c,d). Arrows represent correlations between ordination and environmental variables, arrow direction is direction of correlation, and arrow length is magnitude of correlation (scaled separately in each plot). Physical environmental variables (black) included for both plankton and larval fish NMDS; prey, predator, and phytoplankton environmental variables (grey; log-transformed) included for larval fish NMDS. Only correlations with $r^2 > 0.2$ shown. Stress = 0.15 (continental) and 0.10 (oceanic) for two-dimensional solutions (plankton), and 0.10 (continental) and 0.11 (oceanic) three-dimensional solutions (larval fish). N = 16 (2014 continental, 2014 oceanic), 20 (2015 continental), and 12 (2015 oceanic).

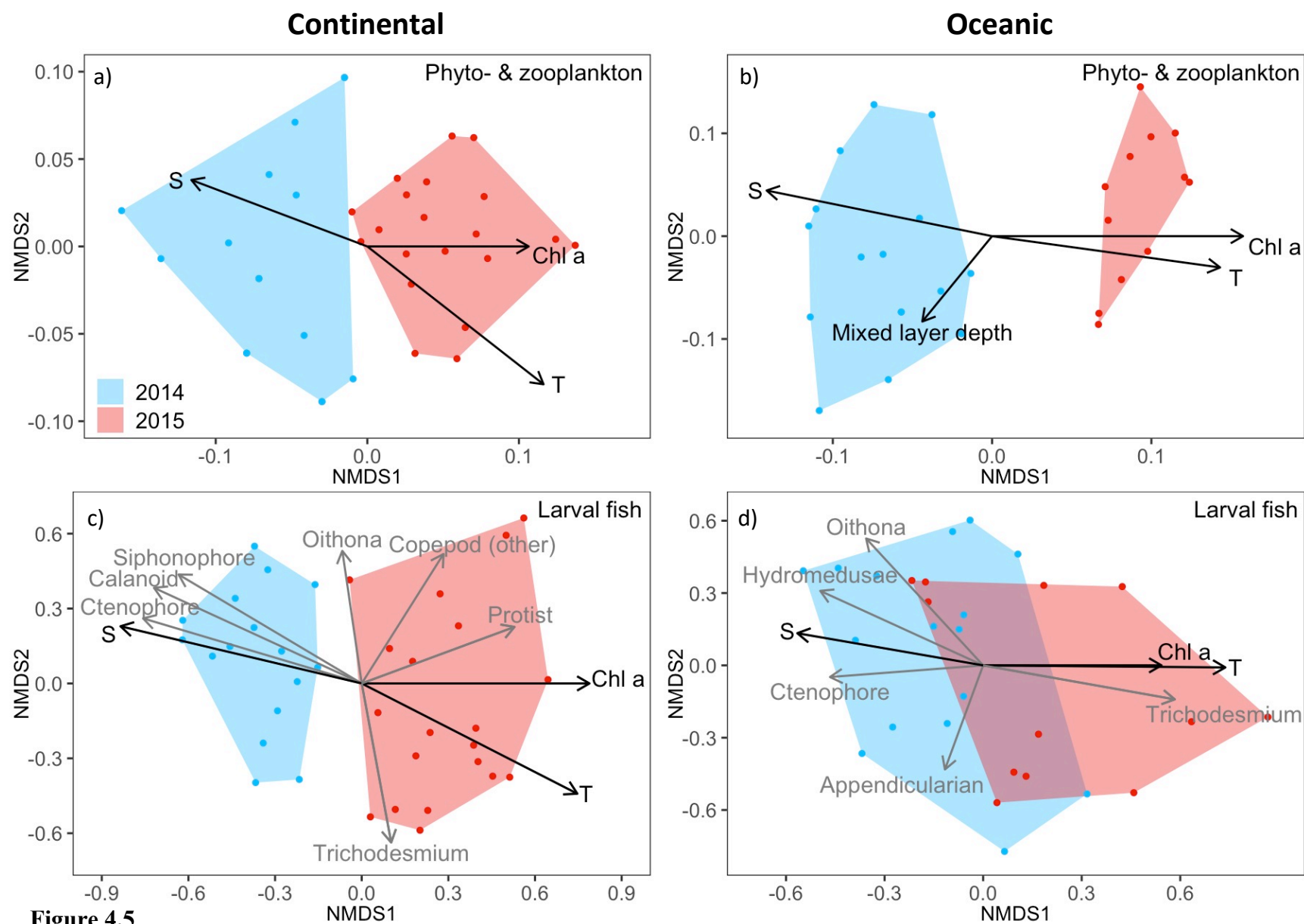


Figure 4.5

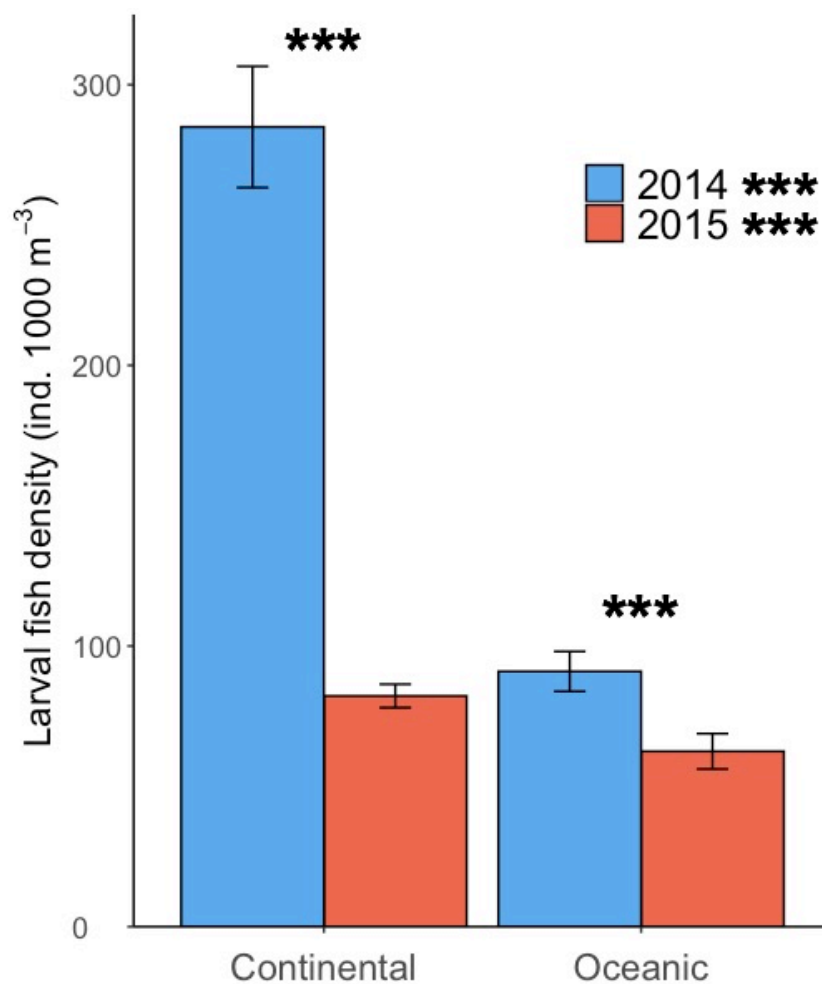


Figure 4.6. Mean densities (ind. 1000 m⁻³) of all larval fishes sampled with nets at depths of 15 m and 30 m (combined) at stations in the Straits of Florida in different regions and years. Error bars represent standard error. Wilcoxon rank sum test p-value (***) p < 0.001) given for interannual comparison with region (above bars) and regional comparison within year (by legend). N = 64 (2014 continental, oceanic), 80 (2015 continental), 48 (2015 oceanic).

Figure 4.7. Mean densities (ind. 1000 m⁻³) of larval fish taxa sampled with nets at depths of 15 m and 30 m (combined) at stations in the Straits of Florida in 2014 vs. 2015 in the (a) continental region, and (b) oceanic region. In each region taxa are list in order of 2014 abundance. Taxa that comprised >1% of all larval fishes in either year in each region shown. Taxa are colored to indicate adult habitat type. N = 64 (2014 continental, oceanic), 80 (2015 continental), 48 (2015 oceanic).

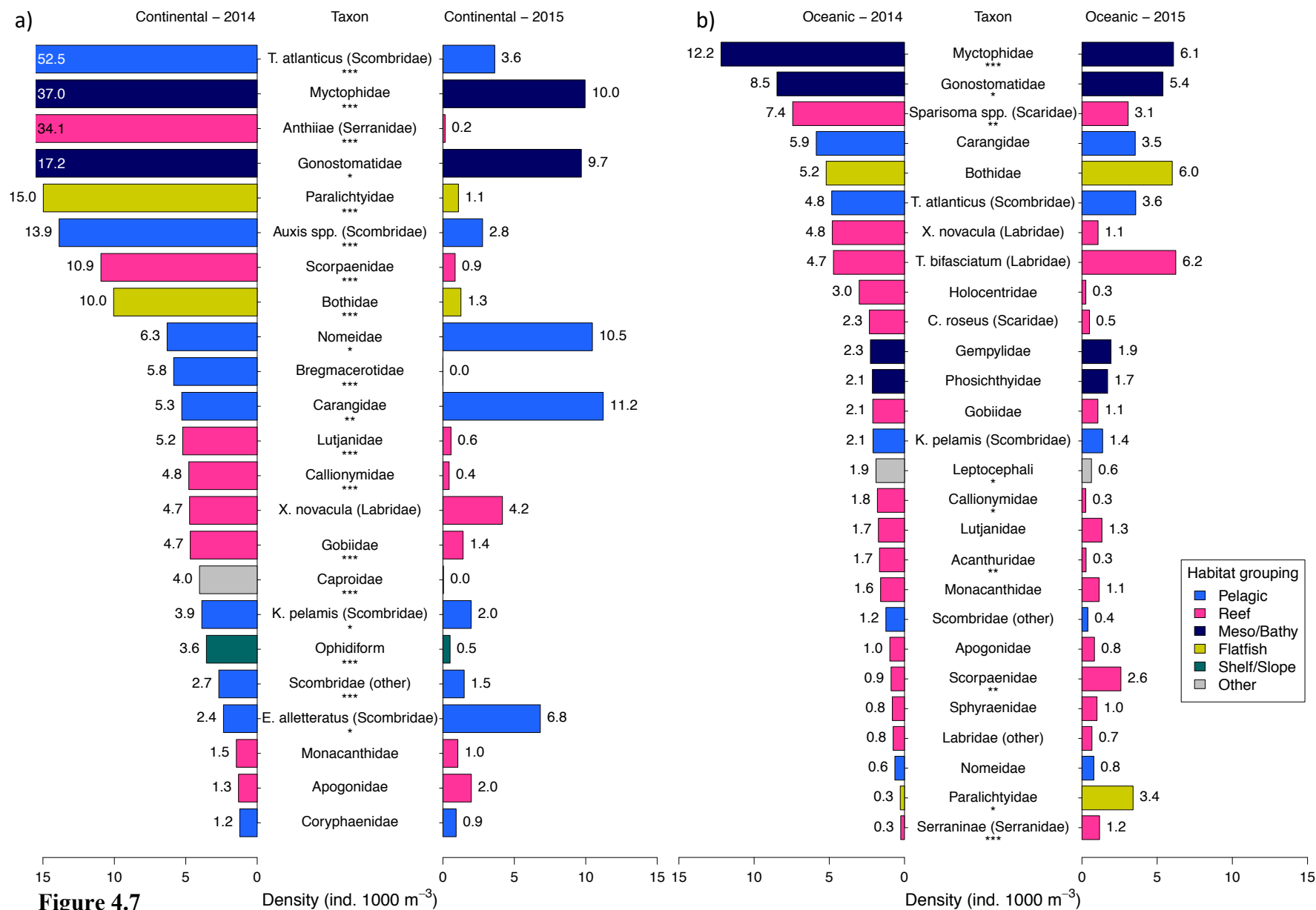


Figure 4.8. Kernel density estimates of standard length (SL) distributions of abundant species and families of larval pelagic and reef fishes sampled with nets in 2014 (blue) versus 2015 (red) in the (a) continental region, and (b) oceanic region. Sample sizes are given since kernel densities are individually scaled. 2014 vs. 2015: Wilcoxon rank sum tests, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

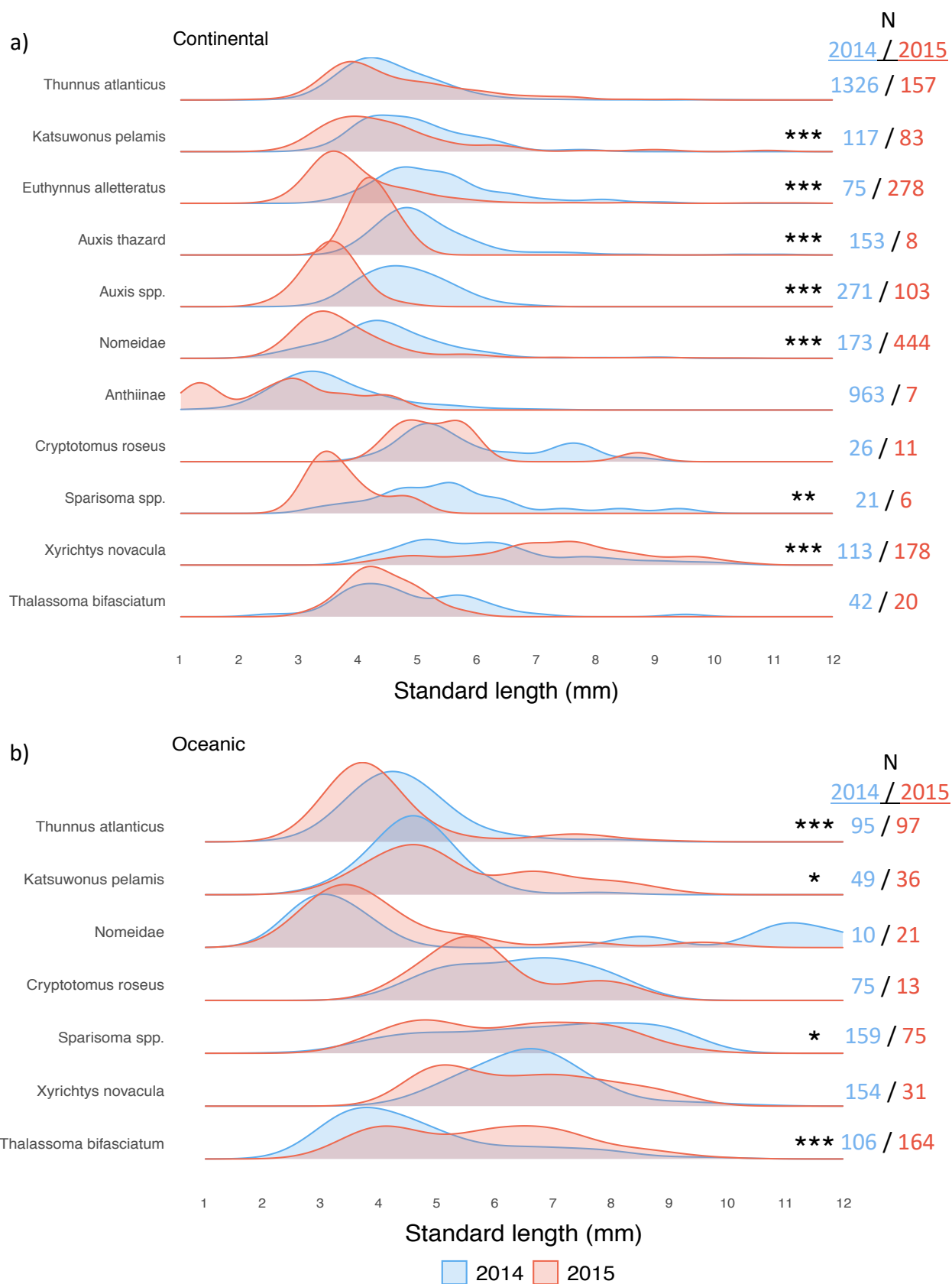


Figure 4.8

Figure 4.9. Linear relationships between densities of abundant taxa of larval (a) reef fishes, (b) flatfishes, and (c,d) tunas and their known prey in the SOF: (a,b,c) calanoid copepods, and (d) appendicularians. Relationships are shown here for correlations > 0.2 from the full analysis (see Supplementary Table C2, C3). Larval fish densities are mean values from replicate net tows in the continental region from (a,b,c) both years and (d) 2014 only. Prey (calanoid copepod and appendicularian) densities are mean values from *ISIIS* half-transects corresponding with net tows. (a) Callionymidae: $r^2 = 0.23$, $p = 0.002$, $n = 36$; Scorpaenidae: $r^2 = 0.25$, $p = 0.001$, $n = 36$, (b) Bothidae: $r^2 = 0.52$, $p = <0.001$, $n = 36$; Paralichthyidae: $r^2 = 0.54$, $p = <0.001$, $n = 36$, (c) *T. atlanticus*: $r^2 = 0.42$, $p = 0.002$, $n = 18$ (15 m depth only, see methods), (d) *Auxis* spp: $r^2 = 0.59$, $p = <0.001$, $n = 16$; *K. pelamis*: $r^2 = 0.53$, $p = 0.001$, $n = 16$; *E. alletteratus*: $r^2 = 0.27$, $p = 0.023$, $n = 16$.

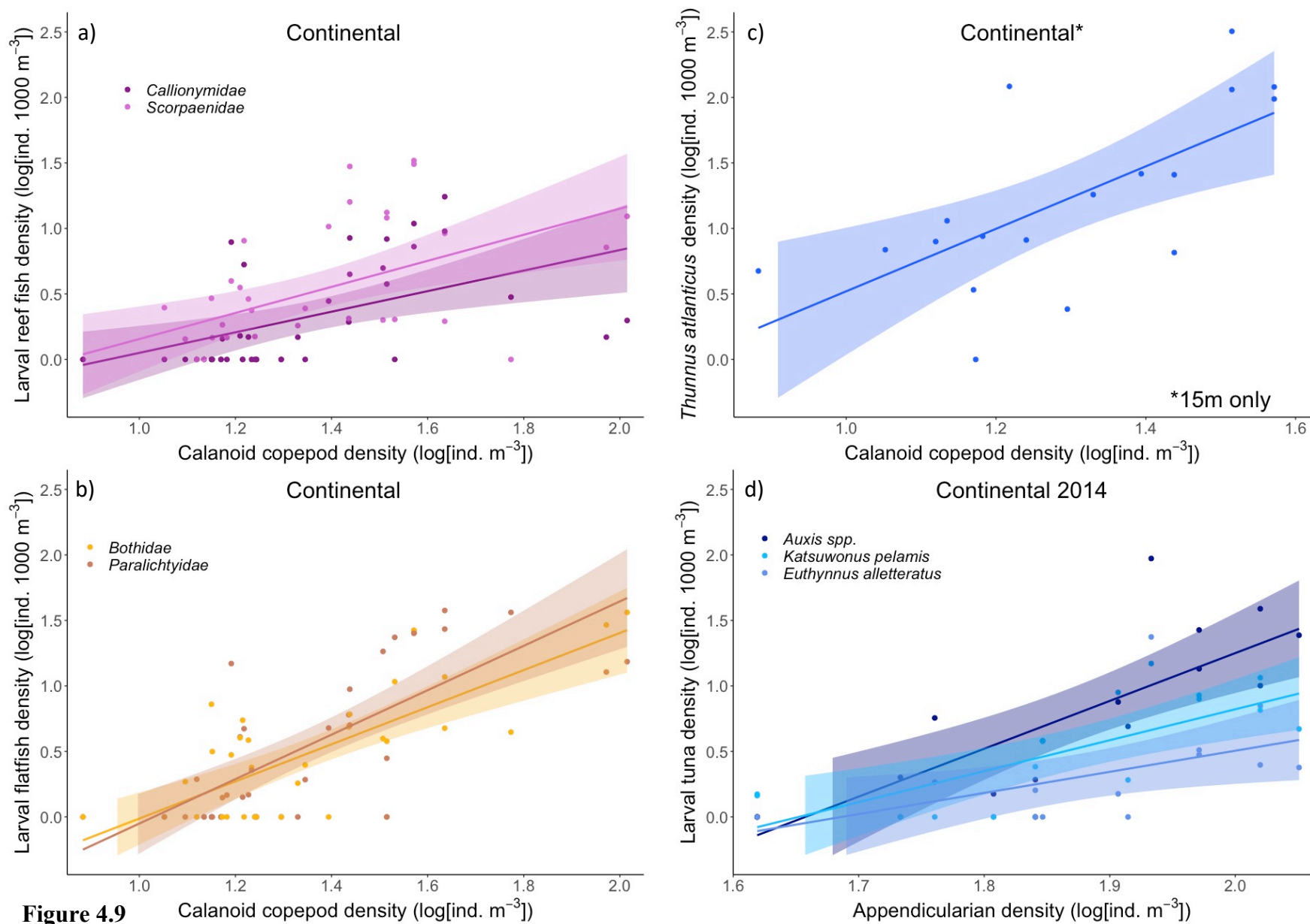
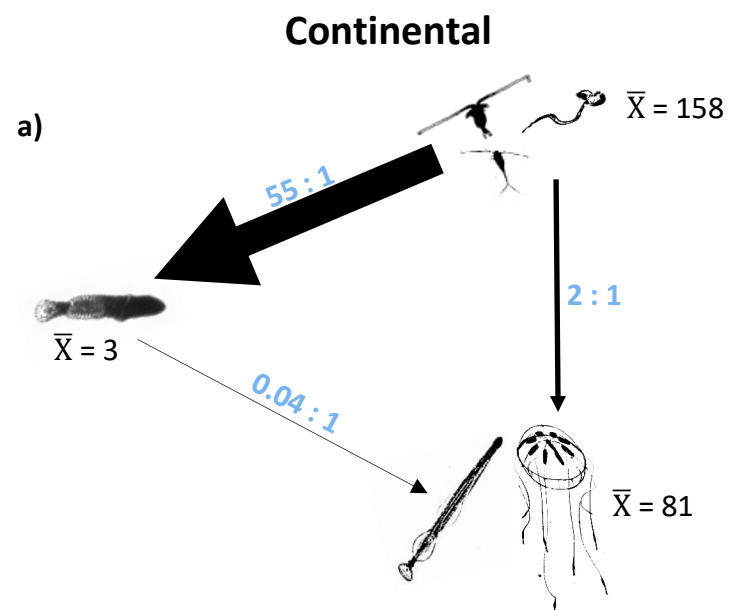
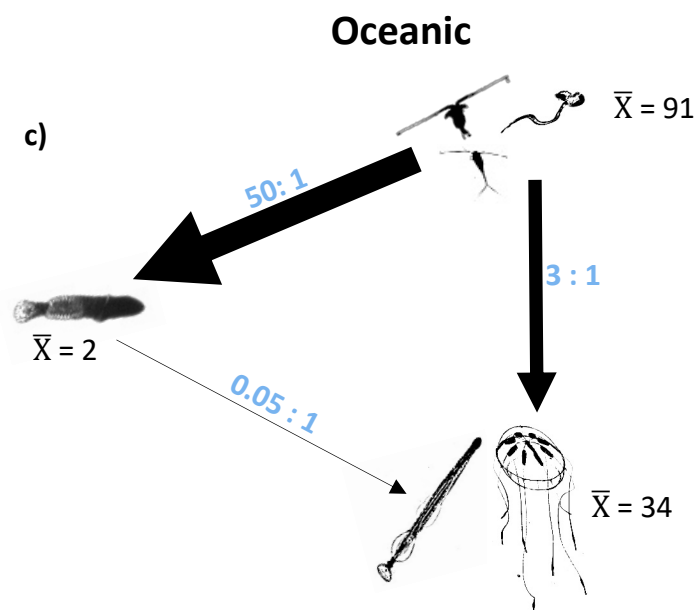


Figure 4.9

Figure 4.10. Schematic of simplified predator-prey interactions between larval fishes, their prey and predators in the continental region in (a) 2014 and (b) 2015, and oceanic region in (c) 2014 and (d) 2015. Mean densities ($\bar{X}$) of larval fishes, prey, and predators from *ISIIS* half-transects are given for each combination of year and region. Arrows point from prey to predator and relative ratios of prey:predator densities (red) associated with each arrow are given. Arrows are scaled to emphasize the differences in relative prey:predator density ratios between years and regions. Prey are the sum of densities of *ISIIS* groups that are potential prey of larval fishes: appendicularians, calanoid, *Oithona*, and other copepods. Predators are the sum of densities of *ISIIS* groups that are potential predators of larval fishes: chaetognaths, siphonophores, hydromedusae, other cnidarians, and ctenophores. An arrow is drawn from the prey of larval fish to the predators of larval fishes to represent a substantial alternative prey for the predators.



2014



2015

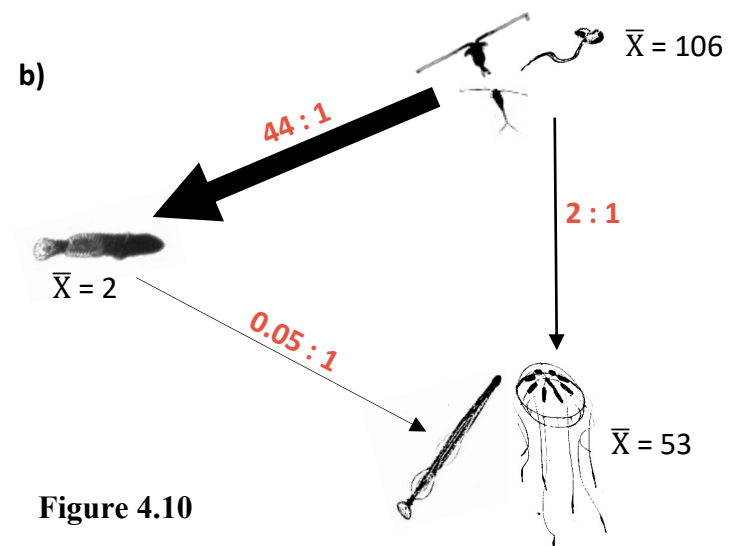
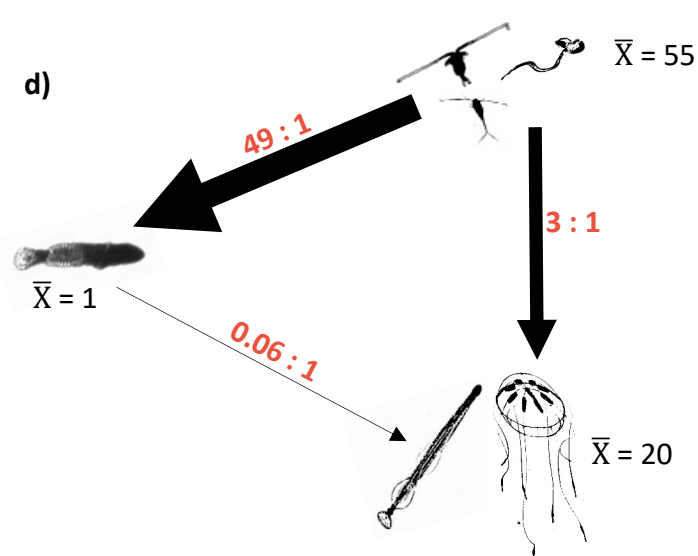


Figure 4.10



CHAPTER 5: GENERAL CONCLUSIONS

Larval fish survival is linked to food web dynamics via a larva's ability to successfully find prey and avoid predation. However, our knowledge of how larval fish diet and growth relate to prey and predator conditions in the natural environment has been limited. To better understand how larval fishes are influenced by predator-prey interactions we utilized a range of sampling systems, (*in situ* imaging, biological net collection), analytical techniques on individual larvae (gut contents and otolith-derived growth analyses), and multivariate statistical approaches. Our sampling encompassed a gradient of prey and predation conditions in the Straits of Florida (SOF), an oligotrophic system, but with regionally enhanced productivity due to physical processes associated with the strong Florida Current.

In Chapter 2, an examination of how fine-scale variability in prey and predator conditions influenced recent larval growth of individual fish larvae revealed that slow-growing (wrasses) and fast-growing (skipjack tuna) larvae had growth patterns that reflected the fine-scale distributions of their prey. Wrasses feeding on patchy prey had faster growth at high prey densities, but also benefitted from dense patches of prey in otherwise low-density regions. In contrast, skipjack tuna had faster larval growth with increasing prey densities, but not patchiness, as their prey were more consistently abundant. Predators also had a strong effect on larval growth patterns. The strength of growth-selective mortality increased with predator densities or occurrence of dense patches of predators, although the direction of selection (e.g., against slow or fast-growers) was taxa specific. Temperature appeared to strongly constrain larval tunas, but not wrasses, evident from growth-temperature relationships that peaked at an optimum intermediate temperature, suggestive of metabolic constraints at high temperatures.

Chapter 3 further demonstrated the dependency of fast-growing tuna larvae (blackfin) on prey availability and the consequences when high temperatures and poor prey conditions coincide. Larvae in high prey-low temperature conditions had fuller guts from eating higher quality prey and faster growth rates; they were larger, older, and more abundant, dominating the larval fish community, compared to blackfin tuna in low prey-high temperatures. Predators and temperature had a strong effect on individual larval fish growth, with strikingly similar patterns to those of the skipjack tunas (Chapter 2). The optimal temperature for

growth for blackfin tuna was well below the thermal maxima for the species, suggesting low prey availability may reduce the thermal optima for fast-growing larvae.

Finally, results of Chapter 4 demonstrated that entire larval assemblages can fluctuate with region-wide changes in prey availability. Quantification of the plankton and larval fish community illustrated contrasting patterns of how larval fishes in coastal-upwelling (continental) compared to oligotrophic (oceanic) conditions respond to interannual variability in productivity. The continental assemblage was dominated by larvae such as fast-growing tunas that were sensitive to variability in prey conditions, with taxon-specific larval abundances positively correlated with that of their prey. The abundance of predators of larval fishes was high in the continental region, but less variable between years. Consequently, a year with higher temperatures coinciding with poor prey conditions coupled further with strong predation pressure had clear consequences for larval survival. In contrast, the oceanic larval assemblage was more consistent over time despite variable prey and temperature conditions. Most of these larvae (e.g., wrasses) have flexible life history traits that are thought to be adaptations to poor or patchy prey environments.

This work connects individual- to community-level responses of larval fishes, illustrating how prey availability is essential to larval fish success and survival. This link was evident between fish larvae and their prey across scales, from taxon-specific fine-scale (meters) distributions of prey, to broader variability across regional productivity (10s kilometers) gradients and years. The contrasting feeding-growth strategies between different types of larvae (wrasses vs. tunas) combined with temperature-growth responses highlighted the sensitivity of larval tunas (and other fast-growing larvae) to environmental variability. Our findings also demonstrated the importance of predation pressure on larval fish in low-latitude regions, with a direct growth-selective effect on larval fish at higher predator densities. Overall these prey, predator, and temperature effects on larval fishes scaled up to community responses, revealing that larval fish in productive continental regions are less resilient to environmental variability than larvae in highly oligotrophic regions with more flexible growth strategies.

Our findings are especially pertinent considering the predicted impacts of climate change in the SOF and other warm-water regions. These changes include increasing temperatures and stratification, which together are likely to result in reduced enrichment

from deep water nutrients and lower productivity (Behrenfeld et al. 2006, Fu et al. 2016). Additionally, the proximity of the SOF to high-density population centers (e.g., South Florida) may result in increasing land-use impacts (e.g., nutrient loading, pollution, resource extraction) on the coastal marine environment (Halpern et al. 2008, Rabalais et al. 2009). With these and other unprecedented future changes, marine systems will face stronger variability in physical processes, environmental variables, and food web dynamics in the future. Our results illustrate the importance of considering food web dynamics when predicting the response of larval fishes, and thus marine fish population replenishment, to ecosystem variability, particularly that associated with ongoing climate change. Our observations of different larval fish feeding-growth strategies that scaled up to community responses are not necessarily unique to warm-water systems, but may occur in other systems where the scope of environmental variability varies over large spatial scales and fish larvae exhibit a range of strategies for survival. For example, larval fishes in any system requiring consistently high prey availability will likely fluctuate in abundance with changes in their prey. Consequently, as future environmental changes impact coastal planktonic food webs, knowledge of larval fish sensitivity or resilience to such changes will be critical in predicting the response of marine fish populations. Future studies in other systems contrasting survival strategies among larval fishes across a range of present conditions can provide important clues to how predator-prey relationships may drive future populations under increasingly variable or prolonged extremes in the environment.

This research addresses fundamental questions in larval fish ecology through a comprehensive examination of the direct influence of prey and predator conditions across different scales of spatial and temporal resolution. The dynamic biophysical drivers of predator and prey distributions, coupled with small scale of individual interactions in a vast ocean have made study of these direct effects previously challenging. With use of a Lagrangian drifter, our sampling was designed explicitly to sample the same water mass with two different systems to almost simultaneously sample larval fishes in the context of their prey and predators. We examined diet, growth, and predator-prey relationships on both an individual and assemblage level, scaling up or down as relevant. However, questions remain about how the range of prey conditions sampled reflects the actual prey field a larva

experiences. Using *in situ* imaging we can begin to answer such questions, and thus link broader patterns to the scale of a larvae.

Ambit of a larval fish

We conducted a pilot analysis as a first attempt to quantify the number of prey an individual larva (captured by *ISIIS* imagery) actually experienced within their foraging ambit (<1m) in the pelagic environment. Since larval fish taxa in the SOF have specific prey preferences (Llopiz & Cowen 2009, Llopiz et al. 2010), we limited the study to a specific larval fish-prey relationship. We focused on *Thunnus atlanticus*, since gut content analyses in Chapter 3 revealed reliance on calanoid copepods, especially in 2014. Additionally, they are often the most abundant larval fish taxa at 15 m depth and rarely co-occur at this depth with other larval tunas, thus we can be confident that any larval fish imaged by *ISIIS* with a scombrid body shape is likely *T. atlanticus*. Using scombrid *ISIIS* images, we calculated the number of calanoid copepods within a range of horizontal distances of up to 1 m from the larva (i.e. 1-8 *ISIIS* images frames at 0.13 m width). We calculated these values for all scombrids (n = 23-64) in three *ISIIS* half-transects with a range of calanoid copepod mean densities.

Based on the selected half-transects, larval *T. atlanticus* rarely co-occurred in the same frame as their calanoid copepod prey. This result was consistent across the range of mean half-transect calanoid copepod densities (15 – 33 ind. m⁻³), suggesting that even in regions of the SOF with the highest densities, larval *T. atlanticus* are required to expend energy to search for calanoid copepod prey by swimming. Larval tunas are highly visual predators, but planktivorous larvae are likely only able to visually detect prey within a few body lengths (Reglero et al. 2011), thus <25 mm for a 5 mm larva. Beyond within-frame distances, the number of *in situ* calanoid copepods scaled closely with mean half-transect calanoid copepod densities. This translated to larvae existing in a high (33 calanoids m⁻³) compared to low (15 calanoids m⁻³) prey regions encountering almost twice the number of calanoids within distances of >0.25 m. For example within a horizontal distance of ~0.40 m from a larval fish, there was an average of one calanoid copepod in a low-density calanoid region, and two calanoids in a high-density calanoid region. Gut contents analysis on larvae in net tows associated with these half-transects revealed larvae had 2-6 calanoid copepods in

their gut, in addition to a similar number of small nauplii and occasionally an appendicularian or *Farranula* copepod (Chapter 3). While we do not know how often these prey move through the gut, if we use the most conservative value that these represent total larval fish feeding activity in a day, we can estimate larval swimming distances. Thus, larvae must be swimming a minimum horizontal distances of 0.4 – >1 m (60 – >150 body lengths) to locate ample calanoid copepod prey. However, actual swim distances are likely greater given that larvae may be feeding on more individual copepods each day as well as larval behavior associated with successfully attacking, capturing, and ingesting prey. Thus, a significant amount of energy is required for these fast growers to sustain their growth rate. While greater availability and consumption of calanoid copepods is directly related to larval success of *T. atlanticus* (Chapter 3, 4), they are generalist feeders with individuals also consuming small nauplii and other prey across a range of sizes. Given the longer swim distances required to locate calanoid copepods, we hypothesize that the smaller nauplii encountered serve as “snacks” to fuel continuous high-energy foraging activities for larger, higher quality “meals” like calanoid copepods that translate to faster growth.

The results of this pilot analysis highlight the insights that *in situ* imaging can provide to connect information about larval success at the scale of a larva to population-level patterns. While it is intuitive that *in situ* prey availability scales with mean densities, this was surprising due to the expectation of plankton patchiness introducing spatial heterogeneity at fine-scales. In Chapter 2 we used *frequency elevated* (FE) to examine prey patchiness with the frequency of elevated fine-scale densities, finding appendicularians to be consistently abundant (FE = 2-5%) and ‘other copepods’ (e.g., Corycaeidae) to be more patchy (FE = 2-14%). In comparison, calanoid copepods were less patchy (FE = 3-7%). Consequently, when zooplankton prey (or predators) of larvae are consistently abundant (compared to patchy), integrating densities over broader distances (4-8 km in this study) may be representative of *in situ* concentrations. In contrast, we expect that rare or patchy plankton will not scale up or down as smoothly. For a full examination, a similar analysis should be conducted across a broader range of prey densities and for other larval fish-prey relationships (e.g., wrasses with patchy prey).

With this analysis we provide an approach for future studies to examine continuities, or discontinuities, between events occurring on the scale of a larval fish and larger population

scales. Our preliminary findings show how *in situ* imaging of wild populations is a valuable tool to accomplish this. While averaging over <10 km distances may scale well with *in situ* densities of abundant organisms, such integration will not capture patchy distributions, or distributions that change across regions with sharp environmental gradients over short distances (e.g., fronts, river plumes). With new technologies, such as *in situ* imaging, we can now tackle previously unanswered, yet fundamental questions in larval fish ecology. As our planet faces ever increasing unprecedented changes, we are more equipped to push the boundaries of our knowledge to better understand climate change, the impacts on the marine environment, and solutions for a more sustainable future.

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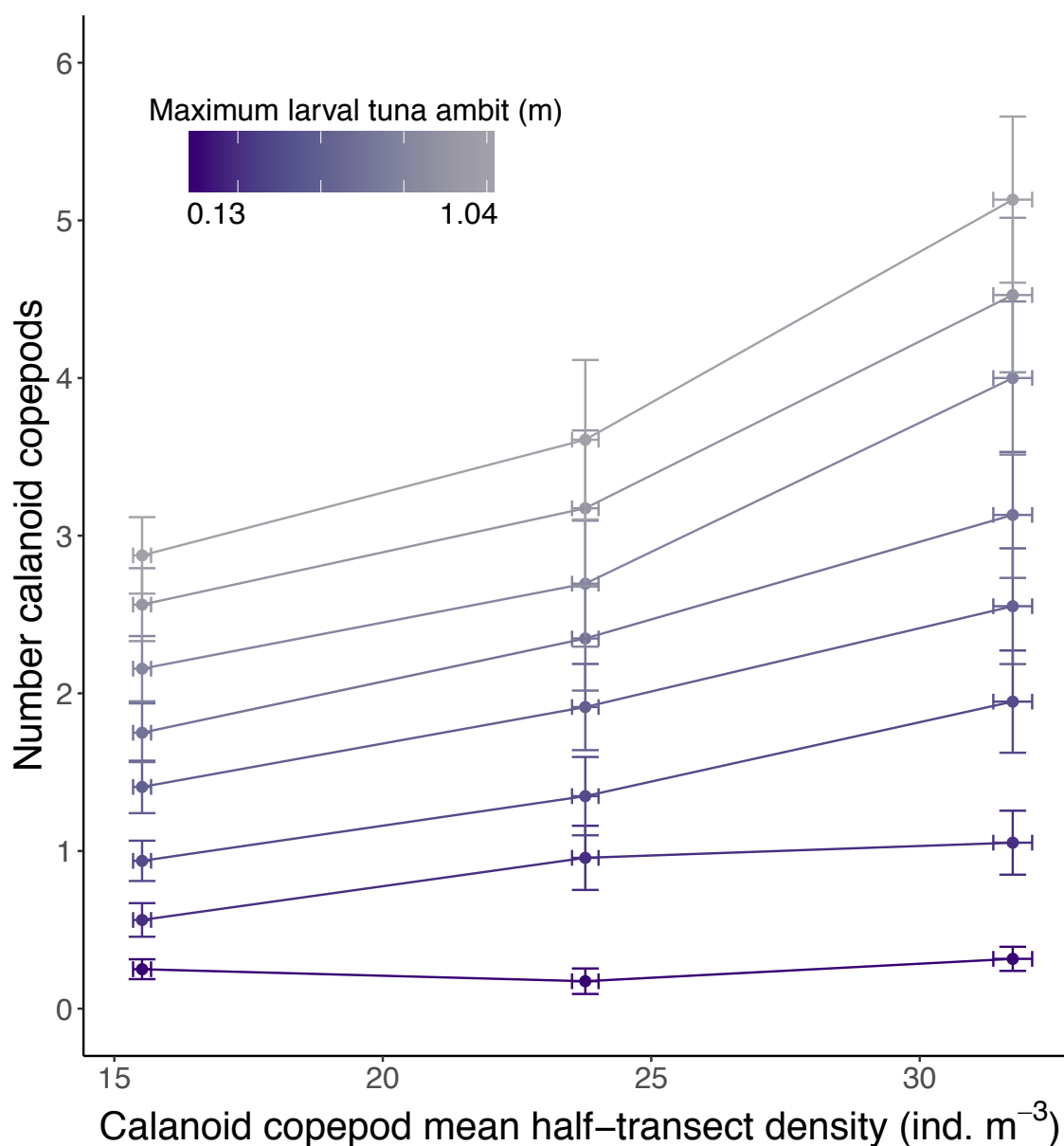


Figure 5.1. Relationships between the numbers of calanoid copepods (from *ISIIS* imagery) within the foraging ambit of larval *Thunnus atlanticus* (blackfin tuna) compared to mean calanoid copepod densities in the associated *ISIIS* half-transect. Half-transects sampled at 15 m depth in locations in the western (continental) Straits of Florida at two locations offshore Miami and one offshore Key Largo. Counts of calanoid copepods were based on number of individuals in the same *ISIIS* frame as the larva, as well as up to 1-7 frames (inclusive of prior frames) before and after the frame with the larva. Since we cannot be certain of within-frame locations of the larva and/or prey, maximum distances based on 13 cm *ISIIS* frame widths are used. Mean values calculated from a subset of fish images confirmed to be scombrids (tunas; $n = 23, 38, 64$) from *ISIIS* half-transects in regions where the majority of larval tunas were *T. atlanticus* (Chapter 3).

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APPENDICES

APPENDIX A – CHAPTER 2 SUPPLEMENTARY TABLES AND FIGURES

Figure A1. Model results of the partial effect of (a) prey background density (*BD*), (b) prey frequency elevated (*FE*), and (c) temperature on recent growth of *Thalassoma bifasciatum*. Predicted recent growth is expressed as a detrended growth index. Fitted lines, 95% confidence intervals (grey shaded areas) and partial residuals (dots) are shown; whiskers on x-axes are field observations for that covariate.

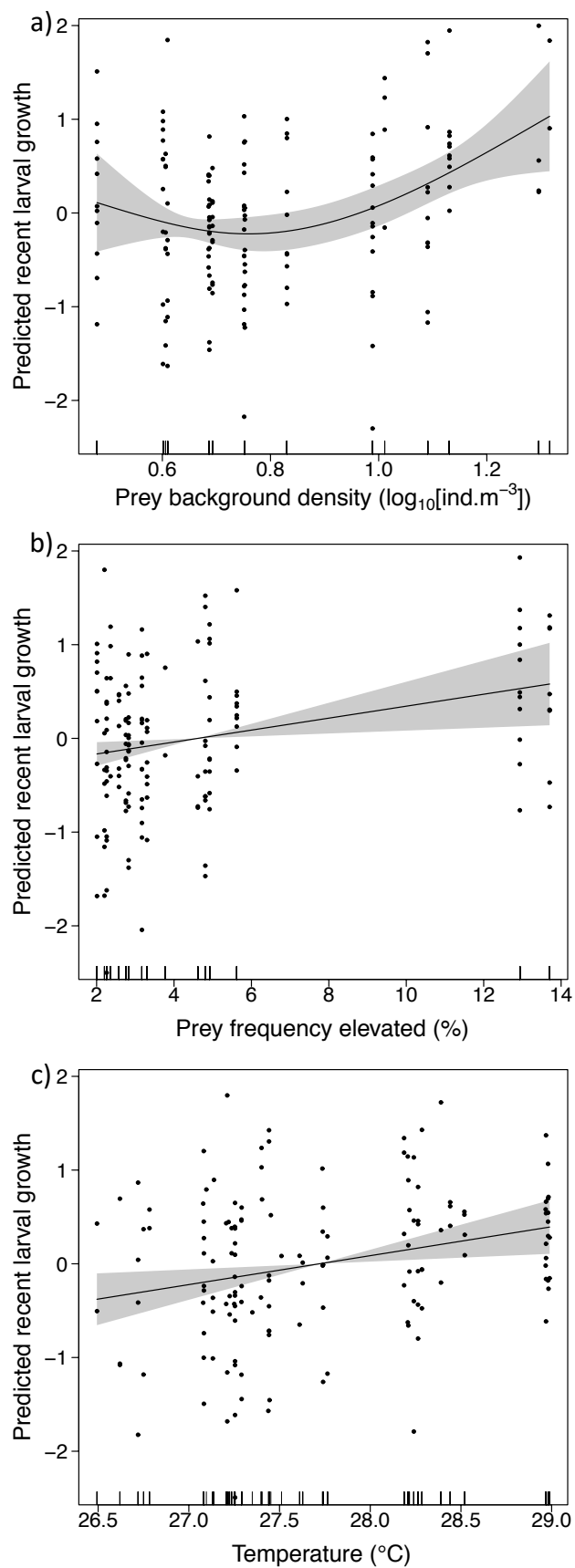
**Figure A1.**

Figure A2. Model results of the partial effect of (a) prey background density (*BD*), (b) prey frequency elevated (*FE*), (c) predator *BD*, (d) predator *FE*, and (e) temperature on recent growth of *Xyrichtys novacula*. Predicted recent growth is expressed as a detrended growth index. Fitted lines, 95% confidence intervals (grey shaded areas) and partial residuals (dots) are shown; whiskers on x-axes are field observations for that covariate.

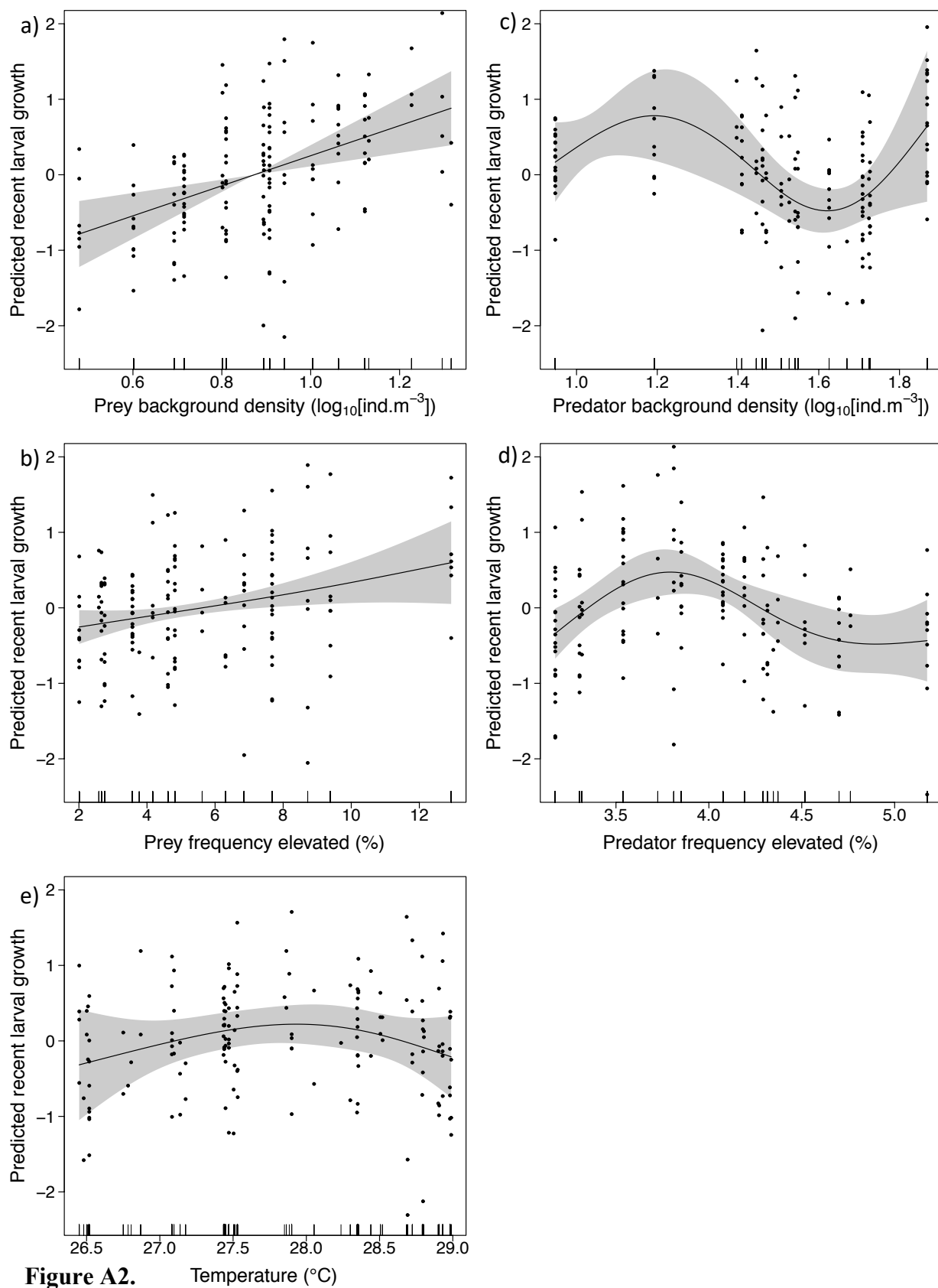
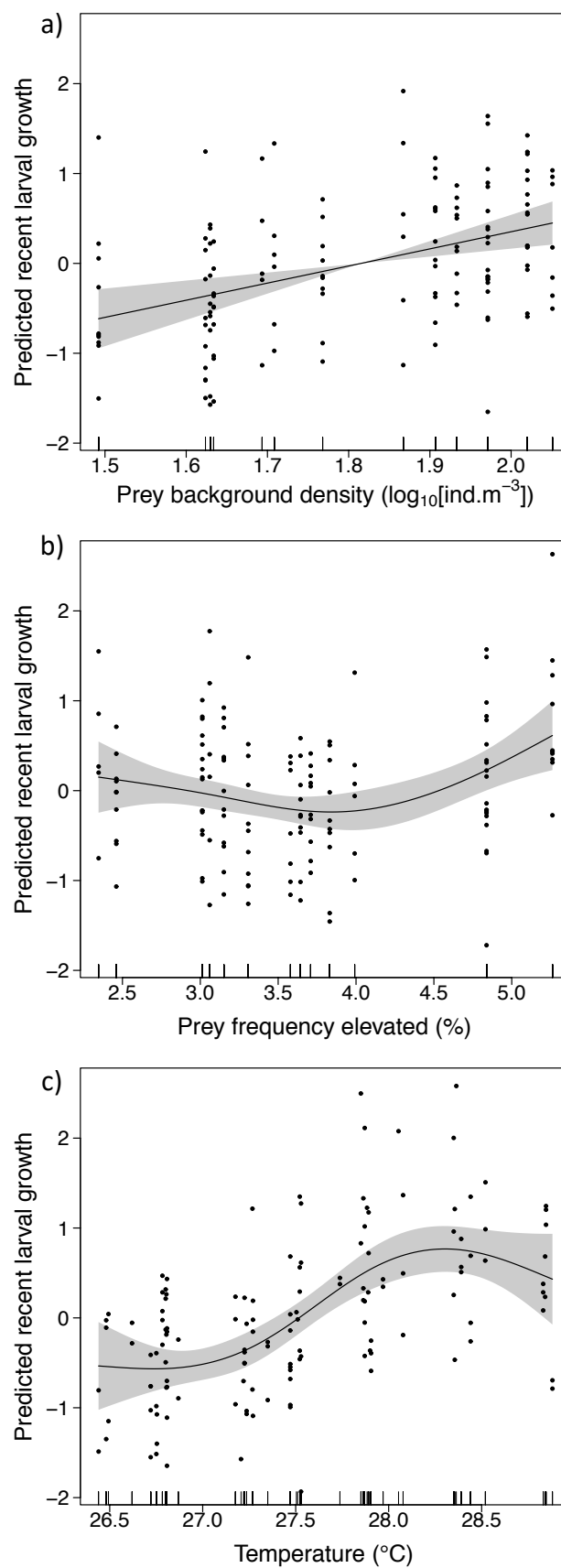


Figure A2. Temperature ($^{\circ}\text{C}$)

Figure A3. Model results of the partial effect of (a) prey background density (*BD*), (b) prey frequency elevated (*FE*), and (c) temperature on recent growth of *Katsuwonus pelamis*. Predicted recent growth is expressed as a detrended growth index. Fitted lines, 95% confidence intervals (grey shaded areas) and partial residuals (dots) are shown; whiskers on x-axes are field observations for that covariate.

**Figure A3.**

APPENDIX B – CHAPTER 3 SUPPLEMENTARY TABLES AND FIGURES

Table B1. Summary of diet data for larval *Thunnus atlanticus* collected in the Straits of Florida. Feeding incidence is the percentage of larvae containing at least one prey item, and the diet is described with both numerical percentages of prey types (%N) and the frequencies of occurrence of prey types (%FO), defined as the percentage of feeding larvae with the prey type present. Includes piscivorous and >7 mm SL larvae.

	2014								2015							
	All		West		Central		East		All		West		Central		East	
	larvae, n = 161		114		32		15		144		88		16		40	
	prey, n = 925		619		254		52		732		436		172		124	
	Size Range (mm SL) 3.2 - 10.7		3.7 - 10.7		3.8 - 8.1		3.2 - 5.1		3.2 - 8.8		3.5 - 7.7		3.4 - 8.8		3.2 - 4.9	
Feeding incidence	0.98		0.97		1.00		1.00		0.99		1.00		1.00		0.95	
Prey type	%N	%FO	%N	%FO	%N	%FO	%N	%FO	%N	%FO	%N	%FO	%N	%FO	%N	%FO
Cladocera																
<i>Evadne</i> sp.	1.0	5.6	0.6	3.5	2.0	15.6	0.0	0.0	1.2	4.9	0.7	3.4	1.7	12.5	2.4	5.0
Unknown	0.6	3.1	0.6	2.6	0.8	6.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Copepoda																
Calanoida	28.9	64.0	25.8	57.0	37.0	84.4	25.0	73.3	9.4	31.3	8.7	28.4	6.4	37.5	16.1	35.0
<i>Farranula</i> sp.	8.2	29.2	8.7	29.8	8.3	37.5	1.9	6.7	3.8	11.1	5.3	13.6	2.3	18.8	0.8	2.5
Harpacticoida	0.1	0.6	0.0	0.0	0.4	3.1	0.0	0.0	0.3	1.4	0.2	1.1	0.0	0.0	0.8	2.5
<i>Oithona</i> sp.	0.3	1.9	0.3	1.8	0.4	3.1	0.0	0.0	0.3	1.4	0.5	2.3	0.0	0.0	0.0	0.0
<i>Oncaea</i> sp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.7	0.0	0.0	0.0	0.0	0.8	2.5
Unknown	3.5	16.8	3.1	14.9	3.9	25.0	5.8	13.3	1.2	4.9	0.7	3.4	1.7	6.3	2.4	7.5
Nauplius	15.8	39.8	15.5	36.8	15.4	50.0	21.2	40.0	21.4	47.9	23.6	52.3	10.5	50.0	29.0	37.5
Pteropod																
<i>Limacina</i> sp.	0.1	0.6	0.2	0.9	0.0	0.0	0.0	0.0	0.3	1.4	0.5	2.3	0.0	0.0	0.0	0.0
<i>Cuvierina</i> sp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.7	0.2	1.1	0.0	0.0	0.0	0.0
Cirripedia, nauplius	6.2	16.1	3.7	14.0	13.0	28.1	1.9	6.7	4.6	18.1	5.0	19.3	4.1	25.0	4.0	12.5
Other crustacean nauplius	10.8	32.9	12.3	33.3	8.3	37.5	5.8	20.0	28.4	46.5	21.6	44.3	51.2	87.5	21.0	35.0
Appendicularia	5.4	14.9	6.9	16.7	1.6	9.4	5.8	13.3	11.2	30.6	13.5	37.5	12.2	56.3	1.6	5.0
Larval fish	3.1	10.6	4.5	14.0	0.4	3.1	0.0	0.0	2.7	9.0	4.6	14.8	0.0	0.0	0.0	0.0
Phytoplankton	0.2	1.2	0.2	0.9	0.4	3.1	0.0	0.0	0.5	2.8	0.7	3.4	0.0	0.0	0.8	2.5
Tintinnid	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.4	2.1	0.5	2.3	0.0	0.0	0.8	2.5
Unknown crustacean rem.	15.7	49.1	17.3	50.9	8.3	34.4	32.7	66.7	10.9	27.8	11.7	27.3	4.1	18.8	17.7	32.5
Unknown soft rem.	0.1	0.6	0.2	0.9	0.0	0.0	0.0	0.0	2.9	5.6	2.1	3.4	5.8	18.8	1.6	5.0

Table B1.

Table B2. Summary of diet data for larval *Thunnus atlanticus* collected in the Straits of Florida. Feeding incidence is the percentage of larvae containing at least one prey item, and the diet is described with both numerical percentages of prey types (%N) and the frequencies of occurrence of prey types (%FO), defined as the percentage of feeding larvae with the prey type present. Includes piscivorous and >7 mm SL larvae.

		Biomass %							
		2014				2015			
		All	West	Central	East	All	West	Central	East
larvae, n =		140	95	30	15	120	71	9	40
prey, n =		868	567	249	52	557	353	80	124
Size Range (mm SL)		3.2-6.9	3.7-6.9	3.8-6.3	3.2-5.1	3.2-7.0	3.5-6.9	3.4-7.0	3.2-4.9
Prey type									
Cladocera									
<i>Evadne</i> sp.		1.6	0.9	3.4	0.0	4.1	3.0	10.4	11.1
Unknown		1.0	0.9	1.4	0.0	0.0	0.0	0.0	0.0
Copepoda									
Calanoida		41.4	37.7	56.9	37.9	11.0	11.2	19.6	24.7
<i>Farranula</i> sp.		19.3	21.8	18.2	7.2	11.6	19.5	13.8	1.8
Harpacticoida		0.2	0.0	0.6	0.0	0.2	0.4	0.0	0.2
<i>Oithona</i> sp.		0.1	0.1	0.1	0.0	0.2	0.3	0.0	0.0
<i>Oncaea</i> sp.		0.0	0.0	0.0	0.0	0.2	0.0	0.0	1.4
Unknown		4.1	3.5	6.0	4.3	0.9	0.6	0.0	4.2
Nauplius		1.9	2.2	1.5	3.7	3.5	4.8	3.7	4.9
Pteropod									
<i>Limacina</i> sp.		1.6	2.5	0.0	0.0	0.0	0.0	0.0	0.0
<i>Cuvierina</i> sp.		0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Cirripedia, nauplius		0.3	0.2	0.6	0.1	0.4	0.5	0.5	0.5
Other crustacean nauplius		8.2	10.8	4.0	5.3	21.3	27.6	26.0	34.2
Appendicularia		4.8	6.4	1.3	11.9	13.4	21.9	16.2	4.6
Phytoplankton		0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Tintinnid		0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Unknown crust. rem.		10.9	12.9	6.0	29.6	6.3	9.0	5.1	8.8
Unknown soft rem.		0.1	0.1	0.0	0.0	1.5	1.2	4.7	3.4

Table B3. Summary of linear regressions between *Thunnus atlanticus* body depth (mm) vs. age (days), and body depth (mm)/standard length (SL; mm) vs. age. N = 133 (2014) and 109 (2015). Excludes piscivorous and >7 mm SL larvae.

Relationship	Year	Slope	Intercept	r ²	p
Body depth vs. Age	2014	0.21	-0.18	0.71	<0.001
	2015	0.16	0.19	0.72	<0.001
Body depth/SL vs. Age	2014	0.02	0.18	0.42	<0.001
	2015	0.01	0.22	0.39	<0.001

Table B4. Summary of ANCOVA (Type 1 SS ANOVA table) for *Thunnus atlanticus* body depth (mm) vs. age (days), body depth (mm)/standard length (SL; mm) vs. age with/without temperature as a covariate. N = 133 (2014) and 109 (2015). Excludes piscivorous and >7 mm SL larvae.

Response	Source of variation	df	Mean square	F	<i>p</i>
Body depth	Age	1	22.13	626.11	<0.001
	Year	1	0.04	1.15	0.285
	Age * Year	1	0.32	8.97	0.003
	Error	257	0.04		
Body depth	Age	1	22.13	658.17	<0.001
	Year	1	0.04	1.21	0.273
	Temp (covariate)	1	0.50	14.98	<0.001
	Age * Year	1	0.26	7.63	0.006
	Error	256	0.03		
Body depth/SL vs. Age	Age	1	0.09	151.53	<0.001
	Year	1	0.01	11.80	<0.001
	Age * Year	1	<0.01	5.10	0.025
	Error	257	<0.01		
Body depth/SL vs. Age	Age	1	0.09	151.03	<0.001
	Year	1	0.01	11.76	<0.001
	Temp (covariate)	1	<0.01	0.42	0.518
	Age * Year	1	<0.01	4.88	0.028
	Error	256	<0.01		

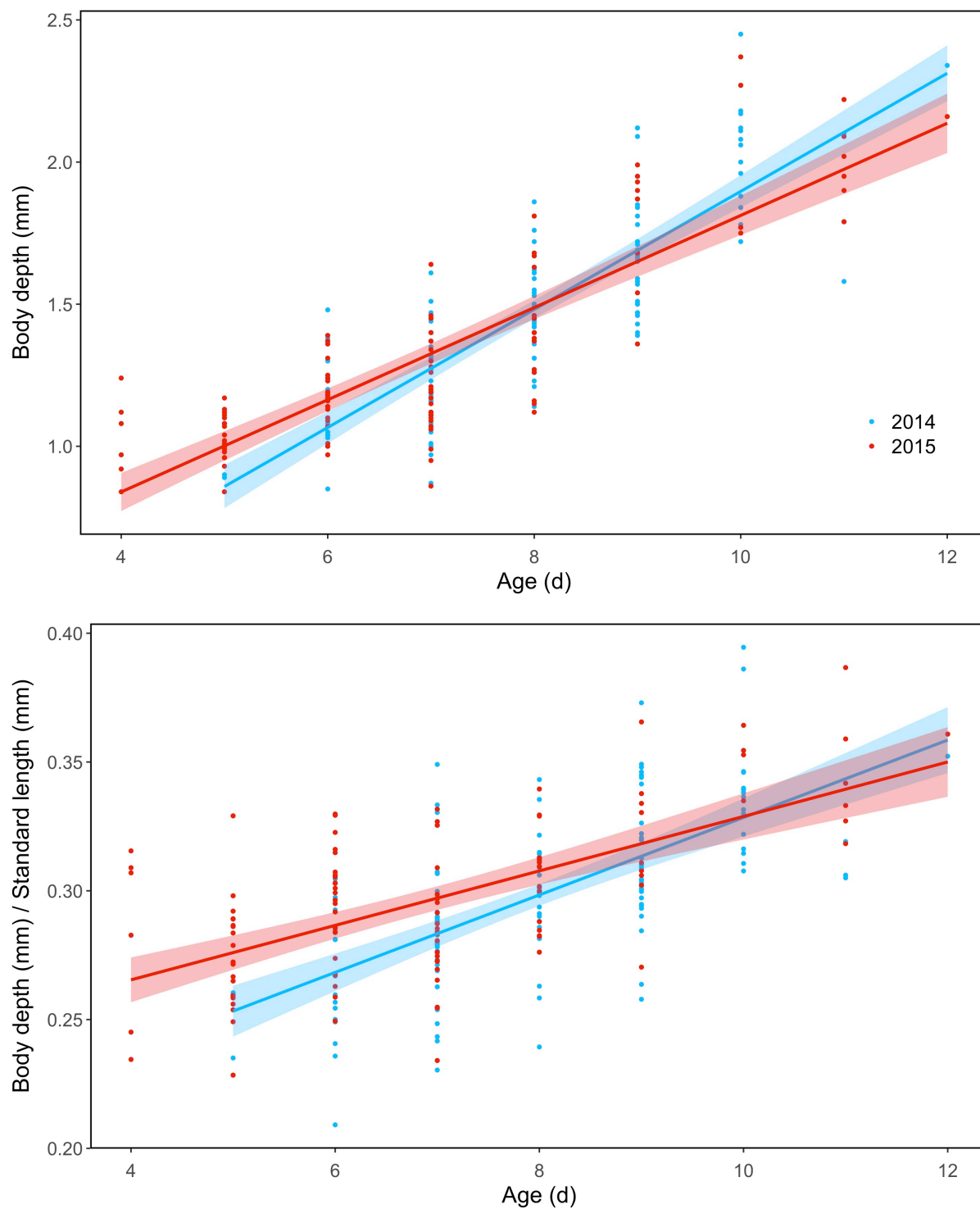


Figure B1. *Thunnus atlanticus* body depth (mm) vs. age (days), body depth (mm)/standard length (SL; mm) vs. age. N = 133 (2014) and 109 (2015). Excludes piscivorous and >7 mm SL larvae.

APPENDIX C – CHAPTER 4 SUPPLEMENTARY TABLES AND FIGURES

Table C1. Mean densities (ind. m⁻³) of all plankton groups rounded to the nearest whole organisms sampled in *ISIIS* half-transects in each combination of region and year. Groups listed in order of abundance based on overall mean sampled.

Group	Continental		Oceanic		Overall mean n = 64
	2014 n = 16	2015 n = 20	2014 n = 16	2015 n = 12	
Diatoms	292	233	156	66	189
Trichodesmium	146	206	29	66	129
Protists	95	157	49	156	114
Appendicularia	76	51	46	32	52
Pelagic tunicates	50	47	25	24	38
Calanoid copepods	41	15	28	11	24
<i>Oithona</i> copepods	36	26	14	6	22
Chaetognaths	32	24	7	7	18
Siphonophores	23	10	19	8	15
Echinoderm larvae	21	11	12	8	13
Hydromedusae	11	9	5	3	7
Other copepods*	7	8	5	5	6
Pteropods	6	5	1	2	4
Larval fish	3	2	2	1	2
Cnidaria (other)	3	2	1	0	2
Ctenophore	2	0	2	0	1
Decapods	1	1	0	0	1
Euphausiids	0	1	0	1	1
Polychaetes	1	0	0	0	1

* a morphological classification including copepods without visible antennae

Table C2. Mean temperature, salinity, chlorophyll *a* (chl *a*), and mixed layer depth (MLD) sampled in the Straits of Florida 2014 and 2015. Data shown for all regions combined and individual cross-strait regions. Temperature and salinity were sampled with a MOCNESS net system at 15 m and 30 m, chl *a* and MLD were sampled with the *In Situ* Ichthyoplankton Imaging System (*ISIIS*) from the surface to 40 m, thus sample sizes differ. Mean and range are reported.

Nets (15m & 30m)	2014			2015		
	All	Continental	Oceanic	All	Continental	Oceanic
Temperature (°C)	27.2 (25.8-28.3)	26.9 (25.8-28.3)	27.4 (27.0-27.8)	28.5 (27.7-29.0)	28.5 (27.7-28.9)	28.5 (27.9-29.0)
Salinity	36.3 (36.2-36.5)	36.4 (35.3-36.4)	36.3 (36.2-36.5)	36.1 (35.9-36.2)	36.1 (35.9-36.2)	36.2 (36.1-36.2)
n	128	64	64	128	80	48
<i>ISIIS</i> Undulation (0-40m)						
Chlorophyll <i>a</i> (mg L ⁻¹)	0.05 (0.05-0.09)	0.06 (0.05-0.09)	0.05 (0.05-0.05)	0.1 (0.1-0.1)	0.1 (0.1-0.1)	0.1 (0.1-0.1)
Mixed layer depth (m)	31.0 (±2.2)	24.9 (±2.8)	37.2 (±1.5)	27.7 (±1.9)	24.8 (±1.7)	32.6 (±3.5)
n	8	4	4	8	5	3

Table C3. Mean densities (ind. 1000 m⁻³) of all larval fish taxa sampled in net tows in each combination of region and year. Mean calculated from individual nets. Taxa listed in alphabetical order. *denotes order, superorder.

Family	Species	Continental		Oceanic	
		2014 n = 64	2015 n = 80	2014 n = 64	2015 n = 48
Acanthuridae	<i>Acanthurus</i> spp.	2.5	0.1	1.7	0.3
Acropomatidae	spp.				0.1
Alepisaruidae	spp.				0.1
Antennariidae	spp.	<0.1			
Apogonidae	spp.	1.3	2.0	1.0	0.8
Ariommatidae	<i>Ariomma</i> spp.	1.8		0.1	
Aulostomidae	<i>Aulostomus maculatus</i>			0.1	
Balistidae	spp.	1.1	0.5		0.1
Blenniodei*	spp.			0.1	
Bothidae	spp.	10.0	1.3	5.2	6.0
Bramidae	spp.	0.3	0.1	0.3	<0.1
Bregmacerotidae	<i>Bregmaceros</i> spp.	5.8		0.1	
Callionymidae	spp.	4.8	0.4	1.8	0.3
Caproidae	<i>Antigonia</i> spp.	4.0	0.0	0.1	<0.1
Carangidae	<i>Alectis ciliaris</i>		11.2		
	<i>Selar crumenophthalmus</i>		0.1		<0.1
	spp.	5.3		5.9	3.5
Carapidae	spp.			0.1	
Ceratioidei*	spp.	0.3	0.2	0.2	0.1
Chaetodontidae	<i>Chaetodon</i> spp.	0.6	0.2	0.4	0.1
Chiasmodontidae	spp.	<0.1			
Chlorophthalmidae	<i>Parasudis truculenta</i>	<0.1		<0.1	
	spp.	0.8	0.1	0.2	0.4
Coryphaenidae	<i>Coryphanea</i> spp.	1.2	0.9	0.1	0.1
Cynoglossidae	<i>Symphurus</i> spp.	1.0	<0.1	<0.1	
Dactylopteridae	<i>Dactylopterus volitans</i>		0.1		0.0
Diodontidae	spp.	0.1		0.1	
Echeneidae	spp.	0.2	0.1		
Elopomorpha*	spp.	1.6	0.7	1.9	0.6
Evermannellidae	spp.		<0.1	0.2	<0.1
Exocoetidae					
Fistulariidae	<i>Fistularia</i> spp.	0.2	<0.1		

Family	Species	Continental		Oceanic	
		2014 n = 64	2015 n = 80	2014 n = 64	2015 n = 48
Gempylidae	spp.	1.1	0.7	2.3	1.9
Gerreidae	spp.				
Giganturidae	<i>Gigantura</i> spp.	<0.1		<0.1	<0.1
Gobiidae	spp.	4.7	1.4	2.1	1.1
Gonostomatidae	spp.	17.2	9.7	8.5	5.4
Hemiramphidae					
Holocentridae	spp.	0.3	<0.1	3.0	0.3
Howellidae	spp.	<0.1			
Ipnopidae	spp.		<0.1		
Istiophoridae	spp.	0.2			<0.1
Kyphosidae	<i>Kyphosus</i> spp.			<0.1	
Labridae	<i>Clepticus parrae</i>	0.3	<0.1	0.4	0.4
	<i>Decodon puellaris</i>	<0.1			
	<i>Doratonotus megalepis</i>	0.1			
	<i>Halichoeres</i> spp.	0.7		0.2	0.2
	<i>Thalassoma bifasciatum</i>	1.8	0.5	4.7	6.2
	<i>Xyrichtys</i> spp.	4.7	4.2	4.8	1.1
	spp.	0.2		0.1	<0.1
Lampridae	<i>Lampris guttatus</i>				
Lampridiformes (order)	spp.	<0.1			
Lophidae	spp.		0.1		
Lutjanidae	<i>Etelis oculatus</i>			0.1	
	<i>Pristipomoides</i> spp.	2.0	0.4	0.1	<0.1
	<i>Rhomboplites aurorubens</i>	1.3			
	spp.	1.9	0.1	1.6	1.3
Luvaridae	<i>Luvarus imperialis</i>	<0.1			
Malacanthidae	spp.	0.2		0.1	
Microdesmidae	spp.		<0.1	<0.1	
Monacanthidae	spp.	1.5	1.0	1.6	1.1
Mugilidae	spp.	0.1		0.2	
Mullidae					
Myctophidae	spp.	37.0	10.0	12.2	6.1
Neoscopelidae	spp.	<0.1			
Nomeidae	spp.	6.3	10.5	0.6	0.8

Family	Species	Continental		Oceanic	
		2014 n = 64	2015 n = 80	2014 n = 64	2015 n = 48
Notosudidae	spp.				0.2
Ogcocephalidae	spp.	1.1	0.2		<0.1
Ophidiform	spp.	3.6	0.5	0.4	0.1
Ostraciidae	spp.	0.2		<0.1	
Paralepididae	spp.	0.4	<0.1	0.7	
Paralichthyidae	spp.	15.0	1.1	0.3	3.4
Phosichthyidae	spp.	2.6	0.1	2.1	1.7
Pomacanthidae	spp.	0.8	0.3	0.1	<0.1
Pomacentridae	<i>Abudefduf</i> spp.				
	<i>Abudefduf saxatilis</i>				
	<i>Chromis</i> spp.	<0.1		0.2	
	<i>Stegastes</i> spp.	0.5		0.1	
	<i>Stegastes partitus</i>	1.1		0.9	0.2
Pomacentridae	spp.	0.1	0.3	0.3	<0.1
		2.5	0.5	0.7	0.5
Priacanthidae					
Rachycentridae	<i>Rachycentron canadum</i>	<0.1			
Scaridae	<i>Cryptotomus roseus</i>	0.1	0.1	2.3	0.5
	<i>Scarus</i> spp.	0.9	0.3	0.3	0.5
	<i>Sparisoma</i> spp.	0.2	0.2	7.4	3.1
	spp.	0.7	0.1	0.1	<0.1
Scombridae	<i>Acanthocybium solandri</i>	1.2	0.5		
	<i>Auxis</i> spp.	8.8	2.6		0.2
	<i>Auxis thazard</i>	5.1	0.2	0.1	
	<i>Euthynnus alletteratus</i>	2.4	6.8	0.1	0.3
	<i>Katsuwonus pelamis</i>	3.9	2.0	2.1	1.4
	<i>Scomberomorus</i> spp.	0.1			
	<i>Thunnus</i> spp.	52.5	3.6	4.8	3.6
	spp.	1.5	0.9	1.2	0.4
	spp.		<0.1		
Scopelarchidae					
Scorpaenidae	<i>Pterois</i> spp.	0.9	0.5	0.6	0.3
	spp.	10.0	0.4	0.2	2.3
Serranidae	Anthiinae (subfamily)	25.1	0.1	0.1	
	<i>Hemanthias leptus</i>	1.4	<0.1		
	<i>Hemanthias vivanus</i>	7.6	<0.1		
	Epinephelinae (subfamily)	0.3	0.1	<0.1	0.3

Family	Species	Continental		Oceanic	
		2014 n = 64	2015 n = 80	2014 n = 64	2015 n = 48
Serranidae	Grammistini (tribe)	0.6	<0.1	0.3	0.5
	<i>Pseudogramma gregoryi</i>	0.4	0.1	0.1	0.2
	Lipropomatini (tribe)	1.0	0.2	0.1	0.2
	Serraninae (subfamily)	1.5	0.3	0.0	0.3
	<i>Serranus</i> spp.	1.1	0.3	0.2	0.9
	spp.	0.1	0.1		0.1
Sphyraenidae	<i>Sphyraena</i> spp.	0.9	0.6	0.8	1.0
Stomioidea	spp.	0.1	0.3	0.4	0.2
Symphasodontidae	spp.				
Syngnathidae	spp.			0.1	0.1
Synodontidae	spp.	0.5	0.2	0.2	0.1
Tetraodontidae	spp.	0.8	0.3	0.2	0.4
Tetraodontiform	spp.		<0.1		
Triacanthodidae					
Triglidae	spp.	0.5			
Xiphiidae	<i>Xiphias gladius</i>	0.1			
Unknown	spp.	2.0	1.2	1.0	0.8

Table C4. Summary of larval fish-prey linear relationships in each region: (top) continental, n = 36, (bottom) oceanic, n = 28. Densities of larval fish taxa and prey groups were log transformed. Larval fish densities are mean values from replicate net tows in the each region. For *T. atlanticus* comparison is from 15 m depth only due to larval abundance patterns (see Methods). Prey (calanoid copepods, *Oithona* copepods, other copepods, appendicularian) densities are mean values from *ISIIS* half-transects corresponding with net tows. Direction of the relationships indicated: positive (+), negative (-). Adjusted r^2 and p-value are given for significant relationships; Bonferroni corrections included for all taxa with multiple comparisons. ** $p < 0.001$, * $p < 0.01$, NS $p > 0.05$ /count of comparisons per taxa.

Table C4.

Continental			Zooplankton prey			
Larval fish predators	Family	Species	Calanoid copepods	Oithona copepods	Other copepods	Appendicularia
	Bothidae	spp.	(+) 0.52**			NS
	Callionymidae	spp.	(+) 0.23*	NS	NS	
	Carangidae	spp.	(-) 0.20*	NS		
	Gobiidae	spp.	NS	NS	NS	
	Labridae	<i>Xyrichtys novacula</i>			NS	
	Lutjanidae	spp.	NS			(+) 0.12
	Monacanthidae	spp.	NS			
	Myctophidae	spp.	(+) 0.12			
	Paralichthyidae	spp.	(+) 0.54**			NS
	Scombridae	<i>Auxis</i> spp.				(+) 0.20*
	Scombridae	<i>Euthynnus alletteratus</i>				NS
	Scombridae	<i>Katsuwonus pelamis</i>				NS
	Scombridae	<i>Thunnus atlanticus</i> ⁺	(+) 0.42*		(-) 0.28*	NS
	Scorpaenidae	spp.	(+) 0.25*	NS	NS	NS
	Serranidae	Serraninae	(+) 0.11			

Oceanic			Zooplankton prey			
Larval fish predators	Family	Species	Calanoid copepods	Oithona copepods	Other copepods	Appendicularia
	Bothidae	spp.	NS			NS
	Carangidae	spp.	NS	NS		
	Gempylidae	spp.	NS		NS	
	Gobiidae	spp.	NS	NS	NS	
	Labridae	<i>Thalassoma bifasciatum</i>			NS	
	Lutjanidae	spp.	NS			NS
	Myctophidae	spp.	NS			
	Scaridae	<i>Sparisoma</i> spp.			NS	
	Scombridae	<i>Katsuwonus pelamis</i>				NS
	Scorpaenidae	spp.	NS	NS	NS	NS

⁺ 15 m depth only

Table C5. Summary of larval fish-prey linear relationships in separate years (2014 / 2015) in the (top) continental region: n = 16 / 20, and (bottom) oceanic region: n = 16 / 12. Densities of larval fish taxa and prey groups were log transformed. Larval fish densities are mean values from replicate net tows in the each region and year. For *T. atlanticus* comparison is from 15 m depth only due to larval abundance patterns (see Methods). Prey (calanoid copepods, *Oithona* copepods, other copepods, appendicularian) densities are mean values from *ISIIS* half-transects corresponding with net tows. Direction of the relationships indicated: positive (+), negative (-). Adjusted r^2 and p-value are given for significant relationships; Bonferroni corrections included for all taxa with multiple comparisons. ** $p < 0.001$, * $p < 0.01$, NS $p > 0.05$ /count of comparisons per taxa.

Table C5.

Continental (2014 / 2015)			Zooplankton prey			
Larval fish predators	Family	Species	Calanoid copepods	Oithona copepods	Other copepods	Appendicularia
	Carangidae	spp.	(-) 0.48* / NS	(-) 0.46* / NS		
	Labridae	<i>Xyrichtys novacula</i>			NS / NS	
	Monacanthidae	spp.	NS / NS			
	Myctophidae	spp.	NS / NS			
	Scombridae	<i>Auxis</i> spp.				(+) 0.59** / NS
	Scombridae	<i>Euthynnus alletteratus</i>				(+) 0.27 / NS
	Scombridae	<i>Katsuwonus pelamis</i>				(+) 0.52** / NS
	Scombridae	<i>Thunnus atlanticus</i> ⁺	NS / NS		NS / NS	NS / NS

Oceanic (2014 / 2015)			Zooplankton prey			
Larval fish predators	Family	Species	Calanoid copepods	Oithona copepods	Other copepods	Appendicularia
	Carangidae	spp.	NS / NS	NS / NS		
	Gempylidae	spp.	NS / NS		NS / NS	
	Labridae	<i>Thalassoma bifasciatum</i>			NS / NS	
	Myctophidae	spp.	NS / NS			
	Scombridae	<i>Thunnus atlanticus</i> ⁺	NS / NS		NS / NS	NS / NS

⁺ 15 m depth only

Figure C1. Proportions of individual larval fish taxa (of all larval fishes) densities (ind. 1000 m⁻³) sampled with nets at depths of 15 m and 30 m (combined) at stations in the Straits of Florida in 2014 vs. 2015 in the (a) continental region, and (b) oceanic region. In each region taxa are list in order of 2014 abundance. Taxa are colored to indicate adult habitat type. Taxa that comprised >1% of all larval fishes in either year in each region shown. N = 64 (2014 continental, oceanic), 80 (2015 continental), 48 (2015 oceanic).

