2008-07-03

The Trophic Ecologies of Larval Billfishes, Tunas, and Coral Reef Fishes in the Straits of Florida: Piscivory, Selectivity, and Niche Separation

Joel Kent Llopiz
University of Miami, jllopiz@rsmas.miami.edu

Recommended Citation

Llopiz, Joel Kent, "The Trophic Ecologies of Larval Billfishes, Tunas, and Coral Reef Fishes in the Straits of Florida: Piscivory, Selectivity, and Niche Separation" (2008). *Open Access Dissertations*. 130.
https://scholarlyrepository.miami.edu/oa_dissertations/130

UNIVERSITY OF MIAMI

THE TROPHIC ECOLOGIES OF LARVAL BILLFISHES, TUNAS, AND CORAL REEF FISHES IN THE STRAITS OF FLORIDA: PISCIVORY, SELECTIVITY, AND NICHE SEPARATION

By

Joel Kent Llopiz

A DISSERTATION

Submitted to the Faculty
of the University of Miami
in partial fulfillment of the requirements for
the degree of Doctor of Philosophy

Coral Gables, Florida

August 2008

UNIVERSITY OF MIAMI

A thesis submitted in partial fulfillment of
the requirements for the degree of
Doctor of Philosophy

THE TROPHIC ECOLOGIES OF LARVAL BILLFISHES, TUNAS, AND CORAL REEF FISHES IN THE STRAITS OF FLORIDA: PISCIVORY, SELECTIVITY, AND NICHE SEPARATION

Joel Kent Llopiz

Approved:

Dr. Robert K. Cowen Professor of Marine Biology and Fisheries	Dr. Terri A. Scandura Dean of the Graduate School
Dr. Su Sponaugle Associate Professor of Marine Biology and Fisheries	Dr. Sharon L. Smith Professor of Marine Biology and Fisheries
Dr. Gary L. Hitchcock Associate Professor of Marine Biology and Fisheries	Dr. Donald L. DeAngelis Research Professor of Biology

LLOPIZ, JOEL KENT (Ph.D., Marine Biology and Fisheries)
The Trophic Ecologies of Larval Billfishes, Tunas, and Coral Reef Fishes in the Straits of Florida: Piscivory, Selectivity, and Niche Separation (August 2008)

Abstract of a dissertation at the University of Miami.

Dissertation supervised by Professor Robert K. Cowen.
No. of pages in text. (177)

The processes influencing larval fish survival in the low-latitude open ocean are poorly understood, especially with regard to feeding. As part of a large-scale study that included two years of monthly sampling in the Straits of Florida (SOF), the objectives of this dissertation were to elucidate the larval fish feeding behaviors and strategies of 1) istiophorid billfishes, 2) tunas, and 3) coral reef fishes, while also 4) characterizing the feeding environment, synthesizing the dominant trophic pathways to fish larvae, and reviewing the literature for evidence of latitudinal distinctions in larval fish trophodynamics. Larval billfishes exhibited highly selective feeding, and their diets were numerically dominated (90%) by two genera of crustaceans, *Farranula* copepods and *Evadne* cladocerans. These prey were consumed throughout early larval ontogeny, from first-feeding through piscivorous lengths (> 5 mm), until piscivory became exclusive near 12 mm. High feeding incidence (0.94) and rapid digestion (~3.5 hrs) suggests frequent and successful feeding by billfish larvae. For tunas, nearly all larvae examined (>98%) contained prey. *Thunnus* spp. exhibited a mixed diet, while skipjack, little tunny, and *Auxis* spp. nearly exclusively consumed appendicularians. All four tuna taxa co-occurred in the western SOF where prey was more abundant, while in the central and eastern SOF (where prey availability was lower), only *Thunnus* spp. and skipjack were present. Additionally, these two taxa exhibited significantly different vertical distributions. Estimates of predatory impact indicated the potential for depletion of resources in the absence of the spatial and dietary niches of larval tunas. Coral reef fish families examined included Serranidae, Lutjanidae, Mullidae, Pomacentridae, Labridae, Scaridae, and Acanthuridae. Feeding incidences were high (0.94 to 1.0) for all taxa except scarids (0.04), and diets were narrow and predator-specific. Cluster analysis yielded clear groupings based on the selective feeding exhibited by the taxa, while within taxa, canonical correspondence analysis illustrated the change in diet with a variety of variables. The physical and biological environment varied markedly across the SOF, largely influenced by the Florida Current. Characteristics examined included thermocline depth, fluorescence, and abundances of total plankton and copepod nauplii. The feeding ecologies of the 21 taxa of fish larvae in this work were synthesized into qualitative and quantitative webs that illustrate the variable trophodynamic strategies of larvae in the SOF and the levels of community reliance upon zooplankton prey types. A review of 170 investigations on larval fish feeding revealed notable distinctions between high- and low-latitude regions, highlighting the substantial variability across environments in the role of larval fishes within the planktonic food web.

ACKNOWLEDGEMENTS

So many people contributed to this work that it doesn't seem right to have only my name on the cover or to get a degree out of it. My advisor Bob Cowen has been an inspirational source of knowledge and guidance, and I cannot thank him enough for the opportunity he has given me and will continue to give me. My committee members Su Sponaugle, Sharon Smith, Gary Hitchcock, and Don DeAngelis were incredible resources and critical to the whole process. An extended committee of several individuals also provided their technical advice, creativity, excitement, and humor—thanks to Claire Paris, Joe Serafy, David Die, Alex Worden, Eric Prince, and Andy Bakun. Others in the more distant past, but no less important, are Sue Barbieri, Luiz Barbieri, and Bill Szelistowki. I would not be where I am without their support or the opportunities they gave me.

The larval billfish project would have been impossible without the help of many. However, David Richardson, by far, contributed the most to this dissertation—the fieldwork, helping identify the 275,000 larvae (including the billfishes molecularly), measuring the tunas, data processing, insightful discussions, and being a friend. The project would have been a bunch of clueless buffoon-scientists on ship in the middle of the ocean without the amazing expertise, critical thought, and hard work of Cedric Guigand. Not only can he design and build a tandem MOCNESS, but his humor and friendship made my experience so much more enjoyable. Critical assistance in the field and lab was generously given by Lisa Gundlach, Amy Exum, Peter Lane, Aki Shiroza, Kevin Leaman, Peter Vertes, Stephen Trbovich, Ian Zink, Klaus Huebert, Kelly Denit, and many, many others. Lisa Gundlach and Amy Exum, in particular, prevented this work from taking 20 years to complete. Very special thanks to Beth Crompton and Lauren Wyatt who worked so hard on their senior theses, and, in turn, contributed to the results for the appendicularian and nauplius analyses presented here. Thanks to Johnathan Kool for the maps.

Many, many thanks to Capt. Bob Loos, Capt. Shawn Lake, and the rest of the crew of the *F.G. Walton Smith* who were amazing in seeing that the 31 cruises and over 100 days at sea were as smooth as possible, even when the seas were not.

Funding for the project, and partially for me, was provided by the National Science Foundation and the Gulf States Marine Fisheries Commission. Other support for me came from the Harding Michel Memorial Fellowship, Capt. Bob Lewis Billfish Challenge Scholarship, and Capt. Harry Vernon, Jr. Memorial Scholarship, with the greatest amount of support from a very generous fellowship from NOAA and the Living Marine Resources Cooperative Science Center.

The friendship and camaraderie of everyone, past and present, in the Cowen/Sponaugle Lab kept the whole journey enjoyable: Evan (Key Largo buddy and great friend), Kelly (inverted keg stands), Cedric, Dave, Claire, Kirsten, Michelle, Mark, Johnathan, Klaus, Stacy, Tauna, Katie, Kristen, and Deanna. So many others in the RSMAS community provided hard work behind the scenes and greater opportunities to learn. Thanks to Karen Wilkening for the many chances to share what I love with the public, especially the aspiring marine biologists.

I cannot duly express my appreciation for my family. My parents have provided me with so much inspiration, moral support, advice, and love—thank you, Mom and Dad.

My brother, Garrett, sister, Tisha, and the rest of my family have always been there for me, providing their love and fun family relaxation.

The one person left has contributed to this work and my life in immeasurable ways. Martha Hauff has gone on cruises, sorted samples, called out data, and proofread every word in this dissertation. Her encouragement, keen intuition, and excitement in my research has made me a better scientist, and her love, and my love for her, has given me a happiness in life I never thought was possible.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

Chapter 1. General introduction and scope of work

The planktonic larval fish is an enigma. It is mere millimeters in length, yet is the offspring of parents perhaps nine orders of magnitude larger; and with no parental care, it slowly drifts with and apart from potentially millions of siblings, heading toward near-certain death. Since most larvae perish prior to becoming juveniles, it could be argued that studying the larval stage of marine fishes is also enigmatic. However, some biological and ecological processes of larval fishes are innate regardless of destiny, and they shape the degree to which slight changes in larval survival may occur. Further, the incremental understanding of some of these processes inherently adds to a present or future capability to protect fish species and the ecosystems in which they live.

Interest in the feeding of fish larvae, and especially the potential influence of feeding, has a long history that largely stems from a desire to understand the population fluctuations of later, exploitable stages (e.g. Hjort 1914). As the majority of the world's fisheries have historically occurred in higher latitudes (Jennings et al. 2001), past interest in larval fish feeding has been largely limited to these regions. This has resulted in an extensive knowledge base on the feeding ecologies of high-latitude larvae. In lower latitudes, the history of larval fish research is much shorter, and the work in these regions has been focused, instead, on questions related to larval transport and variability in recruitment to suitable juvenile habitat (Cowen & Sponaugle 1997). The successful transport of a fish larva to suitable juvenile habitat, however, necessarily depends on the larva's ability to first survive the journey in the plankton. Additionally, larvae of pelagic species such as billfishes and tunas have no need to reach specific benthic habitat.

Therefore, survival to later stages should almost exclusively depend upon successfully feeding and avoiding being eaten.

The influence of feeding on the survivorship of planktonic larval fishes is not limited to starvation mortality. Predation is has come to be regarded as the greatest source of larval mortality (Bailey & Houde 1989), and since mortality rates decrease with growth (Pepin 1991) and growth rates can be influenced by feeding (Houde 1978, Puvanendran & Brown 1999), the feeding process is inextricably linked to levels of predation mortality experienced by a larval population (Cushing 1975, Houde 1987). Considering both the multifaceted influence of feeding on the survival of fish larvae and the dearth of studies in lower latitudes that have investigated larval trophodynamics, a distinct opportunity to make a significant contribution to such work was apparent.

The work presented here is an attempt at that contribution. While its significance may be difficult to assess as of yet, the research was carried out in the context of a larger project that investigated larval fishes and their habitat on an unprecedented scale. Set in the Straits of Florida, the focus of the overlying project was to elucidate the spawning locations, larval distributions and larval ecologies of the poorly understood billfishes (marlins, spearfishes, sailfish and swordfish). While these goals were clearly met, the larger result was one of the most thorough physical, biological and ecological investigations into the planktonic ecosystem of the low-latitude ocean. This endeavor was possible partly due to the hydrography of the Straits of Florida region and the feasibility of frequent collections. Sampling occurred across the narrow, 80-km portion of the Straits of Florida between the Florida shelf break south of Miami to the edge of the Great Bahama Bank. This relatively narrow region, characterized by the funneling of a large upstream area via the rapid Florida Current, was sampled monthly in 2003 and 2004. For the sampling of plankton, a novel variation of the multiple opening closing net and environmental sampling system (MOCNESS) was developed, consisting of two adjoined systems with different opening and mesh sizes (Guigand et al. 2005). This design allowed for the collection of large (rare) and small larvae, but additionally yielded the concurrent collection of larval predators and the spectrum of available zooplankton prey.

The initial goal of the presented research was to simply add to our limited knowledge of larval fish trophodynamics in lower latitudes by examining taxa for which little or no information previously existed. However, the extent of the sampling and the resulting data set allowed for more than just the separate documentation of individual species' diets. Some of the novel and interesting results that were observed raised questions regarding the physical and biological environment, including the spatial distributions of larvae and prey. Answering these questions substantially contributed to the ecosystem approach that this dissertation has ultimately taken.

The larger project's focus on larval billfishes yielded chapter 2 of the presented work. While limited research has been previously conducted on larval billfishes in the Indian and Pacific Oceans (Gorbunova & Lipskaya 1975, Lipskaya & Gorbunova 1977, Uotani & Ueyanagi 1997), the knowledge of larval billfish feeding ecologies in the Atlantic Ocean was based on a total of 45 larvae (Voss 1953, Gehringer 1956, Schekter 1971). From the intense sampling efforts within the Straits of Florida came unprecedented sample sizes of Atlantic blue marlin and sailfish larvae, which allowed for diet analyses on 826 individuals. Larval billfishes were found to exhibit an extremely narrow diet, especially when considering the diversity and abundance of available prey.

Diets also varied across the Straits of Florida, and selectivity analyses suggested the consistently-preferred *Evadne* cladocerans were frequently unavailable in the western Straits of Florida. Though known to feed upon other larval fishes during the larval stage, billfish larvae in the Straits of Florida were found to exhibit piscivory earlier than had previously been documented, and the spatial variability in the frequency of piscivory suggested the possible occurrence of low levels of larval fish prey availability in the central Straits of Florida.

Like larval billfish research, investigations into the feeding of larval Atlantic tunas have been absent from the literature despite extensive work on Indo-Pacific species (e.g. Young & Davis 1990, Margulies 1993, Tanaka et al. 1996, Sanchez-Velasco et al. 1999). The initial objective of chapter 3 was to fill the general void in the Atlantic Ocean, but more than this, the results showed clear distinctions in the trophic and spatial niches of larval tunas. The ‘true’ tunas (tribe Thunnini) are comprised of four genera that inhabit lower latitudes (Collette et al. 2001), all of which occur at high abundances within the Straits of Florida (as *Thunnus* spp., *Auxis* spp., *Katsuwonus pelamis* and *Euthynnus alletteratus*). As a group, the abundance of these four taxa in the Straits of Florida was second only to myctophid (lanternfish) larvae. Prior to an ontogenetic shift to piscivory, three of these taxa fed nearly exclusively upon appendicularians. The horizontal distributions of the taxa illustrated co-occurrence of all four taxa only in the western Straits of Florida. An investigation into the distribution and abundance of appendicularians, and the incorporation of estimates of daily rations of tunas, suggested that levels of appendicularians in the central and eastern regions would possibly be insufficient to support the high levels of tuna larvae that occurred in the west where prey abundance was significantly higher. Vertically in the water column, distributions between the two taxa occurring in regions of low prey availability were significantly different, further illustrating the spatial and dietary niche separation among tuna larvae in the Straits of Florida.

For billfishes and tunas, some previous work had been conducted in various regions, but knowledge of the feeding of larval coral reef fishes was essentially nonexistent for taxa worldwide (but see Sampey et al. 2007 for a cursory examination of several taxa). Chapter 4 focuses on the diet variability within and among 13 taxa of coral reef fish larvae. The most notable findings of the work were the narrow and taxon-specific diets, in addition to feeding incidences for all reef fish taxa except parrotfishes being near 100%, which was similar to the results for billfishes and tunas. The high number of coral reef fish taxa examined in this work, and the many potentially influential variables affecting diet composition, called for a multivariate approach to examining feeding variability both within and among taxa. Cluster analysis and NMDS provided quantitative indices of dietary overlap among taxa, while canonical correspondence analysis (previously unused in larval feeding work) investigated within-taxon feeding variability and its association with several environmental and biological explanatory variables.

The results of these chapters illustrated several surprising distinctions in the trophic ecologies of larval fishes. With the historical lack of thorough data in tropical/subtropical regions, it was often hypothesized within the chapters that these distinctions could be unique to lower latitudes. To address this hypothesis, a formal comparison (by way of a literature review of high- and low-latitude larval feeding dynamics) was one of the three main objectives of chapter 5. A total of 63 published studies, in addition to the tuna and reef fish chapters presented here, allowed for a review of 170 investigations on the feeding ecologies of 130 taxa of larval fishes. Previously hypothesized distinctions between high and low latitudes were largely supported by this review. Among them was higher feeding incidences, narrower diets, and less reliance upon eggs, nauplii and calanoid copepodites in lower latitudes. The second objective of chapter 5 was to describe the physical and biological environment of the Straits of Florida as larval fish feeding habitat. Surveys of the physical environment and its influence on the biology across trophic levels, revealed marked spatial and temporal variability in current structure, thermocline depth, fluorescence, and total plankton and copepod nauplius abundances. The final goal of chapter 5 was to synthesize the feeding information for the 21 taxa examined from the Straits of Florida. To compare different approaches, this was performed with both a qualitative and quantitative subweb of the specific trophic roles that larval fishes have in the planktonic food web of the Straits of Florida. The qualitative web illustrated the various and often-specific linkages between larval taxa and their prey. The quantitative approach was completely novel for larval fish trophodynamic work, and it incorporated both the prey-type proportions consumed by each taxon and the taxon-specific larval abundances in the Straits of Florida throughout the two years of sampling. This allowed for insight into levels of ‘community reliance’ upon each prey type, illustrating what zooplankton prey may contribute the most to the larval fish community as a whole rather than the just the individual species.

Simply considering the diversity of taxa examined and the previous lack of knowledge, this work constitutes a data-rich contribution to our understanding of larval fish feeding in low latitudes. However, it is my hope that it goes beyond a simple documentation of ‘this eats this and that eats that’. While information on specific feeding relationships is interesting and potentially useful, I think that we have taken advantage of the unique opportunity to gain insight into larger ecological processes that can be difficult to elucidate in the immense planktonic ecosystem of the oceans. I say ‘we’ because this research would not have been possible without the help of many.

Chapter 2. Precocious, selective and successful feeding of larval billfishes in the oceanic Straits of Florida

The oligotrophic open ocean of low latitudes is larval fish habitat for a diversity of resident and migratory species. It is hypothesized that these waters, relative to coastal regions, yield reduced predation mortality, but little is known regarding the feeding and feeding environment of these larvae and the extent to which a nutritional tradeoff may exist whereby lower predation mortality is accompanied by poor feeding conditions. Monthly sampling of larval billfishes across the Straits of Florida over two years allowed for an investigation of the temporal, spatial and ontogenetic variability in the feeding of sailfish *Istiophorus platypterus* and blue marlin *Makaira nigricans*. Consumed prey were numerically dominated (90%) by two crustaceans, a copepod (*Farranula*) and a cladoceran (*Evadne*), with relative proportions displaying marked spatial variability. These prey were consumed throughout early larval ontogeny, from first-feeding through piscivorous lengths (> 5 mm), until piscivory became exclusive near 12 mm. High daytime feeding incidence (0.94) and rapid digestion (~3.5 hrs) support generally frequent and successful feeding by billfish larvae. Prey selectivity was illustrated by preference for *Evadne* over *Farranula* and a near absence of calanoid copepods from diets despite high environmental concentrations. Gut fullness exhibited a distinct sunset peak and also differed significantly with larval length and year, but not season or location. A gut evacuation rate was used to estimate a daily ration of 29–75% of gut-free body weight, varying greatly with model selection but also with season (daylight length). Although potentially unique to the Straits of Florida and larval billfishes, these results are counter to the general presumption that the subtropical open ocean is nutritionally constraining for larval fish.

Background

The inherent influence of feeding upon the survival of larval fishes is the basis for nearly a century's worth of research addressing questions of recruitment variability and stock resilience (e.g. Hjort 1914, Cushing 1975). Yet, while high-latitude studies on the early life history of fishes often focus on mortality and trophic aspects, there has been a trend in low latitudes to emphasize the role of transport and settlement processes with little attention to the dynamics of feeding (Cowen & Sponaugle 1997). Transport to suitable settlement habitat is crucial for reef fishes (Cowen et al. 2006), but the larvae of oceanic pelagic species such as istiophorid billfishes do not need to reach settlement habitat. Therefore, the survival of these larvae to later stages should depend more heavily upon the nutrition-mediated processes of starvation, growth and predation. Additionally, billfishes and many other taxa specifically place their progeny in the low-latitude open ocean, often undertaking extensive migrations to do so (Richards et al. 1989, Bakun 1996, Prince et al. 2005), but the potential nutritional costs of this strategy incurred by the larvae are poorly understood.

The low-latitude oceanic environment differs notably from higher latitudes in that it lacks the distinct primary and secondary productivity peaks that may drive similar peaks in fish spawning (e.g. Longhurst & Pauly 1987, Cushing 1990). Instead, many tropical and subtropical fishes have adopted a strategy of spawning multiple times over a protracted spawning season of many months or even throughout the year (Robertson

1991), possibly to ensure the survival of some offspring in an unpredictable and constraining environment. Consequently, investigating larval fish feeding dynamics in lower latitudes at temporal and spatial scales commensurate with those of spawning is essential to understanding the potential role of feeding in survival to later stages.

Previous work on the feeding of larval istiophorid billfishes in the Indian and Pacific Oceans (Gorbunova & Lipskaya 1975, Lipskaya & Gorbunova 1977, Uotani & Ueyanagi 1997) suffers from either low sample sizes or limited analyses, especially regarding variability with space and time. In the Atlantic Ocean, there is an even greater paucity of data, with only a handful of studies reporting on a combined total of 45 larvae (Voss 1953, Gehringer 1956, Schekter 1971). The feeding habits of the youngest individuals, including the first-feeding stage, and any variability with time, space and prey availability, are yet to be described. However, it is clear from previous work that larval istiophorids are piscivorous, with individuals as small as 6 mm standard length consuming other fish larvae, presumably to meet the demands of their characteristically fast growth (Luthy et al. 2005b, Sponaugle et al. 2005).

As part of a large-scale study investigating the early life stages and spawning of billfishes, this work reports on the trophic role of larval istiophorid billfishes in the plankton of the Straits of Florida. Novel sampling techniques and the hydrography of the region allowed for monthly collections throughout 2003 and 2004, and thus the ability to investigate the spatial, temporal and ontogenetic variability in larval sailfish *Istiophorus platypterus* and blue marlin *Makaira nigricans* trophodynamics. We couple the results on diet with prey selectivity analyses and estimates of evacuation rate and daily ration, as well as documentation of the ontogenetic changes of the gastrointestinal tract.

Materials and methods

Area of study and field collection

Plankton sampling occurred within the Straits of Florida (SOF; Fig. 2.1) from the Florida shelf break south of Miami to the Great Bahama Bank south of Bimini, Bahamas (25.5°N parallel). This narrow yet oceanic region, containing the Florida Current and its characteristically strong northerly flow, was sampled monthly along a transect of 17 stations (numbered west to east) during 2003 and 2004. The three western- and eastern-most stations were ~2 km apart with the remaining central stations ~5.5 km apart. Cruises took place near the beginning of each month and larval billfishes included in these analyses were collected from April to Nov 2003 and June to Oct 2004. For subsurface plankton sampling, we utilized a novel design (Guigand et al. 2005) of the multiple opening and closing net and environmental sensing system (MOCNESS; Wiebe et al. 1985) whereby two systems of different opening and mesh sizes were adjoined (4 m^2, 1 mm mesh and 1 m^2, 150 μm mesh). The MOCNESS obliquely sampled depth intervals of 25 m (~5 min $interval^{-1}$ and speed of ~1.5 $m\ s^{-1}$) from 100 m up to 1 m at all but the shallower westernmost station (where sampling was from 50 m depth). Adjoined rectangular neuston nets (2 x 1 m, 1 mm mesh and 0.5 x 1 m, 150 μm mesh) were used to sample the sea surface to ~0.5 m depth. The combined-net approach allowed for the concurrent collection of large and small fish larvae and the prey field. Both net systems were outfitted with flow meters for estimates of water volume filtered. All larvae from the monthly surveys were caught between sunrise and sunset except 20 individuals caught no later than 33 minutes after sunset. All regular transect sampling was performed during daylight hours to minimize diel effects and allow additional physical sampling during the night. Plankton samples were fixed in 95% ethanol and at least 2 d later drained and refilled with 70% ethanol. No correction for length or weight change was made for larval billfishes or their prey due to logistical constraints of live sorting and a lack of appropriate published relationships.

Additional sampling was performed to (1) investigate diel variability, including vertical distributions, and (2) estimate the evacuation rate of gut contents. For the former, a single station near the Florida shelf was sampled every three hours for 42 hours (two day-night cycles) in August 2003. Each sampling period included a neuston and MOCNESS tow as described above. To estimate evacuation rates, sampling occurred during two consecutive evenings near the Florida shelf in June 2005, beginning at sunset with a neuston net tow and following with MOCNESS tows (one net, double oblique to 15 m, ~15 min in length) at the approximate times of 0.5, 1.5, 2.5 and 3.5 hours post-sunset. The observation of empty guts in the early morning and the decline of contents after sunset indicated that billfish larvae, similar to many other taxa, only feed during daylight.

Laboratory data collection

Larval billfishes were sorted from plankton samples and identified to species using morphometrics and lower-jaw pigment patterns (Luthy et al. 2005a) or by molecular techniques (Richardson et al. 2007). These recent developments in istiophorid larval identification allowed for 800 individuals to be identified to species, leaving 26 individuals unidentified, and thus excluded from species-specific analyses. Larval body lengths (BL) were measured through a Leica MZ12 stereomicroscope with a camera and image analysis software (Image Pro-Plus 4.5, Media Cybernetics). Body lengths were recorded as notochord length (pre-flexion) or standard length (post-flexion).

Gut contents were examined under a Leica MZ15 stereomicroscope by excising the entire alimentary canal with a microscalpel and minutien pins and, after transferring to a small amount of immersion oil, teasing out prey items. Prey were counted and identified to the lowest taxonomic level practical. The two dominant crustacean genera, *Farranula* (copepod) and *Evadne* (cladoceran), were analyzed only at the genus level, although of those identifiable to species, all *Farranula* were *F. gracilis* and almost all *Evadne* were *E. tergestina* (except 22 of 2924 that were *E. spinifera*). Most undamaged prey items were measured in length with an ocular micrometer (copepod prosome length, larval fish standard length, and longest dimension in all other prey), as length was observed to be the dimension most often intact. Highly consistent lengths for both *Farranula* and *Evadne* allowed for the assignment of lengths to deformed items or for efficiency (amounting to 28% of these prey). Assigned lengths were the means of ingested individuals from their respective cruises and, for *Farranula*, were usually gender-specific.

Since no length to dry weight relationship is published for any *Evadne* species, and to avoid using extrapolated and potentially inappropriate relationships, we established length to dry weight equations for *Evadne tergestina*. For consistency, a relationship was also established for *Farranula gracilis*. For *E. tergestina*, three replicates of 50 individuals from each of three length classes were dried at 55°C for at least 3 d and weighed on a Cahn C-35 microbalance after attaining constant weights at room temperature (Chisholm & Roff 1990). A linear regression of transformed mean lengths (μm) and weights (μg) for each of the nine subsamples was established (ln W = 2.77 ln L – 17.27, $r^2 = 0.99$). The same method was used for adult *F. gracilis*, but due to distinct sexual dimorphism in size, three replicates of 50 individuals per sex were utilized (ln W = 2.88 ln L – 17.39, $r^2 = 0.99$). Ingested larval fish prey were not converted to dry weight due to identification and measurement only being possible on approximately half of the relatively intact larvae and due to morphological differences between prey taxa. For a subset of sailfish larvae, we established a length (mm) to gut-free dry weight (mg) relationship (GFBW = 0.0004 $BL^{2.62}$, $n = 69$, $r^2 = 0.91$). Gut-free weight was used due to commonly observed gut content weights near 25% of body weight.

Prey availability estimates were made by subsampling a known volume of plankton sample with a Hensen-Stempel pipette and enumerating *Evadne tergestina*, *Farranula gracilis* and calanoid copepodids (juveniles and adults). Subsampling continued until at least 100 individuals per class had been recorded (Postel et al. 2000) or until three subsamples had been quantified (amounting to at least 1.5% of the sample).

Ontogeny of the gastrointestinal tract of sailfish larvae was examined histologically in six individuals (3.5–13 mm BL) preserved in a 4% formalin-seawater solution, specifically noting the development of gastric glands in the stomach, which allow for the efficient extracellular breakdown of proteins (Govoni et al. 1986a). For slide preparation, larvae were embedded in paraffin and 5 μm frontal sections were stained with hematoxylin and eosin.

Data analysis

Feeding descriptors included feeding incidence, defined as the proportion of larvae with food present in the gut, and a similar value for the incidence of piscivory.

Prey-type data included the percentage by number of all prey extracted (%N) and the frequency within feeding larvae that the prey type occurred (%FO). A commonly calculated index of relative importance was avoided due to inherent bias when (1) a diet is of either many small prey or a few large prey, as observed herein, and (2) values are assigned to broad larval size classes that are influenced by both ontogenetic changes in diet and the length-frequency distribution of the larvae inspected.

Variability in gut fullness was analyzed for billfish larvae <7 mm BL containing only *Farranula* and/or *Evadne* prey (n = 393), since these prey accounted for 90% of ingested items. This allowed for analysis by gut content weight without utilizing potentially inappropriate prey length-weight conversions. Analyses were performed via ANOVA on values of relative gut content weight (relGCW), a proxy for gut fullness, calculated as prey dry weight as a percentage of predator gut-free dry weight, to examine the variability with time of day, larval length, season, region, year and species. Due to seasonal differences in day length, time of day collected was converted to a percentage of daylight elapsed relative to daylight length (relTOD). Larvae were grouped in bins of 10% relTOD and 1-mm length classes. A multiway ANOVA compared the random factors of year, time of year, region and predator species, without the significantly different 90–100% relTOD and 2–3 mm BL larvae (see results). Region comprised two groups of stations, the western portion of the SOF (stn. 1–9; faster current and higher primary productivity), and the eastern region (stn. 10–17; slower current and less productive). Time of year groupings were early-season (June–Aug), including the observed peak in larval billfish abundance, and late-season (Sep–Oct). Factor interactions were tested and removed from analyses due to nonsignificance. RelGCW values were

$\log_{10}(x+1)$ transformed and analyses were performed on values from individual larvae with the assumption of independence since larval billfish abundances were very low relative to prey abundances and no correlation between larval abundance and mean relGCW for station samples was observed. The length to gut-free body weight relationship obtained for sailfish was used for both species with the assumption of similar larval morphology at these early stages (Luthy et al. 2005a).

Prey selectivity analyses (following Manly et al. 2002) utilized prey proportions consumed and available to calculate the selection ratio

$$w_i = o_i / \pi_i ,$$

where o_i is the proportion of prey type *i* consumed and π_i is the proportion in the environment. Values >1 indicate selection for a prey type while values <1 indicate selection against a prey type. Selection ratios are near 1 when consumed proportions reflect those of the environment. Confidence intervals (Bonferroni-adjusted) used

$$\mathrm{SE}(w_i) = \sqrt{} \, [o_i \, (1 - o_i) / (u_+ \, \pi_i^2)] ,$$

where u_+ is the total number of prey items consumed. Significant selection for or against a prey type was shown by CI not overlapping with 1. Analyses were performed for the dominant prey, *Farranula* and *Evadne*, for a subset of ten neuston samples representing a broad range of ingested-prey ratios. Selectivity values were calculated for individual samples, pooling prey consumed by all billfish larvae from each sample. The selection ratio (or forage ratio) was chosen due to its simplicity and statistical testability, although CIs are questionable when consumed prey are less than five in any category (Manly et al. 2002). The selection ratio becomes Chesson's α (Chesson 1978) when expressed as a proportion of the sum of selection ratios and is similarly vulnerable to sampling error when prey are rare in the environment (Lechowicz 1982).

The decline in mean relGCW of larvae obtained during the evacuation rate study was used in conjunction with daytime relGCW values to estimate daily rations. Evacuation models describe the change of stomach contents, S, as

$$\frac{\mathrm{d}S}{\mathrm{d}t} = -aS^{b},$$

where a is estimated and b, usually ranging from 0 to 1, is often assumed or can be estimated generally by fit or specifically with nonlinear regression techniques. The most common daily ration models incorporate linear evacuation ($b = 0$; Bajkov 1935, Canino et al. 1991, Bochdansky & Deibel 2001) or exponential evacuation ($b = 1$; Elliot & Persson 1978, Eggers 1979), but square-root evacuation models ($b = 0.5$) have also been appropriate, and possibly more so than described (Jobling 1981, Andersen 1998; but see Persson 1986). Additionally, the general model of Pennington (1985), a Bajkov-like model similar to the modification of Eggers (1979), allows for the use of an estimated value of b for daily ration estimation. As an alternative to assuming a single evacuation model, the data from the evacuation rate experiment were combined with several models and scenarios to better elucidate the effects of evacuation and daily ration model choice on the estimate of daily rations. All evacuation rate regressions were performed on untransformed means, as the use of transformed relGCW values was noted to overestimate daily ration estimates by as much as 30%. Nonlinear regression parameters were estimated using the Marquardt method (NLIN in SAS; SAS Institute Inc. 1999) for each model, with b either fixed or estimated (using eq. 3 of Andersen 1998). Larvae utilized in these analyses were sailfish 3–6 mm BL (minimizing ontogenetic differences) containing *Farranula* only (*n* = 49; 85% of the larvae collected). Abundances of larger, piscivorous larvae were too low after sunset for separate analyses.

Results

Distribution, feeding incidence and diet

Inspected larvae comprised 452 sailfish and 341 blue marlin, each with similar size ranges of 2–23 mm BL and ca. 50% of the individuals <4 mm BL. Only seven white marlin *Tetrapturus albidus* were inspected and 26 istiophorids remained unidentified. Higher numbers of inspected sailfish were collected from the western region of the SOF, while blue marlin were more abundant in the central and eastern regions (Fig. 2.2). This pattern held for the total catch of these species (D. Richardson et al. unpublished data). Vertically, 74% of the inspected larvae were collected at the sea surface with the neuston net and 26% were collected subsurface with the MOCNESS (with only 1% in depth intervals below 25 m). The diel dynamics of the vertical distribution (Fig. 2.3) indicate that larval istiophorids avoid the sea surface during the night.

The feeding incidence for all istiophorid larvae was 0.94 (Table 2.1). Of the sailfish larvae collected at least 30 min after sunrise, the smallest (2–3 mm BL) and largest (8–21 mm BL) subgroups had lower feeding incidences (0.79 and 0.85, respectively) than the 0.99 value for the intermediate 3–8 mm BL class. Nearly all blue marlin (0.97) larvae contained food, including the 2–3 mm BL class, which includes first-feeding larvae as indicated by comparison with identified yolk-sac larvae and the 2–3 d ages of larvae this size (Sponaugle et al. 2005).

Of 6159 prey items extracted from all larvae, the copepod *Farranula* and the cladoceran *Evadne* accounted for nearly 90% (Table 2.2). By species, sailfish consumed more *Evadne* than *Farranula*, while the opposite held for blue marlin. Frequencies of occurrence of *Evadne* were 55% for sailfish and 72% for blue marlin with *Farranula* near 70% for both species. *Farranula* contributed 70% of the dry mass of the total of *Farranula* and *Evadne*, as female *Farranula* are approximately twice the weight of the average *Evadne* (and male *Farranula*). Other prey of less importance were *Corycaeus* copepods and *Limacina* pteropods (both more common at western stations, Fig. 2.4). Larval fish prey %N and %FO were low due to their larger size and presence in the diet only at larger predator lengths, thus these indices are not indicative of their importance. The seven identified white marlin had diets similar to sailfish and blue marlin, with *Farranula* contributing 70% and *Evadne* 22% of the 69 prey items extracted.

Diet variability, prey selectivity and gut fullness

Billfish diets changed little with early ontogeny (Figs. 4a & 4c). First-feeding larvae of both sailfish and blue marlin within the 2–3 mm BL class consumed the same prey as larger larvae, and generally lack a nauplius-feeding stage. The only ontogenetic shift was the inclusion of piscivory at ca. 5 mm BL (corresponding with flexion of the urostyle), which added to a diet of *Farranula* and *Evadne* until larval fish prey were exclusive at later stages. The increase in proportions of *Farranula* consumed with blue marlin size appears to be due to higher numbers of larger larvae collected from the central stations, where greater proportions of *Farranula* were consumed (Figs. 4d & 5), and more smaller larvae collected in the east. Higher proportions of *Evadne* in sailfish are partially influenced by time of year since numbers of *Evadne* consumed were higher in the early summer, overlapping more with the occurrence of sailfish larvae in the SOF (Apr–Nov) and less so with that of blue marlin (July–Nov). A large ‘other’ prey category for 2–3 mm BL sailfish (Fig. 2.4a) results from a greater abundance of smaller larvae in the western region where *Corycaeus* copepods and *Limacina* pteropods are more common prey (Fig. 2.4b).

The incidence of piscivory increased with size as larger larvae became more exclusively piscivorous (Table 2.3). This was illustrated by an increase in prey numbers with larval size (Fig. 2.6) until a decline occurred when relatively large larval fish prey replaced numerous small *Farranula* and *Evadne*. Blue marlin had a higher peak in prey numbers at size with nine larvae 7–10 mm BL containing over 50 prey items each (Fig. 2.6b). With piscivory being the only change in diet, the relationship of prey size to predator size shows an increase in prey size only for larval fish prey (Fig. 2.7).

Approximately half of the extracted larval fish prey were identifiable to at least the family level (Table 2.3), and these prey reflected the spatial variability of the predators (Fig. 2.2). Larval fish prey of sailfish were largely dominated by coastal pelagics (Exocoetidae, Hemiramphidae and Carangidae) and the coral reef fish family Mullidae. Blue marlin larval prey were mostly tunas (Scombridae), especially *Thunnus* spp., and snake mackerels (Gempylidae). Four larval prey of blue marlin were istiophorids, one of which had a larval tuna in its gut, in this instance placing the 23 mm BL predator at perhaps the fifth trophic level.

Temporally, proportions of *Farranula* and *Evadne* consumed were variable but unpredictable, and often switched dominance from month to month, even at the same station (not shown). Spatially, however, there was an overall and common monthly trend for greater numbers and biomass of *Farranula* to be consumed towards the west while *Evadne* composed the majority at several eastern stations (Fig. 2.5).

Of the two dominant prey, *Farranula* copepods and *Evadne* cladocerans, *Evadne* was consumed in greater proportions than available in the plankton, while *Farranula* was consumed in smaller proportions (Table 2.4). Selection for *Evadne* and against *Farranula* was significant for seven samples ($p < 0.001$). The three other samples showed the same trend but the influence of low *Evadne* concentrations precluded significant selection. Calanoid copepodids, which were of similar sizes and up to three times more abundant than *Farranula* and *Evadne* combined (Table 2.5), were not consumed by any larvae. The pattern of consistent selection for *Evadne* and against *Farranula* also held for individual larvae and thus for both sailfish and blue marlin. The possibility for vertical distribution bias is minimal since all larvae and prey for these analyses were collected only from the upper 0.5 m of the water column.

Relative gut content weight (relGCW) with time of day showed a significant increase in the last 10% of daylight for both years combined (Tukey HSD, all $p < 0.001$), a pattern observed each year (Fig. 2.8a). Additionally, the sunset mean near 20% relGCW in the evacuation rate study may indicate a more pronounced evening peak closest to darkness. Significant differences in relGCW with larval length (Fig. 2.8b) were also observed, with the 2–3 mm BL class differing from all but the 6–7 mm BL size class (Tukey HSD, $p = 0.03$–0.001). The nonlinearity of this relationship complicates analyses, yet with and without the 2–3 mm size class, there was a significant difference in relGCW between years, with 2004 higher than 2003 (Table 2.5 & Fig 8a). There were no differences in relGCW between seasons, regions or species (Table 2.5).

Gut evacuation, daily ration and ontogeny

Relative gut content weight declined after sunset until complete gastric evacuation occurred in 3–4 hrs (Fig. 2.9). Ambient water temperature was 30.6 °C. Including the 3.5 hrs post-sunset collection when eight of 10 larvae were empty, the best general model describing evacuation was the square-root model ($b = 0.5$), as the estimation of b yielded a value of 0.44. Excluding the 3.5 hr time period, which may be more appropriate (Bochdansky & Deibel 2001), the decline was linear. Daily ration estimates differed substantially with model choice of both evacuation rate and daily ration (Table 2.6). The Pennington (1985) model estimated a daily ration of 75% gut-free dry body weight during maximum daylight lengths of 14 hours, while use of the linear portion of the evacuation relationship and the approach of Bochdansky and Deibel (2001) yielded a daily ration estimate of 34%. Aside from model choice effects, daily rations were up to ca. 23% greater in June and July (14 hrs of daylight), a time of year potentially occurring at the peak of spawning (D. Richardson et al. unpublished data), than in November (11 hrs of daylight)..

Histological analyses of gastrointestinal tract ontogeny showed the early development of a blind sac, the enlargement of the stomach with gastric glands developing throughout the mucosa, and a corresponding decrease in relative intestinal volume (Fig. 2.10). Gastric glands were first observed in a 4.2 mm BL sailfish in the stomach's blind sac (Fig. 2.10a). The only smaller specimen examined (3.5 mm BL) had a much smaller blind sac without gastric glands.

Discussion

Feeding incidence, diet and ontogenetic diet shifts

Larval istiophorid billfishes consistently exhibited a high feeding incidence over broad ontogenetic, temporal and spatial scales. Although the presence of prey alone does not preclude the possibility of suboptimal feeding and eventual starvation, high feeding incidence (0.94 overall and 0.79–0.97 for first-feeding larvae), in conjunction with rapid gut evacuation, indicates the likelihood that feeding by the larval population as a whole is frequent and successful. Extrapolating these results to levels of starvation mortality is not possible, but the ability to withstand an empty gut for 7–10 hrs during the night (a non-feeding period of 10–13 hrs) suggests that empty daytime guts should be present prior to larvae dying from starvation. High feeding incidences have been reported for a variety of species, including Indo-Pacific billfishes (Gorbunova & Lipskaya 1975, Uotani & Ueyanagi 1997), although in other taxa they are often much lower. For example, in the tropical Indian Ocean, only ca. 50% of larval scombrids collected during daylight hours had prey present in the gut (Young & Davis 1990). Possibly due to the extensive and protracted spawning by many species in lower latitudes, and the limited spatial and temporal scope of many studies, it has been difficult to infer how representative previously observed feeding incidence data are. However, with monthly sampling for two years in the SOF, the present study provides evidence that high feeding incidence may occur throughout the extended period of larval billfish presence.

Diets of larval billfishes were notably narrow, with *Farranula* copepods and *Evadne* cladocerans numerically dominating throughout early ontogeny. Such a narrow diet, as indicated by the selectivity analyses, was not a reflection of what was available since calanoid copepods usually occurred in higher concentrations than *Farranula* and *Evadne*. *Farranula* copepods may be the most reliable resource since they have been shown to occur year-round and have the highest reproductive activity of all copepods off Jamaica (Webber & Roff 1995). Indo-Pacific larval billfishes had similarly narrow diets, consuming *Evadne* and *Corycaeus* copepods (Uotani & Ueyanagi 1997). Adjacent to the SOF in the Gulf of Mexico, sciaenid larvae fed upon prey similar to billfishes, including cyclopoid copepods and *Limacina* pteropods, and were also shown to do so selectively among many available prey types (Govoni et al. 1983, Govoni et al. 1986b). Such diets differ from many other larval fishes that consume more diverse prey that are often dominated by calanoid copepods (e.g. Pepin et al. 1987). If broader diets are more prevalent in higher latitudes, larval fish diversity and the potential for competition may be low enough in these regions, especially during bloom periods, such that specific dietary niches are unnecessary.

Many species of fish larvae consume copepod nauplii during the first feeding stage. However, larval billfishes are precocious at first feeding, possessing the mouth, sensory capability and gut capacity to feed on larger adult copepods and cladocerans (though *Farranula* and *Evadne* are small relative to many other zooplankters). With the first and only ontogenetic diet shift for larval billfishes being to piscivory, such a consistent diet throughout ontogeny with only one substantial increase in prey size is contrary to many studies that show a more constant increase in prey size, usually including shifts from copepod eggs and nauplii to calanoid copepodids and larger adults (e.g. Pepin et al. 1987, Anderson 1994, Sabates & Saiz 2000). Perhaps the most advanced first-feeding larvae are the coastal mackerels *Scomberomorus* spp. that are first-feeding piscivores (Jenkins et al. 1984, Shoji et al. 1997), a strategy presumably dependent upon higher larval fish prey abundances near the coast. For larval billfishes, the inclusion of piscivory was after a period of crustacean feeding (>5 mm BL) and complemented the crustacean diet until nearly exclusive at much greater lengths (~12 mm BL).

Gut evacuation and daily ration

The estimation of gut evacuation rates is possible with field or laboratory studies, each having advantages and disadvantages. The laboratory setting affords the ability to eliminate the potential slowing of gut passage times due to discontinuous feeding (Wuenschel & Werner 2004), yet it is unknown how these rates relate to those in the natural environment. As larval billfishes are difficult to maintain alive in the laboratory (Post et al. 1997), field efforts are currently the only option, and consequently, daily rations may be underestimated. In addition to this limitation, it was shown that estimating daily rations may be less straightforward than often implied in the larval fish literature, and that estimates of daily rations can vary substantially depending on both evacuation and daily ration model choice. In this study, two evacuation models for larval sailfish appeared most appropriate, depending upon the inclusion of the last collection period (3.5 hrs post-sunset) in which eight of 10 larvae were empty. Although it is often recommended to truncate data usage once empty guts appear, when these data were included, the best general model was the square-root model, as the estimated b parameter in the decline of contents (0.44) was near 0.5. With the daily ration model of Pennington (1985), consumption estimates were near 75% of gut-free body weight per day with 14 hrs of feeding. Without the 3.5 hr period, evacuation was distinctly linear. Utilizing the approach of Bochdansky and Deibel (2001), termed the redefined linear model, daily rations were over 50% lower (34% with 14 hrs of daylight). Such lower estimates than the non-linear approaches have been noted (Bochdansky & Deibel 2001). For larval sailfish, a linear relationship may result from the use of converted weights (essentially ingestion = egestion, similar to the use of prey numbers) rather than actual remaining biomass, and therefore, the redefined linear model may be most appropriate. Earlier developed linear approaches (Bajkov 1935; Canino et al. 1991) appear to greatly underestimate daily rations for sailfish larvae (i.e. about half of the estimate is consumed in the last 10% of the day); this conclusion has also been drawn for other taxa (e.g. Hillgruber & Kloppmann 2001).

One clear potential cause of daily ration variation is daylight length. Estimates for 14 hrs of feeding were substantially greater than those for an 11-hr feeding period, which is experienced by larvae spawned late in the protracted spawning season of billfishes. The effect of water temperature on these differences is not accounted for, although monthly mean surface-water temperatures ranged from ca. 26 to 30 °C during larval billfish occurrence. The cooler temperatures together with the shortest daylight lengths should only add to the seasonal difference in daily rations. Comparisons to other taxa are difficult due to a variety of approaches, however other work has estimated larval daily rations of 25–30% for oceanic tunas *Thunnus* spp. from the Indian Ocean (Young & Davis 1990) and ~120% for coastal, piscivorous Japanese Spanish mackerel *Scomberomorus niphonius* (Shoji et al. 2001). Laboratory efforts focused on estuarine species just inshore of the SOF yielded values near 50% when prey concentrations were held similar to the natural environment (Houde & Schekter 1981). For comparative purposes, the greatest potential caveat in this and several studies is the use of preserved larvae and prey, which can influence estimates if effects of weight loss by preservation on predator and prey are not similar. Otherwise, for an evacuation rate, the approach used herein should be preferable due to the avoidance of using techniques such as (1) the assumption of an evacuation rate; (2) the potentially unsuitable use of prey numbers without a correction for size; and (3) the linear fitting of transformed gut fullness data for parameter estimation instead of employing nonlinear techniques.

Feeding variability and implications

Aside from its role in starvation, feeding can influence total numbers of larval billfishes surviving to later stages if growth rates are reduced by suboptimal feeding (Cushing 1975, Houde 1987). Such an effect could be large since the annual egg production of blue marlin in the SOF is estimated to be in the trillions (D. Richardson et al. unpublished data). This possibility is supported by differences in blue marlin larval growth between the SOF and nearby Exuma Sound (Sponaugle et al. 2005). The dynamics of piscivory in the present study may offer insight into how feeding could affect growth. Sailfish, more common along the western SOF, consumed a variety of larval fish prey, including coral reef fishes and coastal pelagics. With a more diverse and likely larger source population of spawning adults upstream along the Florida Keys, sailfish near the western shore may be less vulnerable to fluctuations in ichthyoplankton availability. In contrast, the majority of larval fishes consumed by blue marlin in the central SOF were of a few taxa, largely oceanic tunas and snake mackerels. The reliance upon a less diverse resource could mean greater vulnerability to factors affecting the abundance of prey larvae, including fluctuations in adult abundances or spawning times and locations (especially of tunas). Supporting evidence for potential mismatches between piscivorous blue marlin and prey larvae may be seen in the relationships of number of prey ingested and predator size (Fig. 2.6). The greatest number of prey items within a sailfish was 44; yet nine blue marlin of piscivorous lengths collected in the central SOF contained 50 to 64 crustacean prey (predominantly *Farranula*) instead of larval fish prey. This peak indicates the likelihood of occasionally low larval fish prey abundances for piscivorous blue marlin. This is further supported by our data on total larval fish abundance across the SOF showing fish larvae are approximately twice as abundant in the western SOF when compared to the central SOF (unpublished data). Without linking growth and feeding, only the potential for growth effects can be noted, but direct relationships have been shown for piscivorous Japanese Spanish mackerel larvae (Shoji & Tanaka 2006). Additionally, swordfish *Xiphias gladius* larvae exhibit a distinct increase in linear growth rates once piscivory begins (Govoni et al. 2003), and for istiophorids, the exponential growth of blue marlin and sailfish larvae (Luthy et al. 2005b, Sponaugle et al. 2005) is much faster at later, piscivorous lengths.

Evadne cladocerans were selected for in each of the samples analyzed for prey selectivity, but were commonly not consumed at many station-month combinations, indicating the likelihood they are often unavailable. If larval billfishes select *Evadne* due to greater profitability, perhaps including higher capture success, less handling time, or a higher energy to bulk ratio (Whelan & Brown 2005), the net result should be faster growth and thus higher overall survival when *Evadne* is available. If *Evadne* are actively selected for, such selection for a smaller prey type is generally counter to optimal foraging theory and other work showing higher condition while feeding on larger prey (Anderson 1994). The alternative is that there may not actually be selection of *Evadne* over *Farranula*. If optimal foraging theory holds for larval billfishes such that less profitable prey are either always attacked upon encounter or never attacked (dependent upon relative abundances; Stephens & Krebs 1986), the inclusion of *Farranula* in diets throughout a broad range of abundances relative to *Evadne* may suggest that *Evadne* is not selected over *Farranula*. If so, the discrepancy between consumed and ambient proportions of *Evadne* and *Farranula* could be due to factors such as greater capture success or detection distances for *Evadne*, or occurrence in micropatches or aggregations, for example at the air-sea interface. Furthermore, the term ‘selectivity’ may be less appropriate for larval billfishes since prey concentrations are so low in these waters relative to a larva’s search volume (Munk & Kiorboe 1985, Pepin & Penney 1997), resulting in few simultaneous encounters with more than one prey type. Concentrations of *Farranula* and *Evadne* were less than 2 individuals 10 l^{-1} in over half of the samples used in the selectivity analyses. Such low prey abundances contrast with the highly productive periods in higher latitudes during which prey can occur at concentrations of 100 to >1000 individuals 10 l^{-1} (Hillgruber et al. 1995, Pepin & Penney 1997).

The use of relative gut content weight (relGCW) as a proxy for gut fullness for larval billfishes helped account for the rapid increase in gut capacity with growth (Fig. 2.6), allowing for better resolution of the observed peak in feeding prior to sunset. This increase in feeding intensity significantly contrasted with relGCW values throughout the rest of the day, which were quite variable and ranged from near 0% to 13%, illustrating not only greater filling of guts but also a synchrony of filling in the last part of the day. Prey availability data from these samples are unavailable, but work on diel vertical migrations of both *Farranula* and *Evadne* indicate abundances near the surface are actually lower at nighttime (Mullin & Onbe 1992, Paffenhofer & Mazzocchi 2003), suggesting this peak may not be due to an increase in prey availability. One possibility is that greater levels of polarized light during crepuscular periods enhance prey detection (Novales Flamarique & Browman 2001). However, a similar peak in gut fullness near sunrise was not observed. If prey are not more abundant and there is no enhancement of prey detection or capture success, it may be possible that an optimal feeding rate exists during the day (e.g. allowing thorough digestion without unnecessary energy expenditure) with an increase and synchronization of feeding activity before a nightly non-feeding period. Although generally uncommon, evening peaks in gut fullness have also been shown in other taxa (Anderson 1994, Fortier & Villeneuve 1996, Conway et al. 1999), but they are much less pronounced than those observed in this study for larval billfishes.

The differences in relGCW with size class may reflect a changing allometry of gut capacity with ontogeny, but more importantly draw attention to the potential influence such a difference may have on other analyses. Although the greatest difference in size-class means of relGCW was ca. 1.5% of larval weight, ignoring this difference and including the 2–3 mm BL size class in the analysis of temporal and spatial effects would have yielded an erroneous conclusion of significant seasonal differences in relGCW. In this situation, the greater relGCW in the late-season group would have been an artifact of the greater proportion of larger larvae collected during this time (i.e. fewer recently spawned 2–3 mm BL larvae).

Significantly greater gut fullness in 2004, independent of any ontogenetic influence, indicates the possibility for interannual differences in feeding conditions, which could translate to differences in growth and overall survival. Possibly due to temporal and spatial constraints of sufficient sampling, previous studies in tropical/subtropical waters have been unable to investigate interannual feeding variability. Similar studies in higher latitudes, which are also somewhat limited in interannual comparisons, are usually associated with the temporal match or mismatch of the feeding of fish larvae with secondary productivity peaks (e.g. Anderson 1994), or ignore feeding behavior altogether and only relate larval abundance peaks or recruitment levels to zooplankton peaks (e.g. Cushing 1990). Due to the narrow diet of larval billfishes, the use of general secondary production indices to infer feeding success may be inappropriate if *Farranula*, *Evadne* or larval fish prey did not follow the pattern of the zooplankton as a whole.

The trophic ecologies of larval sailfish and blue marlin are distinct from many taxa in both high and low latitudes. Attributes include a high feeding incidence, a narrow diet throughout ontogeny, highly selective feeding within a diverse prey environment, and the precocious ability to rely upon adult copepods at first feeding and then piscivory at a lengths of 5 mm BL. Such behaviors are counterintuitive when considering the potential constraints of the subtropical, oceanic SOF. The physical limitations in lower latitudes include shorter summertime daylight lengths and higher temperatures, resulting in less time foraging with an increase in metabolic activity and caloric demands. Biologically, low-latitude oceanic waters are oligotrophic and generally have low levels of productivity (although the contributions of small crustaceans (Turner 2004) and the microbial food web (e.g. Landry 2002) are becoming better understood). Because of these constraints, the broad utilization of the low-latitude open ocean as larval habitat by resident and migratory species (Johannes 1978, Richards et al. 1989, Bakun 1996) seems paradoxical, yet this is the basis for hypotheses that implicate larval fish predation, not starvation, driving the evolution of spawning strategies (Bakun & Broad 2003). Although much remains unknown, especially in other low-latitude regions, the successful feeding by larval billfishes despite the presumed constraints suggests that the Straits of Florida may be more conducive to larval fish survival than previously assumed.

Table 2.1. Istiophoridae. Feeding incidence (proportion of larvae with prey present in gut) for all larvae, which were collected between sunrise and shortly after sunset, and length classes of sailfish and blue marlin collected after 30 min post-sunrise. Values for after 30 min post-sunrise minimizes bias due to time of day collected, as larvae were observed to be daylight-only feeders. Illustrating this was the lower feeding incidence of larvae collected 0–30 min post-sunrise in conjunction with nighttime collections and evacuation rate sampling.

	n	Feeding incidence
All istiophorid larvae	826	0.94
Sailfish	452	0.90
Blue marlin	340	0.98
White marlin	7	1.00
Collected >30 min post-sunrise		
Sailfish		
2–3 mm	89	0.79
3–8 mm	296	0.99
8–21 mm	41	0.85
Blue marlin		
2–3 mm	62	0.97
3–8 mm	220	0.99
8–23 mm	49	1.00
Collected 0–30 min post-sunrise		
All species	36	0.44

Table 2.2. *Istiophorus platypterus* and *Makaira nigricans*. Ingested prey items summarized by numerical percentage (%N) and the frequency of occurrence in feeding larvae (%FO). Raw numbers of prey are in parentheses for infrequent prey types and *n* is the total number of prey items excised.

	Sailfish		Blue marlin	
Prey	%N (*n* = 2687)	%FO	%N (*n* = 3134)	%FO
Tintinnida	0.07(2)	0.25	-	-
Foraminifera: *Globigerina*	-	-	0.03(1)	0.30
Gastropoda				
Thecosomata: *Limacina*	2.72	5.16	0.73	3.90
Prosobranchia: Atlantidae	-	-	0.03(1)	0.30
Unknown dextral	0.19(8)	1.23	-	-
Cladocera: *Evadne*	53.3	54.8	42.1	72.1
Copepoda				
Farranula	32.0	69.5	51.2	70.1
Corycaeus	7.55	28.5	2.11	16.2
Oncaea	0.11(4)	0.74	-	-
Unknown corycaeid	0.15(4)	0.74	0.10(4)	0.90
Calanoid	0.33(9)	1.47	0.19(6)	0.90
Harpacticoid	0.04(1)	0.25	-	-
Nauplius	0.22(6)	1.23	0.35(12)	1.80
Unknown copepod	0.45	1.97	0.22	1.80
Ostracoda	0.04(1)	0.25	0.03(1)	0.30
Amphipoda	-	-	0.03(1)	0.30
Larval fish	1.97	10.6	2.14	15.0
Unknown crustacean remains	0.82	4.91	0.64	4.20
Unknown	0.04(1)	0.25	0.06(2)	0.60

Table 2.3. *Istiophorus platypterus* and *Makaira nigricans*. Dynamics of larval piscivory, including the smallest larva with evidence of piscivory, proportional incidence of piscivory, identifiable prey taxa and proportions of total, and mean larval prey lengths (expressed as a proportion of predator length). Numbers of larvae examined are in parentheses. Largely intact prey larvae were identifiable to at least family level for 25 of 55 sailfish prey and 39 of 67 blue marlin prey.

	Sailfish	Blue marlin
Smallest piscivore	5.0 mm BL[a]	5.1 mm BL
Incidence of piscivory		
6–8 mm BL	0.30 (47)	0.36 (39)
8–10 mm BL	0.85 (13)	0.82 (22)
10–18 mm BL	0.86 (21)	1.00 (25)
Prop. of identifiable prey larvae		
Myctophidae	0.04	0.08
Exocoetidae	0.12	-
Hemiramphidae	0.20	-
Holocentridae	0.04	0.05
Carangidae	0.12	-
Gerreidae	0.04	0.05
Mullidae	0.24	0.05
Gempylidae	-	0.18
Scombridae (total)	0.20	0.59
Thunnus spp.	0.12	0.33
Katsuwonus pelamis	-	0.05
Unidentifiable	0.08	0.13
Istiophoridae	-	0.10
Mean larval prey length	0.52	0.53
Maximum observed	0.88	0.68

[a] Two piscivorous sailfish larvae, each 4.4 mm BL, were collected during the 2005 evacuation rate study.

Table 2.4. Istiophoridae. Prey selectivity analysis and environmental prey concentrations for ten samples collected in 2004. Numbers of prey excised from larval billfishes are indicated by u_F for *Farranula* and u_E for *Evadne*. Significant selection for ($w_i > 1$) or against ($w_i < 1$) a prey type is denoted by asterisks, all at $p < 0.001$. No calanoid copepodids were consumed despite relatively high concentrations available in the environment. Stn. = station number.

				w_i		Env. concentration (m^{-3})		
Mo.	Stn.	u_F	u_E	*Farr.*	*Evadne*	*Farr.*	*Evadne*	Calanoid
June	5	9	57	0.36*	1.38*	25	41	118
June	10	4	77	0.10*	1.82*	50	55	126
June	16	27	6	0.87	3.03	116	7	201
July	16	4	22	0.25*	2.16*	254	164	150
Aug	10	35	38	0.56*	3.81*	129	20	95
Aug	11	3	76	0.13*	1.38*	327	749	399
Sep	8	8	136	0.12*	1.82*	45	49	311
Sep	9	44	172	0.26*	3.53*	245	72	351
Oct	6	27	3	0.94	2.17	113	5	332
Oct	8	127	3	0.99	1.71	279	4	482

Table 2.5. *Istiophorus platypterus* and *Makaira nigricans*. ANOVA results investigating variability in gut fullness with year, season, region in the SOF, and predator species. Only the same collection months each year (Jun–Oct) were included, and the significantly different relative time of day prior to sunset and the 2–3 mm BL size class were excluded.

Source	df	MS	*F*	p
Year	1	0.369	10.7	0.001
Season	1	0.017	0.49	0.49
Region	1	0.024	0.70	0.40
Species	1	0.000	0.001	0.97
Residual	268	0.034		

Table 2.6. Istiophoridae. Evacuation rate and daily ration models used to estimate daily rations. Evacuation models are fit to data in Fig. 2.9 with parameter *b* fixed or estimated. Daily ration estimates, as percent of gut-free body weight, given for minimum and maximum daylight lengths (duration of feeding) when billfish larvae are present during the protracted spawning season of approximately April to November.

Gut evacuation		Daily ration estimate		
Model	*b*	Model	11 hrs	14 hrs
Linear	0	Canino et al. (1991)	15.4	19.7
		Bochdansky & Deibel (2001) with Eggers (1979)	29.3	34.3
Exponential	1	Elliot & Persson (1978)	41.7	50.2
		Eggers (1979)	45.0	54.3
Square-root	0.5	Thorpe (1977)	44.5	49.4
		Pennington (1985)	59.4	72.6
b-estimated	0.44	Pennington (1985)	61.5	75.3

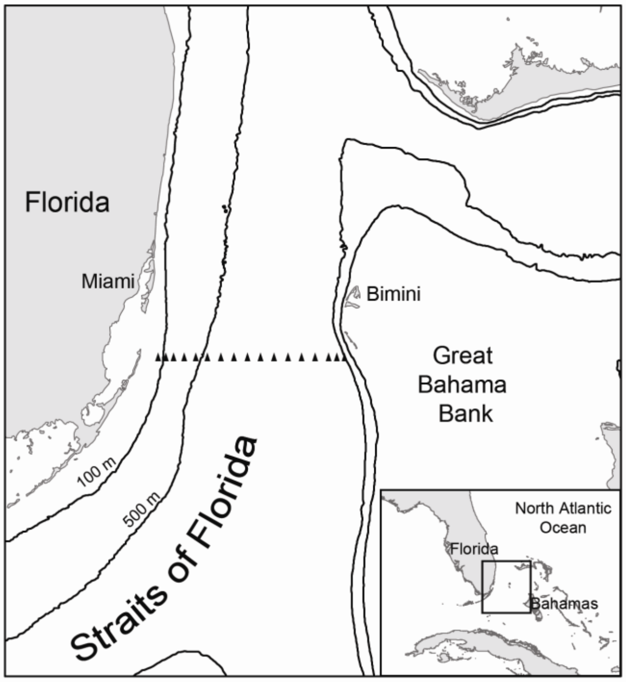


Figure 2.1. Western North Atlantic (inset) and the Straits of Florida region where a transect of 17 stations (numbered west to east) from the Florida shelf break just south of Miami, Florida to the Great Bahama Bank south of Bimini, Bahamas was sampled monthly in 2003 and 2004.

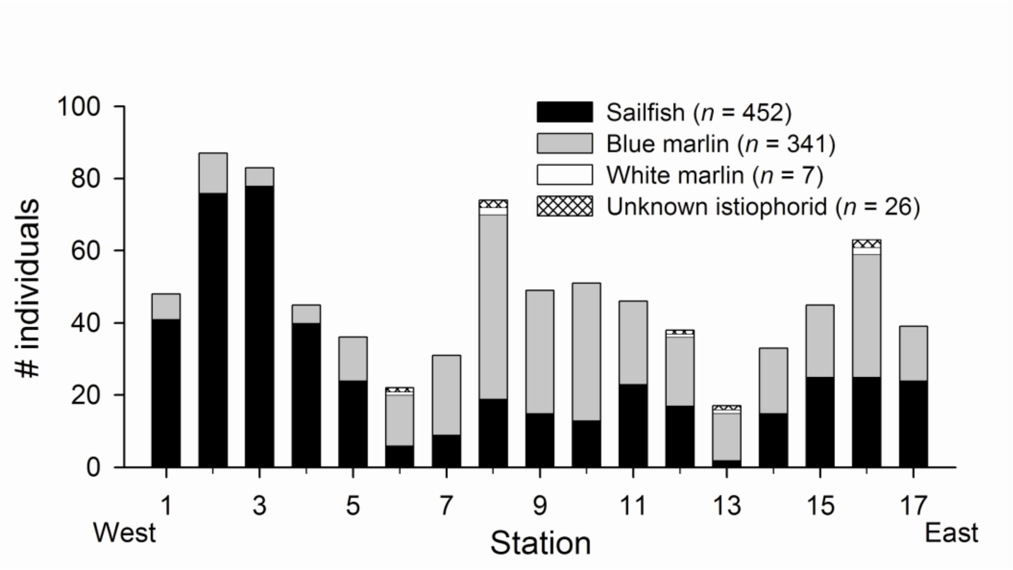


Figure 2.2. Istiophoridae. Spatial distribution of inspected larval sailfish *Istiophorus platypterus*, blue marlin *Makaira nigricans*, white marlin *Tetrapturus albidus* and unidentified istiophorids across the Straits of Florida. Stations are numbered west to east, from the Florida shelf break to the Great Bahama Bank.

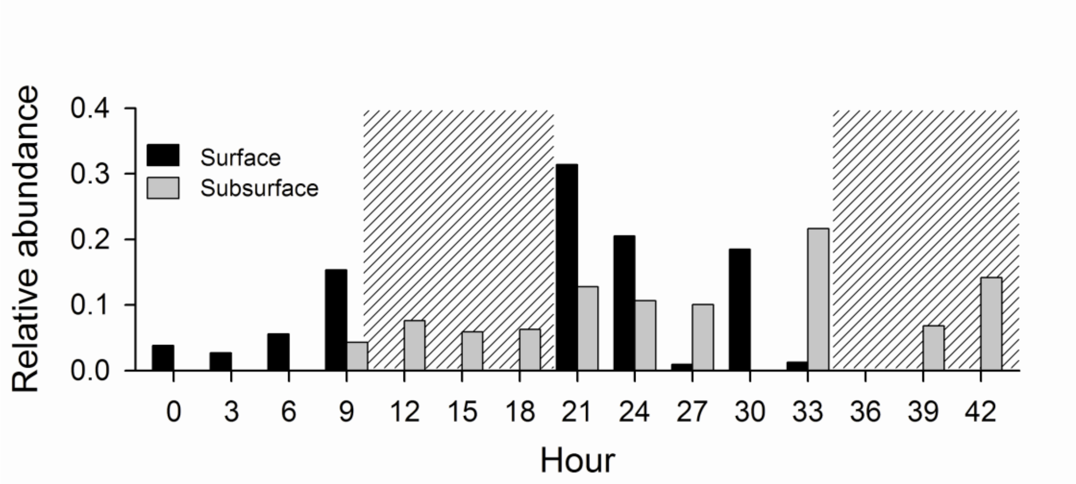


Figure 2.3. Istiophoridae. Diel vertical distribution of larvae during a 45-hour study with three-hour sampling intervals. Relative abundance values are the larval concentrations (larvae m^{-3}) expressed as proportions of the sum of concentrations for the entire study within each depth interval. A neuston net sampled the sea surface and a MOCNESS sampled subsurface. All subsurface larvae were collected in the 1–25 m depth interval. Shaded areas indicate periods of darkness.

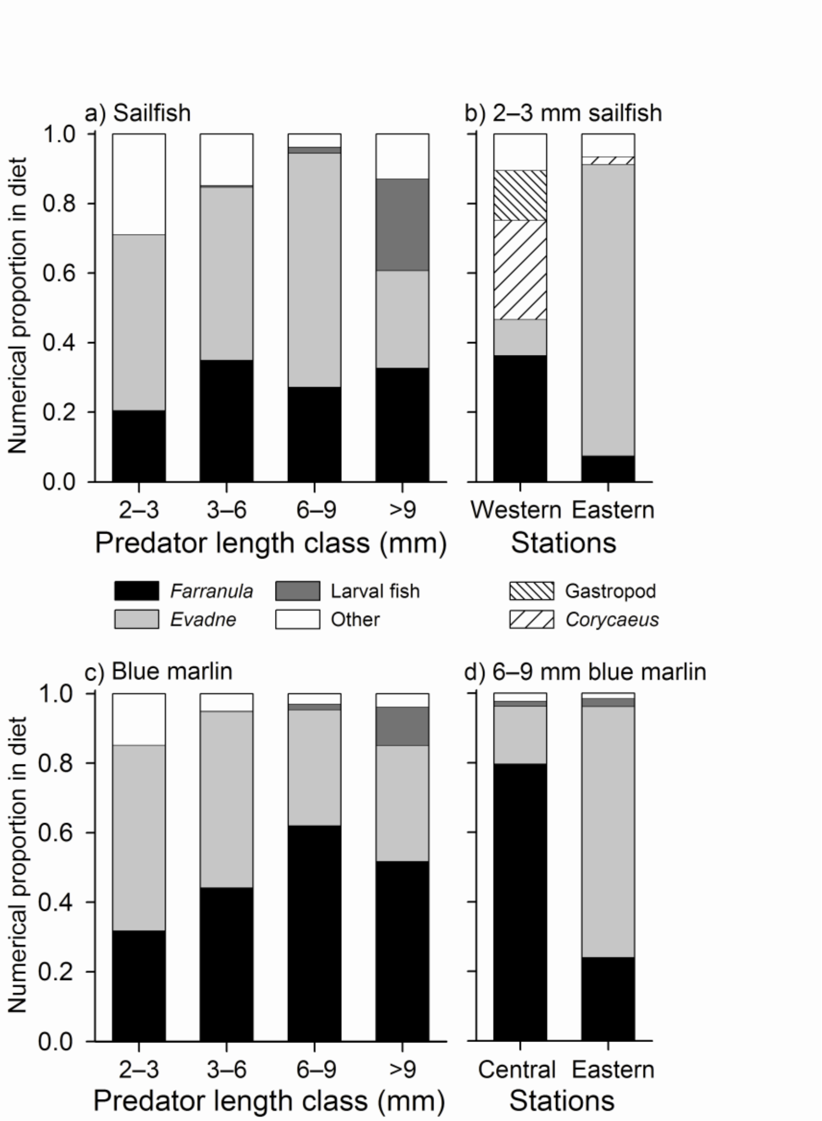


Figure 2.4. *Istiophorus platypterus* and *Makaira nigricans*. Numerical proportions of ingested prey types with larval growth for (a) sailfish and (c) blue marlin. Spatial differences, not capability, appear to explain the 'other' category for (b) 2–3 mm BL sailfish that largely consists of *Corycaeus* copepods and gastropods. For blue marlin, the increase in *Farranula* with larval size is a spatial effect of larval catch differences, illustrated by (d) 6–9 mm BL larvae having differing proportions of *Farranula* and *Evadne* between the central and eastern regions of the SOF. Station numbers for (b), western: 1–6, eastern: 9–17. Station numbers for (d), central: 6–9, eastern: 11–15. 'Other' category in (a), (b) and (c) includes *Corycaeus* and gastropods.

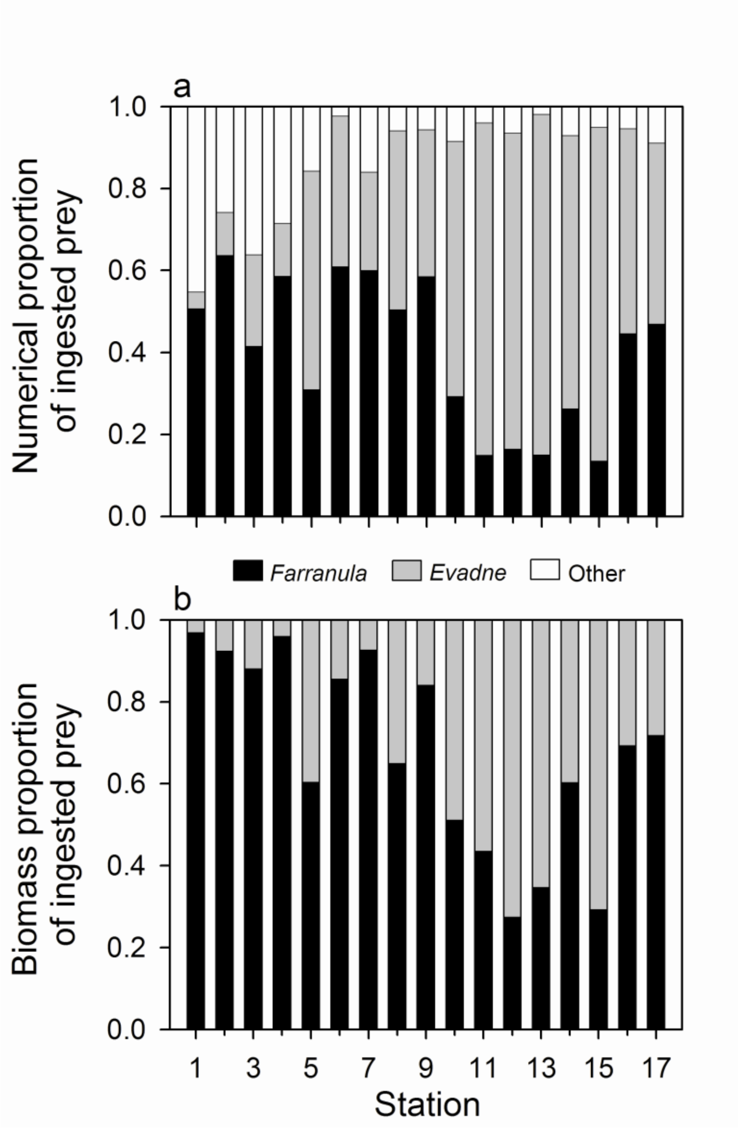


Figure 2.5. Istiophoridae. Spatial distribution of (a) numerical and (b) biomass proportions of ingested prey across the Straits of Florida for all billfish larvae. Biomass proportions are from converted dry weight and only include proportions of the total of the dominant prey types *Farranula* and *Evadne*.

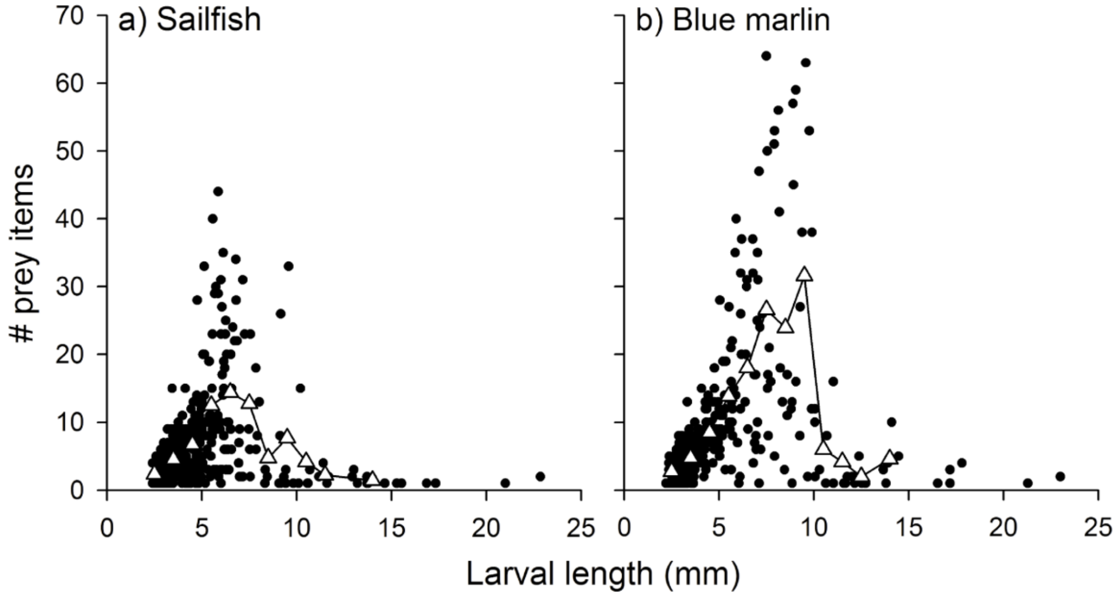


Figure 2.6. *Istiophorus platypterus* and *Makaira nigricans*. Relationships of number of prey items per larva and larval predator length for (a) sailfish and (b) blue marlin. Circles represent individual larvae and open triangles are size class means.

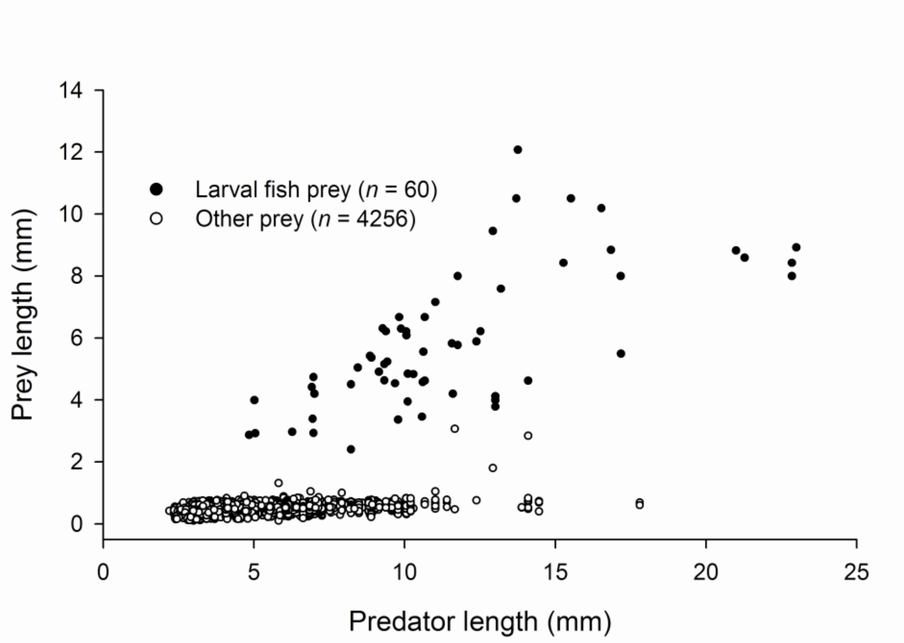


Figure 2.7. Istiophoridae. Relationship of individual ingested prey lengths and larval predator length.

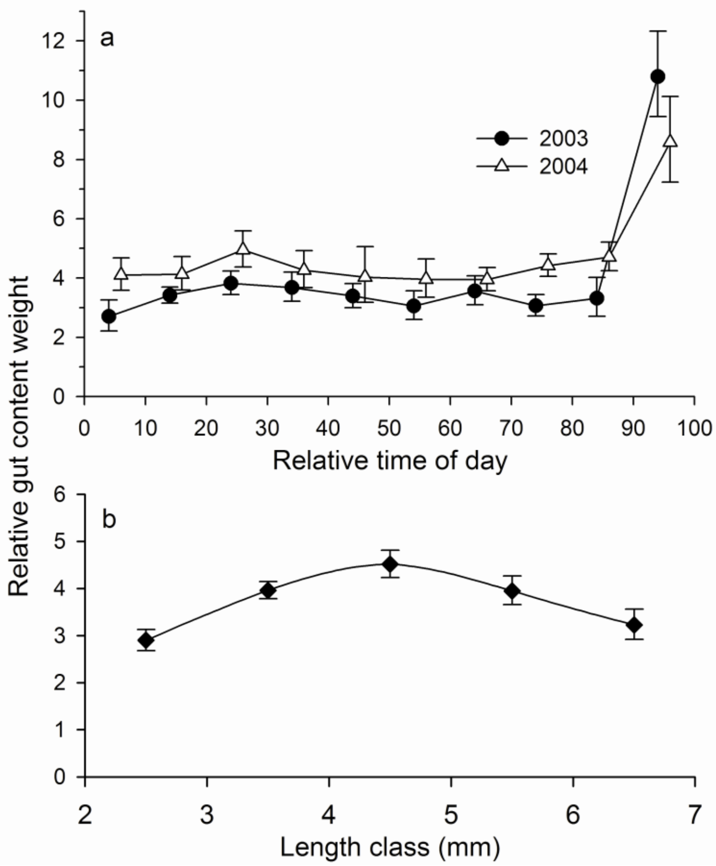


Figure 2.8. Istiophoridae. Relationship of relative gut content weight (percentage of gut-free body weight) to (a) time of day (*n* = 393) and (b) larval length (*n* = 368). Data are back-transformed means ±SE (from $\log_{10}(x + 1)$). Relative time of day (relTOD) is the percentage of daylight elapsed from sunrise to sunset. Data and analysis in (b) are for both years and exclude 90–100% relTOD.

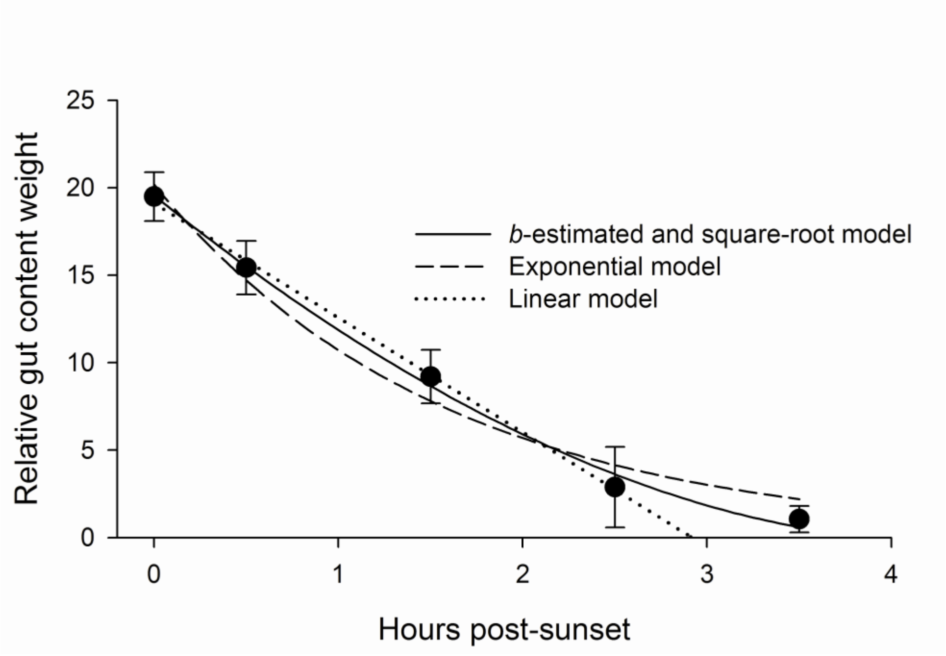


Figure 2.9. *Istiophorus platypterus*. Mean ±SE relative gut content weight (percentage of gut-free body) at time post-sunset for larvae collected to estimate the rate of gut evacuation. Nonlinear regression lines are from models that describe the decline in contents with different values for the parameter *b* (see 'Materials and methods' and Table 2.6). The *b*-estimated model ($b = 0.44$) and the square-root model ($b = 0.5$) essentially share the same regression line. The linear model excludes the 3.5 hr collection (Bochdansky and Deibel 2001). $n = 49$, including eight larvae containing no prey at 3.5 hrs post-sunset.

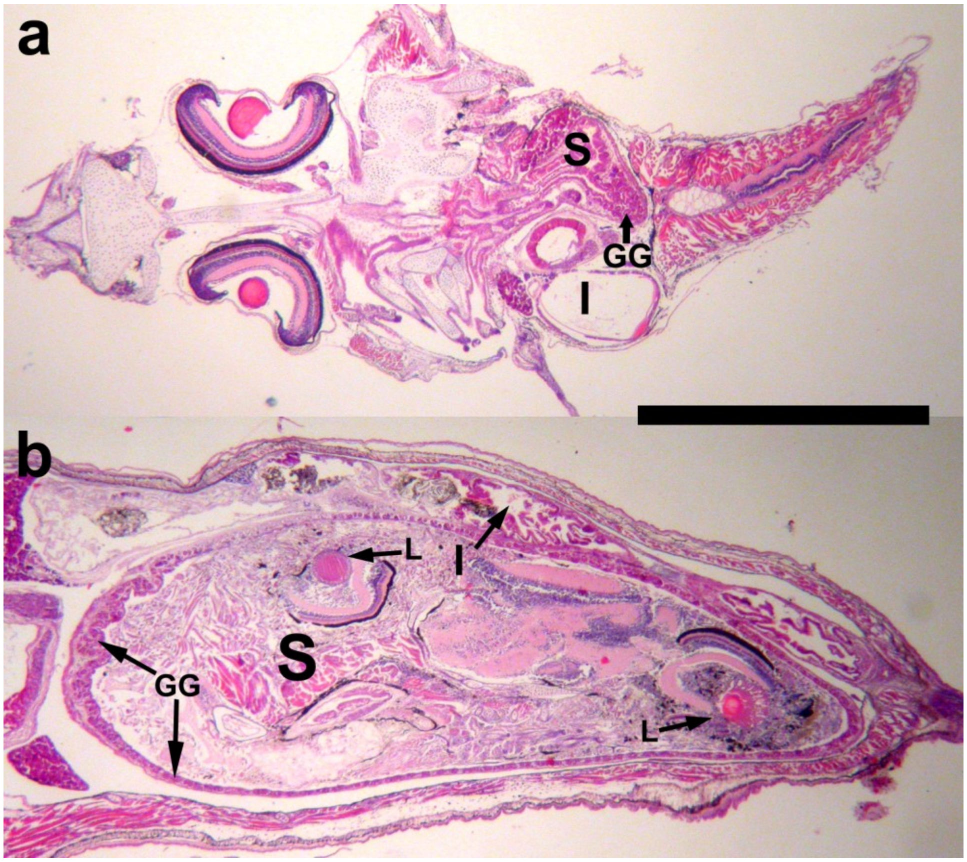


Figure 2.10. *Istiophorus platypterus*. Frontal histological sections of (a) an entire 4.2 mm BL larva and (b) the gastrointestinal region of a 13 mm BL larva. Gastric glands (GG) have developed in the posterior stomach (S) of the small larva and fully surround the stomach of the large larva that contains two ingested fish larvae, including the lenses (L) and surrounding eye. The relatively large intestine (I) in small larvae (containing a *Farranula* copepod in (a)) becomes relatively narrow along the margin of the coelom as the large stomach develops. Scale bar = 1 mm.

Chapter 3. Spatial and dietary niche separation among planktonic larval tunas in the subtropical ocean

The planktonic larvae of marine fishes often exhibit unique dietary and spatial characteristics. However, an understanding of how such distinctions relate to co-occurring larval fish taxa and the environment over ecologically relevant scales remains largely elusive, especially in the diverse low-latitude ocean. Monthly sampling of four taxa of larval tunas (family Scombridae, tribe Thunnini) across the Straits of Florida (SOF) over two years allowed for a description of taxon-specific feeding ecologies and horizontal and vertical distributions. Nearly all larvae examined (>98%) contained prey, and prior to piscivory as late larvae, *Thunnus* spp. exhibited a mixed diet of crustaceans and appendicularians, while skipjack *Katsuwonus pelamis*, little tunny *Euthynnus alletteratus*, and bullet and frigate mackerel *Auxis* spp. displayed nearly exclusive reliance upon appendicularians. The environmental abundances of both appendicularians and larval fish prey declined from west to east across the SOF. In the western SOF where prey was more abundant, tuna larvae were also abundant and all larval tuna taxa co-occurred, indicating not only the sharing of resources by the larvae, but also the sharing of general spawning grounds upstream in the Florida Current by the adults. In the central and eastern SOF, where prey was less abundant, only *Thunnus* spp. and skipjack tuna larvae were present. These two taxa exhibited significantly different vertical distributions, minimizing spatial overlap and possible competition for resources. Gut evacuation of appendicularians occurred in ca. 3 hrs, and this rate was used to estimate size-specific daily rations, allowing for estimates of the predatory impact of larval tunas upon ambient abundances of appendicularians. Predatory impacts occurring in the western SOF could potentially be unsustainable by appendicularian levels in the eastern SOF; however, specific knowledge of appendicularian growth and predation is limited. The spatial and dietary niches of these four abundant taxa of larval tunas highlight the possible influence of evolved larval and adult behavior on feeding-related larval fish survival.

Background

The planktonic organisms of the low-latitude open ocean occupy one of the largest and most poorly understood ecosystems. While characteristics of underlying phenomena occurring in oceanic plankton (e.g. species distributions and trophic links) are often described, inherent sampling limitations often preclude capturing overarching ecological processes that might explain why these specific characteristics exist. These broad-scale processes are elucidated through examining several aspects of the ecosystem (including the interactions of multiple taxa) concurrently over ecosystem-relevant temporal and spatial scales. Although distinct patterns have been revealed in the oceanic plankton, especially for phytoplankton and crustacean zooplankton (e.g. McGowan & Walker 1979, Venrick 1990), such work is limited for planktonic larval fishes.

The reproductive strategy of most marine teleost fishes involves the release of hundreds to millions of eggs into the planktonic environment (e.g. Elgar 1990, Winemiller & Rose 1993), resulting in extremely altricial offspring that are required to feed exogenously in a potentially food limited environment. Although the larval and adult stages of marine fishes are distinctly decoupled, selective forces governing larval survival can operate during both larval and adult life. For example, many larvae possess specific feeding, swimming and vertical distribution behaviors (Cowen 2002, Leis and Carson-

Ewart 2003, Llopiz and Cowen, 2008) that presumably enhance survival, while the spawning behavior of adults, including specific spawning times and locations (e.g. Iles & Sinclair 1982), can place offspring in an environment optimal for survival. For fishes such as tunas, the swimming capabilities and highly migratory nature of the adults have been hypothesized to allow for the placement of offspring in favorable larval habitats despite potentially long distances between such regions and those best suited for adult feeding and growth during non-spawning periods (Bakun 1996, Block et al. 2001).

The limited understanding of larval fish ecologies in lower latitudes suggests there may be substantial differences between the tropics/subtropics and higher latitudes, especially regarding larval fish trophodynamics (Sampey et al. 2007, Llopiz and Cowen 2008). High latitude larvae often exhibit broad diets that appear to be regulated more by prey size than prey type, resulting in little resource partitioning (Economou 1991, Pepin and Penney 1997 but see Last 1978). This may be due to a lower diversity of both fish larvae and their prey, or to an abundance of food (and associated reduction in competition) since spawning seasons in higher latitudes are often temporally contracted to correspond to brief periods of high secondary productivity (Cushing 1990). In contrast, most regions of the low-latitude open ocean are characterized by low secondary productivity that has little seasonal variability or temporal consistency (Longhurst & Pauly 1987), and, as such, fishes in these regions usually exhibit frequent spawning over protracted reproductive seasons, perhaps as a bet-hedging strategy for an unpredictable environment (den Boer 1968, Robertson 1991). Such an environment, coupled with a higher diversity of both fish larvae and planktonic prey, may result in selective larval feeding behaviors and specific trophic niches. Spatially, the vertical distributions of fish larvae and the spawning locations of the adults (influencing the horizontal distribution of the larvae) could also contribute to a reduction in both inter- and intraspecific competition for resources.

Here, we integrate larval diets, prey availability, predatory impact and vertical and horizontal distributions of four taxa of larval tunas in the Straits of Florida (SOF). Individually, such work can describe unique characteristics of the organisms or ecosystem, yet together and over relevant scales, it may yield insight into the evolved behaviors of both larval and adult fishes that presumably enhance offspring survival during the vulnerable larval stage. The four taxa of tuna larvae considered, oceanic tunas *Thunnus* spp., skipjack tuna *Katsuwonus pelamis*, little tunny *Euthynnus alletteratus*, and bullet and frigate mackerels *Auxis* spp., represent all four genera of ‘true’ tunas (family Scombridae, tribe Thunnini) that occur in the tropical and subtropical open ocean. Within the SOF, they composed 97% of scombrid larvae, and were second only to lanternfish (Myctophidae) larvae in abundance (unpublished data). These taxa co-occur in the SOF from ca. Apr to Nov, and are morphologically similar, having relatively precocious development and the capability for piscivory during the larval stage (Tanaka et al. 1996). Considering the observed high abundance and general temporal and spatial overlap of tuna larvae in the SOF, we address the following questions: 1) Is there selective and taxon-specific feeding by larval tunas? 2) Do the horizontal and vertical distributions of larval tunas correspond to the availability of their prey? 3) Could larval tuna consumption result in limited prey availability? 4) Are there taxon-specific horizontal and/or vertical distributions of tuna larvae that would reduce potential inter- and intraspecific competition or resource depletion? These specific questions allow for the ultimate goal of describing the potential influence of larval fish feeding and prey availability on the observed larval behaviors and distributions of several co-occurring taxa.

Materials and methods

Field sampling

The SOF region is a tropical/subtropical oceanic environment that contains the rapidly northward flowing Florida Current (nearer the Florida shelf break) that, to the north, becomes approximately one third of the total transport of the Gulf Stream (Leaman et al. 1989). A transect of 17 stations (numbered west to east) across the SOF between Miami, Florida and Bimini, Bahamas (Fig. 3.1A) was sampled monthly in 2003 and 2004 (following Llopiz and Cowen 2008). Plankton was sampled using two adjoined multiple opening closing net and environmental sensing systems (MOCNESS; Wiebe et al. 1985) of different opening and mesh sizes (4 m^2, 1-mm mesh and 1 m^2, 150-µm mesh; Guigand et al. 2005), which allowed for the concurrent collection of larval fishes of a broad size range and the available zooplankton prey. Similarly, adjoined rectangular neuston nets (2 x 1 m, 1-mm mesh and 0.5 x 1 m, 150-µm mesh) sampled the sea surface to a depth of ~0.5 m. The MOCNESS obliquely sampled the upper 100 m at all but the shallower western-most station (to 50 m) with nominal discrete-depth intervals of 25 m. Flow meters in each net system allowed for calculations of water volume sampled. Monthly transect sampling occurred during daylight to minimize diel effects (including any caused by the observed cessation of feeding by larval tunas during the night). Plankton samples were fixed in 95% ethanol and later drained and stored in 70% ethanol.

Gut evacuation rates were estimated with additional sampling at nighttime (a non-feeding period) that was conducted on two consecutive nights along the Florida shelf break in June 2005. MOCNESS tows of 15 min duration to a depth of 15 m were performed at ca. 0.5, 1.5, 2.5 and 3.5 hours post-sunset. This sampling allowed for modeling the decline in gut contents with time.

Laboratory procedures

Larval tunas were sorted from the samples of the 1 mm mesh nets and identified by pigment patterns (Richards 2005). Body lengths (BL) were measured as notochord length (pre-flexion) or standard length (post-flexion) with an ocular micrometer. Oceanic tunas *Thunnus* spp. were grouped at the genus level, although molecular techniques (Richardson et al. 2007) indicated 95% of collected *Thunnus* larvae were blackfin tuna *T. atlanticus* (Richardson et al. in review). Furthermore, no species differences in diets were observed between molecularly identified blackfin tuna and the far less abundant yellowfin tuna *T. albacares*. *Auxis* spp. larvae were also grouped together due to similarities in diet and distributions. Molecular analyses showed that frigate mackerel *Auxis thazard* and bullet mackerel *A. rochei* were approximately equally abundant in the SOF (Richardson et al. in review).

Subsamples of tuna larvae from 2003 were inspected for gut contents (*n* = 789). For the more abundant and widely distributed *Thunnus* spp. and skipjack tuna, only larvae from even-numbered months and stations were inspected. *Auxis* spp. larvae from even months and all stations, and little tunny from all months and stations, were inspected. Within each taxon, no more than five larvae were inspected from each combination of station, depth interval, and 2-mm BL size class. After excising the entire alimentary canal, prey items were teased out with minutien pins, identified, and enumerated.

Environmental concentrations of appendicularians, the most common and often exclusive prey of larval tunas, were estimated from the 1-m^2 MOCNESS samples for each depth interval of the even-numbered stations and months of 2003, and for select samples in 2003 and 2004 where predatory impact of larval tunas was highest. Appendicularians (whole or tails only) from a subsample (Hensen-Stempel pipette) of a known volume of plankton sample were enumerated, and subsampling occurred until at least 100 ind. were counted (Postel et al. 2000) or three subsamples had been analyzed (at least 1.5% of the sample). Subsamples taken throughout the year and across the transect for taxonomic purposes indicated that 99% of the appendicularians were of the genus *Oikopleura*, with the majority appearing to be *O. longicauda*.

Data Analysis

For the horizontal distributions of larval tunas, taxon-specific abundances (ind. m^{-2} sea surface to maximum depth sampled) at each station were summed over both years and all months of general co-occurrence of the four tuna taxa (Apr to Nov in 2003, Apr to Oct in 2004 due to incomplete sampling of stations in Nov) and expressed as a relative abundance (to the total of all four taxa). Total fish larvae (i.e. the prey of piscivorous tuna larvae) abundances were calculated similarly and for the same periods.

Vertical distributions were investigated using abundance proportions at depth calculated for each cruise for the entire larval population across the SOF. Surface layer abundances (from neuston nets) were added to the 0–25 m MOCNESS net. Abundances from each depth interval were standardized to 25 m of depth since not every net sampled exactly 25 m (93% were within 3 m of target interval). Abundances (m^{-2}) in each nominal 25 m depth interval over all stations sampled in a cruise were summed and expressed as a proportion of the total in all depth intervals. Collections from several cruises allowed for differences in taxon-specific proportions at depth to be tested with ANOVA and Tukey's hsd for pairwise comparisons. Proportions at depth were arcsine transformed (arcsin $p^{1/2}$). Distribution centers (e.g. Fortier & Leggett 1983) were also calculated for each cruise (following Röpke 1993) and similar results were obtained. However, the largely confined nature of *Thunnus* spp. to the upper 25 m depth interval biased error estimates. Vertical distribution analyses included the months of general co-occurrence (Apr–Nov) in 2003, and excluded the shallower and thermally constrained (shoaling thermocline) westernmost station and, for little tunny, three cruises where ≤10 ind. were collected.

Feeding and diets were described with feeding incidence (the proportion of larvae with prey present in the gut) and the frequency of occurrence of prey types (%FO; expressed for each type as the proportion of larvae with the prey type present). Frequencies of occurrence should better illustrate differences in prey choice and diversity, especially when prey sizes substantially differ as observed here for larval tunas. For the calculation of daily rations and establishing evacuation rates, estimates of appendicularian numbers present in guts were made. While inherently difficult to distinguish due to their soft bodies, consumed appendicularians progressed from fully intact and undigested individuals in the stomach of larval tunas to increasingly digested but somewhat distinct appendicularian 'packets' (enhanced by the different trunk, tail and 'house' regions) towards the posterior intestine.

Evacuation rates were estimated for little tunny and *Auxis* spp. larvae, which fed nearly exclusively upon appendicularians. Fifteen larvae of each taxon (4–8 mm BL) from each of the four post-sunset sampling periods were inspected (n = 120). Appendicularians were enumerated and expressed as a proportion of gut capacity (yielding a measure of gut fullness), standardizing for the increase with larval length. Gut capacity at length was established by a linear relationship of the maximum number of appendicularians observed in 1-mm BL intervals from the monthly transect sampling (Little tunny: $F_{1,4} = 48.4$, $P = 0.002$, $r^2 = 0.93$; *Auxis* spp.: $F_{1,4} = 52.7$, $P = 0.002$, $r^2 = 0.93$). Perhaps due to the use of prey numbers (ingestion = egestion) rather than remaining prey weight, the decline in gut fullness was distinctly linear. As such, evacuation models for each taxon, following Bochdansky and Deibel (2001), were estimated by weighted least squares regression (Neter et al. 1996) on raw gut fullness data at time post-sunset. The guts of all 30 larvae at 3.5 h post-sunset were empty and thus not included in the regression, and one extreme *Auxis* spp. outlier (possibly net or sample contamination) at 2.5 h post-sunset was excluded. Average gut fullness values from the monthly transect samples, which were similar throughout the day, were used in conjunction with the evacuation models to obtain estimates of daily rations (Eggers 1979) in units of multiples of gut capacity. The gut capacity with size relationship then yielded size-specific daily rations in numbers of appendicularians. Variability (SE) around estimates of daily rations was calculated using Gaussian error propagation (Lo 2005) to incorporate error associated with estimates of daytime average gut fullness and evacuation regression parameters.

Estimates of the predatory impact of larval tunas upon appendicularians used mean daily ration at length relationships together with larval concentrations and individual lengths to obtain a removal rate of appendicularians ($m^{-3} \cdot d^{-1}$) that was related to environmental appendicularian concentrations. Daily rations at size for skipjack tuna were assumed to be the midpoints of the relationships for little tunny and *Auxis* spp. This assumption agrees with the observation that development of little tunny is the most precocious of the three taxa and *Auxis* spp. the least. Predatory impact estimates only included larvae at lengths prior to low reliance upon piscivory (<8 mm for skipjack and little tunny and <15 mm for *Auxis* spp.). The consumption of *Thunnus* spp. was not included in estimates due to their mixed diets of appendicularians and crustaceans.

Results

Feeding variability

Of the 789 tuna larvae subsampled for feeding analyses, over 98% had prey present in the gut. Feeding incidences by taxa were 98% for *Thunnus* spp. (*n* = 323) and 99% for skipjack tuna (*n* = 170), *Auxis* spp. (*n* =162), and little tunny (*n* = 134). Despite morphological similarities (Fig. 3.1b), the diets of *Thunnus* spp. were distinctly different from the other three taxa of larval tunas (Fig. 3.2). *Thunnus* spp. diets were mixed throughout larval ontogeny, consisting of copepod nauplii and copepodids (calanoid and cyclopoid), appendicularians, *Evadne* cladocerans and larval fish. Similar to *Thunnus* spp., all other taxa exhibited piscivory (although to varying degrees and beginning at different lengths). Prior to piscivory, however, skipjack tuna, little tunny and *Auxis* spp. larvae displayed marked and nearly exclusive reliance upon appendicularians.

Consumption of appendicularians by *Thunnus* spp. increased with larval length to a maximum when nearly 80% of the larvae 7–11 mm BL had appendicularians present.

Predator and prey distributions

The horizontal distributions of tuna larvae across the SOF showed the highest total abundances and the co-occurrence of all four taxa in the western region (Fig. 3.3). In the central and eastern SOF, abundances were lower, and little tunny and *Auxis* spp. were nearly absent while skipjack tuna and *Thunnus* spp. co-occurred. Vertically in the water column, all taxa were primarily limited to the upper 50 m (Fig. 3.4a). *Thunnus* spp. larvae were found at significantly shallower depths than the other three taxa. This pattern held regardless of horizontal region, and vertical separation was most pronounced between *Thunnus* spp. and skipjack tuna. The extent of this separation is likely masked by the large depth intervals, since relative larval concentrations (i.e. m^{-3}, rather than m^{-2}) in the upper 0.5 m of the water column were 43% for *Thunnus* spp., whereas no skipjack tuna were collected at the surface.

The greatest levels of available appendicularians were also found in the upper 50 m of the water column (Fig. 3.4b), coincident with the highest abundances of tuna larvae. Horizontally, abundances of appendicularians in the upper 50 m were significantly greater in the western SOF where all four taxa of tuna larvae co-occurred, as compared to the central and eastern SOF where only *Thunnus* spp. and skipjack larvae were abundant (Student's $t_{30} = 2.04$, $P = 0.02$). Appendicularian concentrations by station (Fig. 3.5a) were greatest at the westernmost station (mean of 77 ind. m^{-3} in upper 50 m), declining towards the east to a minimum in the eastern central SOF (Stn 12 with 20 ind. m^{-3}). Abundances of all fish larvae (potential prey of piscivorous tuna larvae) were also highest in the western SOF (Fig. 3.5b). The average abundance in the west (Stn. 1–5) was twice the average of the central and eastern SOF, with a 3.5 fold difference between the stations with the highest and lowest abundances (Stn. 1 & 12).

Daily rations and predatory impact

Gut evacuation of appendicularian prey by little tunny and *Auxis* spp. larvae was completed in less than 3.5 h (Fig. 3.6a). Mean size-specific daily ration estimates for little tunny and *Auxis* spp. larvae (Fig. 3.6b) increased with size from 10–18 appendicularians d^{-1} for larvae of 3 mm BL up to 50–57 appendicularians d^{-1} for larvae of 10 mm BL. These estimates are for 14 h of feeding during the longest daylight lengths (Jun–Jul), which is near the center of temporal overlap and peak spawning of all four taxa of tuna larvae. Estimates for November (11 h of daylight) are 82% of 14-h values.

Observed monthly maximum estimates of potential predatory impact by tuna larvae (Table 3.1) ranged from 0.4–4.9 appendicularians$\cdot m^{-3} \cdot d^{-1}$ during the months of highest larval tuna abundance (Jun–Sep). All maxima for these months occurred in the western SOF, with four of eight at the westernmost station. Environmental concentrations of appendicularians where these maxima occurred were variable, ranging from 29–268 ind. m^{-3}, yielding percent removal estimates of appendicularians ranging from 0.3–3.5% d^{-1}. If related to the average level of appendicularians in the eastern SOF (26 ind. m^{-3}), observed maximum values of predatory impact (occurring in the western SOF) could have hypothetically removed 1.3–18.9% d^{-1}.

Discussion

We have utilized spatially explicit abundances of larval tunas and their prey in conjunction with estimates of predatory impact to examine the potential evolutionary influence of prey levels upon larval tuna distributions and behavior. Many of our observations are consistent with the hypothesis that larval and adult tuna behaviors are adapted to larval resource availability to maximize survival during the larval stage. With regard to the distribution of larval tunas and their prey across the SOF, *Thunnus* spp., skipjack tuna, little tunny and *Auxis* spp. all co-occurred in the western SOF, likely corresponding to upstream spawning off the Florida Keys and within the core of the Florida Current. Appendicularians, which were the nearly exclusive prey of all but *Thunnus* spp., were also most abundant towards the west, suggesting prey levels are high enough for coexistence of all four taxa. Abundances of total fish larvae, the prey of piscivorous tuna larvae as small as 5 mm BL, were also greatest in the western SOF. The greater abundance of prey in the western SOF may allow for coexistence of the four tuna taxa, resulting in less inter-specific competition. In addition, greater prey availability may also support high abundances of individual tuna species, thereby reducing intra-specific competition and even cannibalism. This is supported by the observed high abundances of little tunny in the western SOF that largely accounted for the high predatory impact in July and August 2004.

As prey availability declined towards the east, little tunny and *Auxis* spp. became nearly absent in the central and eastern SOF. The vertical distributions and diets of the remaining *Thunnus* spp. and skipjack tuna further support that prey availability may influence the ecologies of larval tunas. *Thunnus* spp. and skipjack larvae exhibited significantly different vertical distributions, and thus were distinctly spatially separated despite overlapping horizontally across the SOF. Additionally, the pre-piscivorous diet of skipjack tuna was almost exclusively composed of appendicularians (demonstrating a clearly selective feeding behavior given the greater abundances of other zooplankters [e.g. Llopiz & Cowen 2008; S. Smith unpublished data]), but *Thunnus* spp. fed upon multiple crustacean taxa while exhibiting an increasing reliance upon appendicularians with size. The taxon-specific diets observed in co-occurring tuna larvae suggest that feeding behaviors have evolved to maximize survival, and if so, the more diverse diet of *Thunnus* spp. may be a different strategy to assure successful feeding in variable or low prey environments or to minimize competition. The possibility for prey switching by the other taxa of tuna larvae if appendicularians were unavailable cannot be ruled out; however, appendicularians continued to be consumed despite low environmental abundances.

The dynamics of predatory impact by larval tunas offer further support for a link between larval distributions and prey availability. For each month during the period of peak larval tuna abundance (Jun–Sep), the maximum observed predatory impact upon larvaceans occurred in the western SOF (most often at the westernmost station), due to high total abundances of tuna larvae and the occurrence of all taxa. Percentages of appendicularians removed at these stations had a range of 0.3–3.5% d^{-1}, averaged 1.5% d^{-1} and were clearly dependent upon the highly variable abundances of both tuna larvae and appendicularians. If the observed maxima of predatory impact in the west had occurred at the average environmental concentration of appendicularians in the eastern SOF (26 ind. m^{-3}), percent removal rates would be substantially higher, including values for Jul and Aug 2004 that were 19% d^{-1} and 13% d^{-1}, respectively. Knowledge of appendicularian population growth is necessary for placing removal rates into a context of what is sustainable; however, work in this area is limited, and especially so in warm, oligotrophic waters and on the commonly observed appendicularian *Oikopleura longicauda*. Some estimates of generation times for *O. dioica* are 3–5 d at temperatures of 20–22 °C (Fenaux 1976, Troedsson et al. 2002) and 1–2 d at 29 °C (Hopcroft & Roff 1995), a temperature similar to the observed surface-water average in the SOF in the summer. Such rapid growth, which is notably greater than that of crustacean zooplankton, would allow for high levels of predation and, thus, the high reliance upon appendicularians by abundant larval tunas. Without knowledge of the predatory impact of the many other appendicularian predators (Purcell et al. 2005), including several larval reef fish taxa in this region (Llopiz & Cowen in prep), the proportional contribution by larval tunas to appendicularian predation mortality is unknown. It appears, however, that occasionally high predatory impacts by larval tunas in the western SOF could be excessively large for the maintenance of appendicularian abundances at eastern SOF levels, thus supporting potentially evolved spawning habitat selection by adult little tunny and *Auxis* spp. that is limited to the western SOF and results in maximizing larval feeding success and offspring survival.

Although the average state of the prey environment may be important, the variability of prey resources may also have implications. If there is a threshold level of appendicularian abundance below which tuna larvae feed unsuccessfully or can substantially deplete the resource, the frequency with which larvae experience such levels may influence total larval survival. If so, it is likely that the western SOF will less frequently exhibit constraining prey levels. In the context of a bet hedging strategy of frequent spawning over a long season, the western SOF would be a better bet for experiencing larval prey levels above any potential minimum prey threshold. However, there are resources available in the central and eastern SOF, and skipjack tuna and *Thunnus* spp. may occupy these niches to their own benefit and to the exclusion of other taxa. Adult skipjack tuna and *Thunnus* spp. may also distribute their reproductive output more consistently, compared to the potentially periodic high spawning output of little tunny (as observed in Jul and Aug 2004), which may only be supported by the higher prey availability in the western SOF. Yet, even in the western SOF, appendicularian abundance was observed to vary considerably between months at the same location, and between nearby locations in the same month. For example, in Aug 2003 at the westernmost station, the appendicularian concentration was 220 ind. m^{-3}, but the month before at the same station there were only 38 ind. m^{-3}. Although the degree of fine-scale patchiness of appendicularians is unknown, this variability highlights the possibility of mismatches between larval fish predators and their zooplankton prey, though on distinctly smaller spatial and temporal scales than those exhibited in higher latitudes that are driven by the seasonality of primary and secondary productivity peaks (Cushing 1990). Such a possibility has been largely unaddressed despite the long standing hypothesis that frequent spawning over large temporal and spatial scales by many fish species in low latitudes is a bet hedging strategy for an unpredictable environment.

There are limitations to our estimates of predatory impact; however, we have utilized a more direct approach that eliminates several broad assumptions that are necessary when data are not highly spatially and temporally resolved, or daily rations and concurrent distributions of prey and predator are unavailable. With regard to evacuation and daily ration estimates, the linear evacuation model used here yields daily ration estimates lower than those of most models (Bochdansky and Deibel 2001, Llopiz and Cowen 2008), and estimates of gut evacuation during a non-feeding period (after sunset) may be slower than those from periods of continuous feeding (e.g. Canino & Bailey 1995). Additionally, only the taxa that fed nearly exclusively upon appendicularians were used in the analyses (the more broadly feeding *Thunnus* spp. larvae were excluded). Therefore, our estimates of predatory impact should be conservative, with the observed pattern and potential implications remaining valid. Largely unknown, however, is the influence of predator and prey patchiness (e.g. Lough & Broughton 2007) or the potential bias of net samples for estimating appendicularian abundance (Remsen et al. 2004), although the small mesh size and the counting of both whole individuals and tails should reduce the chance for underestimates. Furthermore, while this is the first study to directly measure evacuation rates of appendicularians in a larval fish, the potential for inaccuracies in estimating the number of appendicularians present in the gut, especially the hindgut, must be acknowledged.

A common descriptor of larval fish feeding success is the feeding incidence, or the proportion of larvae with food present in the gut. In combination with the rapid digestion exhibited by larval tunas, the daytime feeding incidence of nearly 99% indicates that feeding is frequent and rather successful for larval tunas in the SOF. Although these are the first data for larval tunas in the western North Atlantic, daytime feeding incidences in other regions were near 55% for *Thunnus* spp. and 42% for skipjack tuna in the eastern Indian Ocean (Young & Davis 1990), and ca. 60% for both black skipjack *Euthynnus lineatus* (a congener of little tunny) and *Auxis* spp. in the Gulf of California (Sanchez-Velasco et al. 1999). Furthermore, it has been inferred that larval tunas in the eastern Pacific Ocean may experience high levels of starvation mortality (Margulies 1993). Without knowledge of spawning output or larval feeding success by tunas in other Atlantic Ocean regions, the relative advantage conferred by the SOF ecosystem to larval survival is unknown. However, the high abundances and successful feeding of tuna larvae in the SOF indicate that this region is likely to be important to the persistence of these species.

Spawning within oligotrophic oceanic waters by tunas, often after lengthy migrations, has been hypothesized to have evolved in order to reduce predation on larvae with the potential tradeoff of experiencing poor larval feeding conditions (Bakun & Broad 2003). This theory is largely supported by evidence that many regions may often be nutritionally limiting (Young & Davis 1990, Margulies 1993, Sanchez-Velasco et al. 1999), even potentially yielding density-dependent feeding and growth (Jenkins et al. 1991). However, the SOF appear to provide a relatively favorable feeding environment, possibly due to appendicularian abundances. This is supported by not only higher feeding incidences, but also higher reliance upon appendicularians exhibited by *Thunnus* spp., *Auxis* spp. and little tunny compared to the same genera in other regions (Young & Davis 1990, Sanchez-Velasco et al. 1999). For tunas, the energy demands of fast growth and warm temperatures (25–30 °C in the SOF) add to the challenge of feeding in an unproductive habitat. The reliance upon appendicularians may be a nutritional ‘loophole’ (cf. Bakun & Broad 2003) that helps larvae overcome these constraints. Appendicularians are known to rapidly filter and ingest much smaller particles than most zooplankton, assimilating nano- and picoplankton that dominate low latitude oceanic waters (King et al. 1980, Alldredge 1981, Deibel & Lee 1992), thereby essentially exploiting the microbial loop to fuel their extremely high growth rates. Larval tunas, in turn, obtain relatively large, energy rich prey items (Purcell et al. 2005) that are generally abundant and reliably available in an otherwise oligotrophic environment. Early piscivory should also confer a nutritional advantage due to the high diversity of consistently available fish larvae in the SOF that, although relatively rare, provide much larger and more nutritious prey items.

The characteristics of the spatial and dietary niches of larval tunas are generally related either to the behavior of the individual larvae or the spawning of the adults. Clear distinctions in diets and vertical distributions are evident in larvae, and while causality cannot be definitively assigned, there is support for the possible influence of food acquisition, as larval tuna behaviors are in accordance with resource partitioning and reducing competition. The horizontal distributions across the SOF, which are a function of the locations of upstream spawning, similarly relate to the nutritional resources of the larvae. An alternative explanation is that spawning locations are more related to the survival and feeding of the adults. It is also possible that such clear distinctions may not exist, as adult ecologies may be inherently related to offspring survival, or the conditions optimal for each could be correlated. While considering the spatial scales, intricacies and innumerable unknowns in the open ocean, we can only present a possible role of larval tuna feeding and survival on their apparent niche separation in the oceanic planktonic ecosystem.

Table 3.1. Predatory impact upon appendicularians by larval tunas.

Cruise	Max pred. impact (append.$\cdot$m$^{-3}\cdot$d^{-1})	Stn	Env. append. abund. (m^{-3})	% consumed (d^{-1})	% consumed of avg. east append. abund. (d^{-1})
Jun 2004	1.3	2	70	1.9	5.0
Jul 2004	4.9	3	142	3.5	18.9
Aug 2004	3.3	4	268	1.2	12.8
Sep 2004	0.7	1	29	2.4	2.6
Jun 2003	0.5	1	64	0.8	2.0
Jul 2003	0.5	1	38	1.4	2.0
Aug 2003	0.6	1	220	0.3	2.3
Sep 2003	0.4	6	62	0.4	1.3

Notes: For each month during the period of peak larval abundance (Jun–Jul), a maximum observed predatory impact by larval tunas was related to ambient appendicularian concentrations to estimate a potential daily percentage of appendicularians removed. Maxima were also related the average appendicularian concentration in the eastern Straits of Florida (26 ind. m^{-3}), yielding estimates of hypothetical percentages removed if the maxima of predatory impact occurred in this region. All values corrected for daylight length differences in daily consumption. Stn = station.

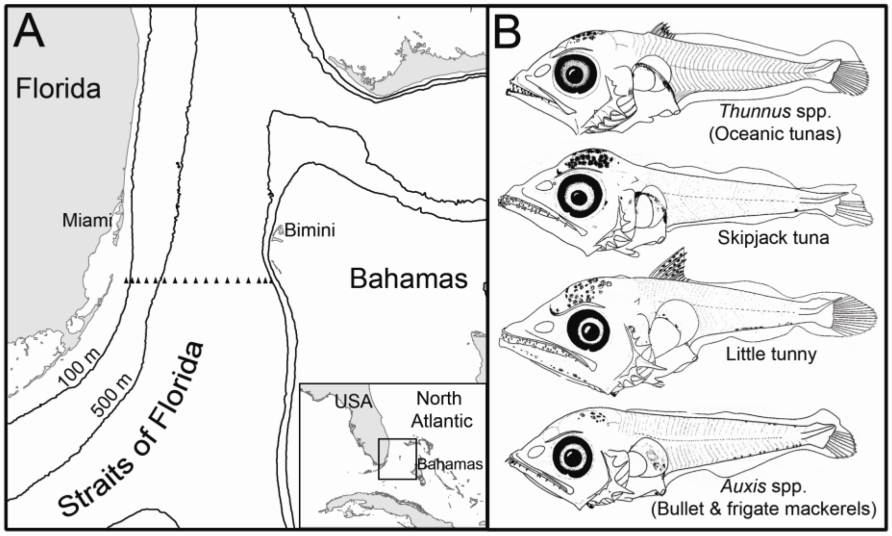


Figure 3.1. A) Map of the Straits of Florida where a transect of 17 stations (triangles) was sampled monthly in 2003 and 2004. B) The four taxa of 'true' tunas (tribe Thunnini) that occur in the Straits of Florida illustrating their morphological similarities. Body lengths are ca. 6 mm for all taxa, except *Auxis* spp., which is ca. 5 mm. *Thunnus* spp. drawing from Richards 2005, others from Collette et al. 1984.

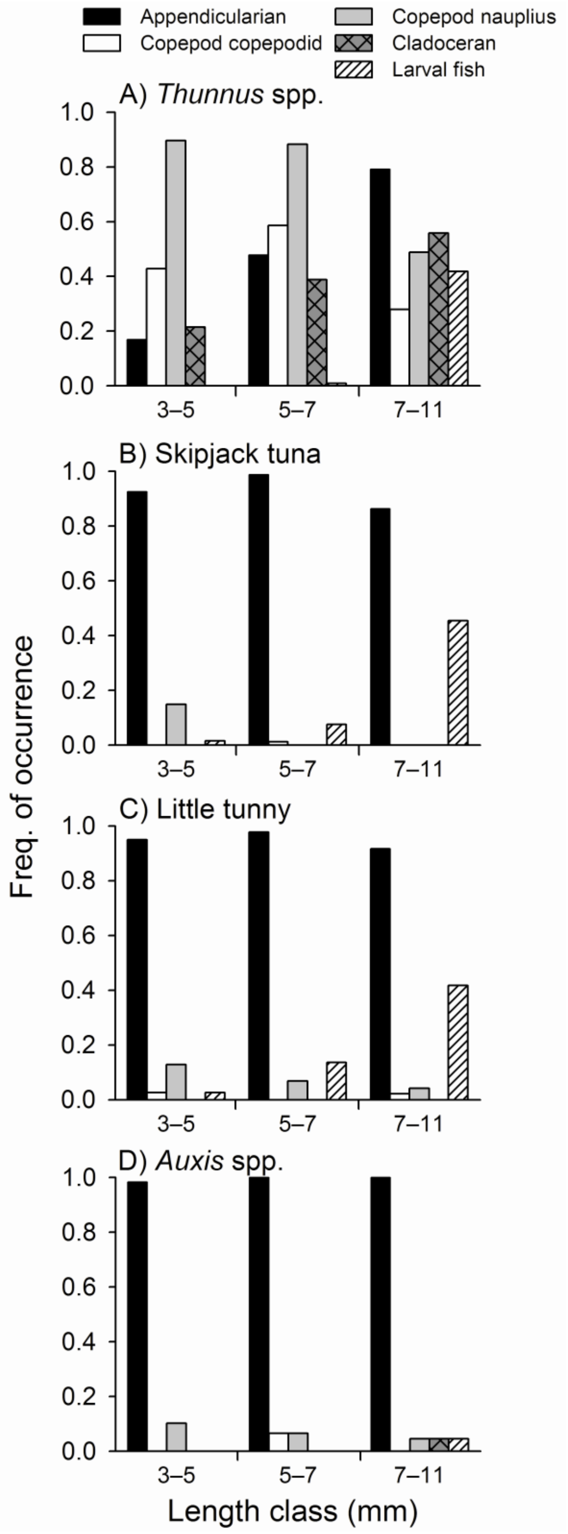


Figure 3.2. Frequency of occurrence of prey types (percentage of larvae with prey type present) by length class for A) *Thunnus* spp., B) skipjack tuna, C) little tunny, and D) *Auxis* spp. larvae.

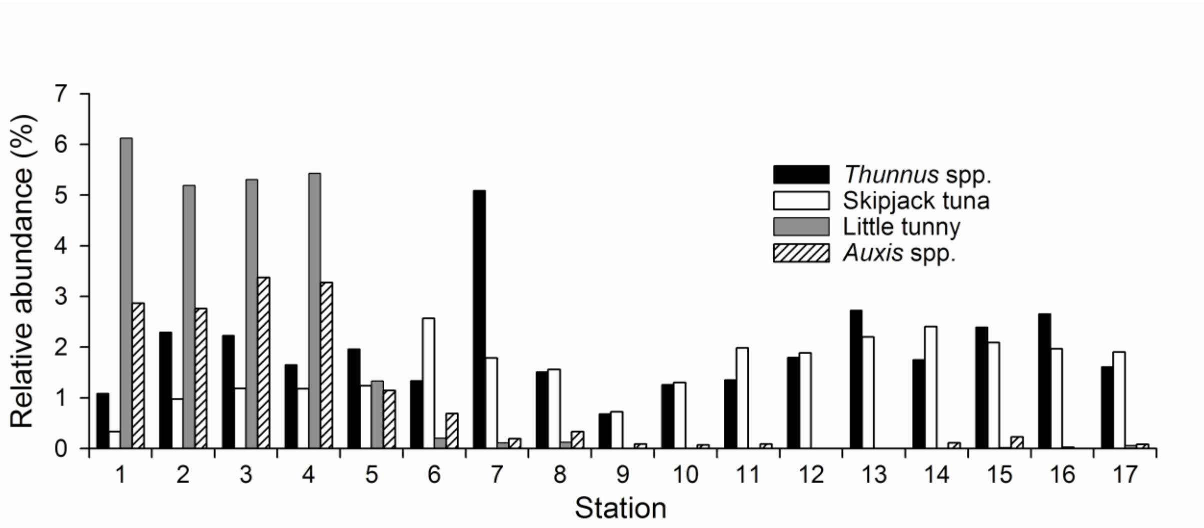


Figure 3.3. Relative abundances of tuna larvae at each of the 17 stations (numbered west to east) sampled across the Straits of Florida (*n* = 8156).

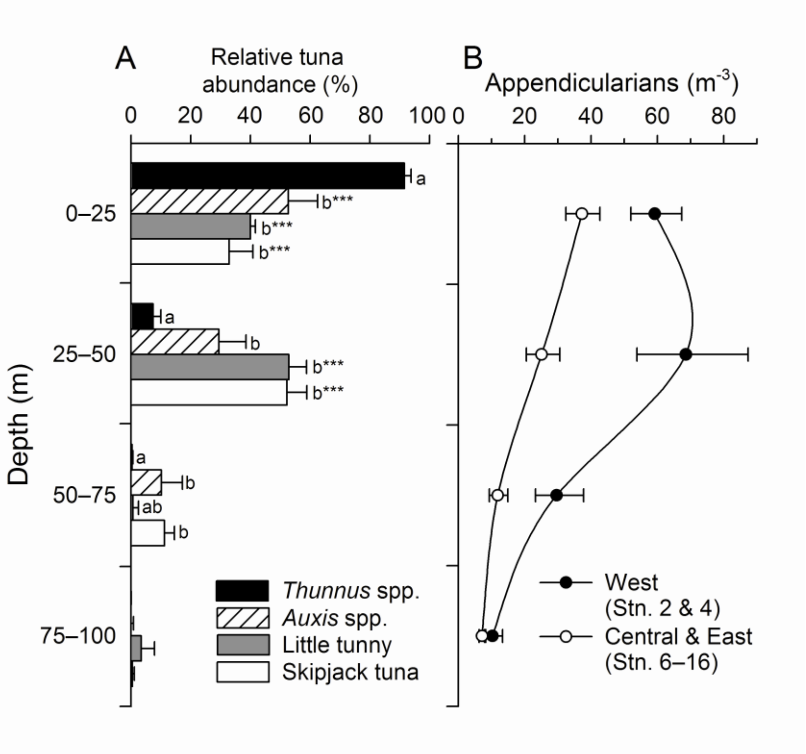


Figure 3.4. Vertical distributions of larval tunas and appendicularians. A) Mean (+SE; backtransformed) larval tuna relative abundances by taxa in 25 m depth intervals calculated from monthly values of the entire larval population across the SOF. Significant differences between taxa combinations within each interval are indicated by unshared letters ($P < 0.05$ or ***$P < 0.001$). B) Geometric mean (±SE; backtransformed) environmental concentrations of appendicularians at depth interval for stations where all taxa of tuna larvae co-occurred (2 & 4) and those where only *Thunnus* spp. and skipjack tuna larvae occurred (6–16).

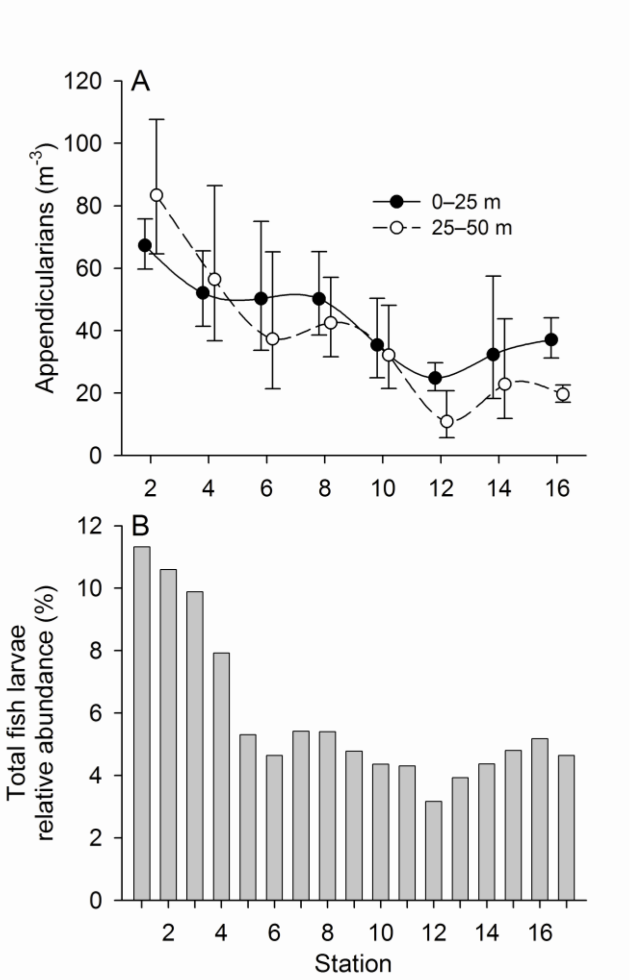


Figure 3.5. Environmental abundances of two dominant prey of larval tunas by station (numbered west to east) across the Straits of Florida. A) Geometric mean (±SE; backtransformed) of appendicularians, and B) relative abundance of all fish larvae in the upper 50 m (*n* = 90,246).

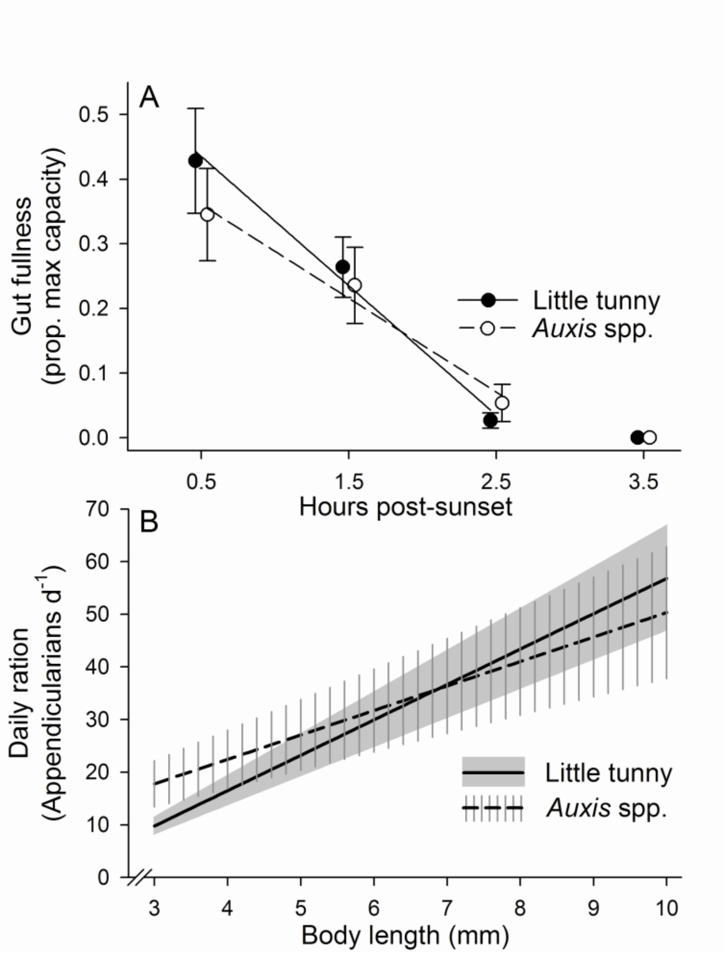


Figure 3.6. A) Mean (±SE) gut fullness, expressed as a proportion of maximum capacity, of little tunny and *Auxis* spp. larvae collected during periodic post-sunset sampling to estimate gut evacuation rates. Total $n = 119$, including 30 empty larvae at 3.5 h post-sunset excluded from the weighted least squares linear regression. Means are offset for clarity. B) Size-specific relationship of daily consumption estimates, in numbers of appendicularians, for little tunny and *Auxis* spp. larvae. Black lines represent model estimates with shaded areas the SE calculated from Gaussian error propagation of evacuation rate and daytime gut fullness SE. Estimates are for 14 h of feeding (i.e. summer, also the approximate period of maximum larval abundance).

Chapter 4. Trophodynamic strategies among larval coral reef fishes in the oceanic plankton

The successful transport of larval coral reef fishes to juvenile habitat is inherently tied to surviving the planktonic journey. Yet, the processes governing survival of coral reef fish larvae are not well known, and notably lacking are sound data regarding the trophic ecologies of these larvae. Regular sampling across the Straits of Florida allowed for highly resolved data on the diets and diet variability of several taxa of coral reef fish larvae. Included were the families Serranidae, Lutjanidae, Mullidae, Pomacentridae, Labridae, Scaridae, and Acanthuridae. In total, 1266 larvae over broad spatial, temporal and ontogenetic scales were examined for gut contents. Feeding incidences were high (0.94 to 1.0) for all taxa except *Sparisoma* spp. scarids (0.04). Diets were generally narrow and predator-specific. Diets of *Serranus* spp. (Serranidae) changed little with growth and were composed almost entirely of calanoid copepods, while the labrids *Thalassoma bifasciatum* and *Xyrichtys* spp. nearly exclusively consumed harpacticoid and cyclopoid (*Farranula* and *Oncaea*) copepods throughout ontogeny. Increasing reliance upon appendicularians with growth was exhibited by lutjanine and acanthurid larvae, and mullids exhibited an ontogenetic shift from nauplii to calanoid copepodites and appendicularians. Cluster analysis examining diet similarity among taxa yielded clear groupings of small acanthurids, labrids, appendicularian-feeders, and a fourth group with subgroups of larvae having calanoid and mixed diets. Within larval taxa, canonical correspondence analysis illustrated the change in diet with a variety of environmental and larva-specific variables. Diets were most associated with larval length, but other significant variables were time of year (acanthurids, mullids and *T. bifasciatum*), collection depth (acanthurids, *T. bifasciatum* and *Xyrichtys* spp.), and longitude and gut fullness (mullids, *T. bifasciatum* and *Halichoeres* spp.). The trophic niche breadth of four larval taxa significantly decreased with growth, while other taxa exhibited no significant change. Many of these results highlight distinct differences between high and low latitude regions, including the narrow taxon-specific trophic roles and greater niche separation of larval fishes in the diverse planktonic food webs of lower latitudes.

Background

The larval stage of most marine fishes is characterized by a planktonic period during which there is high vulnerability to both starvation and predation. Despite the potential influence of these two processes on total survival to later stages (Houde 1987), our understanding of them is limited; this is especially so for the larvae of coral reef fishes. As predation mortality is inextricably linked to growth (Cushing 1975), and consequently to feeding (Buckley & Lough 1987), a necessary step toward understanding survival in the early life stages of fishes is identifying their specific trophic roles in the complex planktonic food webs of the ocean.

The tropical/subtropical ocean is generally oligotrophic and unproductive with fluctuations in productivity that are low in magnitude and temporally inconsistent (Longhurst & Pauly 1987). These conditions, which could represent a nutritionally constraining environment for altricial larvae, differ from those of higher latitudes where there are distinct secondary productivity blooms with which fish spawning periods often coincide (Cushing 1990). Additionally, the low-latitude open ocean is habitat for a higher diversity of larval fishes (Richards 2005) and their potential zooplankton prey (van der

Spoel & Pierrot-Bults 1979, Hillebrand 2004) relative to higher latitudes. High larval fish diversity in an unproductive and diverse prey environment raises the possibility of evolved species-specific feeding niches, and while building evidence supports this hypothesis (Sampey et al. 2007; Llopiz and Cowen 2008), elucidation of such processes necessarily requires increasing the number of taxa studied, but with sufficient spatial, temporal and ontogenetic resolution.

Fish larvae that generally develop well offshore may be subjected to lower predation (e.g. Bakun & Broad 2003) but could suffer from low food availability or the unsuccessful transport to suitable juvenile habitat (Hare & Cowen 1991). Modeling studies in lower latitudes have focused on the transport success of larvae between spawning and settlement locations (Cowen et al. 2006); however, the connectivity of marine populations is inherently tied to larval survival en route. This subject has, in large part, been a black box for modelers, and a need for more work empirically investigating the biological processes occurring in the planktonic phase, especially with regard to temporal, spatial, and taxonomic variability, is becoming increasingly apparent (Paris et al. 2007). Feeding studies are particularly important, for without knowledge of the specific diets of the larvae that are being modeled, the relation of general zooplankton indices to larval survival (especially without first relating them to growth rate variability) is tenuous.

Empirical larval fish research nearer the tropics notably lags behind the extensive body of work in higher latitudes, presumably due to historical interest in understanding and maintaining the important fisheries in temperate regions. However, as the coral reef ecosystems of the world are increasingly threatened by anthropogenic pressures, such as overfishing, habitat degradation, and climatic effects (Hughes et al. 2003, Pandolfi et al. 2003), the piecewise understanding of the ecological processes governing coral reefs and their fish populations is critical to conservation efforts.

This contribution reports on the diets and diet variability of several taxa of coral reef fish larvae that occur in the oceanic waters of the western North Atlantic Ocean. In addition to taking a comparative approach, our goal was to maximize temporal, spatial and ontogenetic resolution of feeding variability by examining relatively large numbers of larvae collected throughout the year in the Straits of Florida. In this region, the oceanic waters of the Caribbean Sea and Gulf of Mexico pass through a bottleneck between Florida and the Bahamas, allowing for the sampling of disparate water masses along a narrow 80 km transect. Due to the many physical and biological variables, we also incorporate multivariate analyses to understand the trophic ecologies of these larvae and the factors that may influence feeding variability. Overall, we address the following questions: Are larval coral reef fishes generally successful feeders? Do they exhibit taxon-specific diets, and if so, to what degree do diets differ among taxa? Are there ontogenetic diets shifts in prey types and/or prey sizes? What variables of the environment and of the larvae themselves may influence prey type? Do the larvae conform to the general assumptions regarding trophic niche breadth?

Materials and methods

Area of study and field sampling

The Straits of Florida (SOF) encompass the waters between Florida and both Cuba and the Bahamas. The region is dominated by the rapid northerly flow of the

Florida Current (nearer the Florida shelf) that links the oceanic waters of the Gulf of Mexico and Caribbean Sea to the Gulf Stream of the western North Atlantic Ocean. In 2004, ichthyoplankton was sampled monthly along an east-west transect of 17 stations across the SOF (Fig. 4.1) between the Florida shelf and Great Bahama Bank (Llopiz & Cowen 2008). For subsurface sampling, we utilized a multiple opening closing net and environmental sensing system (MOCNESS; Wiebe et al. 1985) with a 4 m^2 opening and 1-mm mesh nets. Discrete-depth sampling occurred at nominal intervals of 25 m from a depth of 100 m at all but the shallower westernmost station (where sampling was from 50 m). A fluorometer attached to the MOCNESS continuously measured fluorescence. A rectangular neuston net (2 x 1 m, 1-mm mesh) sampled the surface waters to a depth of ca. 0.5 m. All sampling occurred during daylight hours. Plankton was preserved in 95% ethanol and later transferred to 70% ethanol.

Laboratory procedures

Fish larvae were sorted from plankton samples and initially identified to varying degrees of taxonomic resolution following Richards (2005). Ten taxa of coral reef fish larvae (generally abundant as larvae or adults, or of economic importance) were subsampled for gut content inspection (total *n* = 1266). Taxa included the families Lutjanidae (snappers), Pomacentridae (damselfishes), Acanthuridae (surgeonfishes), and Mullidae (goatfishes), the serranid subfamilies Serraninae (seabasses) and Epinephelinae (groupers), the labrids (wrasses) *Halichoeres* spp., *Xyrichtys* spp. and *Thalassoma bifasciatum*, and *Sparisoma* spp. scarids (parrotfishes). For most taxa, subsamples were taken from the even-numbered stations of cruises taken in even-numbered months, and consisted of no more than 10 individuals from each of three regions of the SOF (west:

stn. 1 to 5; central: stn. 6 to 11; east: stn. 12 to 17). If >10 ind. were collected within each region, larvae were selected ca. proportionally to both horizontal and vertical total abundances, and, within each sample, to their size distributions. Exceptions were *T. bifasciatum*, which followed the same scheme described above but with a maximum of 20 ind. in each region-cruise combination, and epinepheline groupers, of which all individuals collected throughout the year and transect were inspected (due to low abundances). All taxa co-occurred in the SOF throughout the year.

Prior to inspection, most serranine and pomacentrid larvae were further identified to the genus level, and lutjanid larvae to subfamily. Larval body length (BL; notochord/standard length before/after flexion of the urostyle) and lower jaw length (LJL; mandible) were measured with the ocular micrometer of a stereomicroscope (Leica MZ15). Larvae were dissected with a microscalpel and minutien pins, and the contents of the entire alimentary canal were teased out and identified. Due to the increase in gut capacity with larval growth, gut fullness was estimated for each larva and assigned a value of 0 (empty), 1 (< half-full), 2 (> half-full) or 3 (full). The most anterior (least digested) prey items, up to a maximum of 5 per larva, were measured for length (prosome length for copepod copepodite stages except of harpacticoids, carapace length for other relevant crustaceans, and the longest dimension in all other prey, including harpacticoid copepods but excluding the caudal rami). Appendicularians were not measured due to their soft bodies. Appendicularian enumeration became more difficult with the degree of digestion (posteriorly in the intestine), but was estimated by the distinctiveness of the trunk, tail and house regions of the organism and the repeatedly observed anterior to posterior gradient of digestion state. Reference to copepod orders follows Boxshall and

Halsey (2004). If identified, only copepod genera are referenced, and no distinction was made between juvenile and adult copepodite stages.

Data analysis

The feeding incidence of a taxon of fish larvae was calculated as the proportion of individuals with food present in the gut. The overall diet of each taxon of larval fish was described with an index of relative importance (IRI) for each prey type observed, and was calculated as the product of the numerical percentage of a prey type and its frequency of occurrence (percentage of larvae) in feeding larvae (Govoni et al. 1983, Young & Davis 1990). Values were converted to a percentage of the sum of IRI values (%IRI). Although IRI values may be biased by prey size variability and length-frequency distributions of inspected larvae (Llopiz & Cowen 2008), their use here for several taxa allow for easier interpretation and comparison among the taxa and with other studies. The numerical percentage of prey types was used in further analyses, including the description of ontogenetic changes in diets within each larval fish taxon.

Indirect gradient analysis was used to examine diet similarity among larval fish taxa (Field et al. 1982). Both hierarchical clustering and non-metric multidimensional scaling (NMDS) were performed on a Bray-Curtis dissimilarity matrix (SYSTAT Software Inc. 2004) constructed from the average arcsine-transformed numerical percentages of prey types for each taxon of larval fish. Taxa that exhibited distinct ontogenetic diet shifts or seasonal differences were further subdivided *a priori* into two size classes or two periods of the year. Prey categories used in the analyses were those composing at least 5% of the prey items for at least one of the larval fish classes and excluded unidentifiable prey. This yielded 12 prey categories (variables) and 18 larval fish classes (samples). Hierarchical clustering used the unweighted arithmetic average method (Legendre & Legendre 1998) and main groupings were chosen at the 55% similarity level with subgroups of the largest group at the 65% level. NMDS ordination was in two dimensions and used the Kruskal method with a monotonic regression. Cluster groupings were projected on the NMDS ordination for visualizing the consistency between the methods.

To investigate diet variability within taxa and how it was related to variables of the environment and individual larvae, the direct gradient analysis technique of canonical correspondence analysis (CCA; ter Braak 1986) was employed. CCA is an ordination method that directly relates species or community composition to environmental or other explanatory variables. Here, within a taxon of larval fish, the prey type composition was related to the explanatory variables of larval BL, gut fullness, longitude, collection depth, daylight length (proxy for time of year), and fluorescence (proxy for primary productivity). Samples consisted of the prey consumed by larvae within the same cruise-station-depth-BL (1-mm interval) combinations containing at least 4 prey items. Collection depth and fluorescence were calculated as the means of the respective net sampled by the MOCNESS, and when multiple larvae were grouped, the mean gut fullness was used. Prey values were the arcsine-transformed numerical proportions within a sample. A forward stepwise selection method (ter Braak and Verdonschot 1995) determined which explanatory variables significantly contributed to explaining the variability in prey types (Monte Carlo permutation tests, 999 permutations, $\alpha = 0.05$). Ordination diagrams allowed for interpretation of how the explanatory variables (arrows) were related to prey type consumption. Along the gradient for each explanatory variable (including in the opposite direction of the arrow), each prey type location, which represents its weighted mean, can be related to the distance along the gradient (with the origin being the mean for the explanatory variable). This allows the relative locations of all prey to be compared with each other, but also, for each prey type, it illustrates how much above or below the average explanatory variable the prey type tended to be consumed. Additionally, arrow length relates to the importance of the variable, and the angle between any two arrows represents their correlation. CCA was performed with the computer program CANOCO (ter Braak & Simlauer 2002) incorporating biplot scaling with a focus on interspecies distances. The five larval taxa analyzed were those with sufficiently large sample sizes or diet variability, and prey classes included were those composing ≥1% of the total diet within each taxon.

Taxonomic differences in the allometry of jaw development (linear in all taxa) were tested using ANCOVA (GLM, SYSTAT). Pairwise differences in slope (significant BL and taxon interaction) were tested using a Bonferroni correction, and if nonsignificant, further tested for differences in intercept. To better standardize morphological differences between larval fish taxa in both jaw development and body shape, LJL (instead of BL) was related to prey size to examine the change and variability of prey size with larval growth. For each taxon, the lengths of consumed prey were grouped in LJL intervals of 0.1 mm (0.05 for acanthurids). Intervals contained ≥10 prey, or no more than two LJL intervals were combined to reach a minimum of 10 prey. Trophic niche breadth for each interval was calculated as the SD of the log-transformed prey lengths (Pearre 1986). It is generally hypothesized that the range of prey sizes increases with mean prey size (and larval growth), but the trophic niche breadth, which standardizes for the increase in mean prey size, should remain relatively constant throughout growth (Pearre 1986). However, evidence for an increase in trophic niche breadth has been shown (Pepin & Penney 1997).

Results

Feeding incidence, diets and ontogenetic variability

For nearly all larval coral reef fish taxa examined, the proportions of larvae with food present in the gut were high, ranging from 0.94 to 1.0 (Table 4.1). The only exception to this was *Sparisoma* spp., of which only 4% contained prey. The size ranges of larvae were broad and included some of the earliest stages; however, they likely excluded the first-feeding stage.

Diets of larvae were often narrow with clear distinctions among larval taxa (Table 4.2). *Serranus* spp. larvae consumed calanoid copepodite stages almost exclusively while the confamilial *Centropristis* spp. consumed a mixture of ostracods and calanoid and cyclopoid copepodites. Winter- and spring-spawned epinepheline groupers consumed mostly calanoids, yet those occurring in the summer and fall added *Farranula* copepods to their diet. (Subsampling of these larvae for genetic species identification indicated these groups of epinephelines are largely composed of different species [Richardson et al. unpublished data]). The labrids *Xyrichtys* spp. and *Thalassoma bifasciatum* relied heavily upon *Farranula*, *Oncaea*, and harpacticoid (mostly *Microsetella*) copepods while consuming almost no calanoids or nauplii. Appendicularians, absent from many diets entirely, had high %IRI values in lutjanine snappers (58.3) and acanthurids (18.1), and they were consumed at lower levels by eteline snappers, mullids and *Halichoeres* spp.

labrids. Acanthurid diets were also composed largely of *Limacina* pteropods and excluded copepodite stages of copepods. Pomacentrids consumed a mixture of copepodite copepods but few nauplii. Differences between pomacentrid genera included the greater importance of calanoids in the diet *Chromis* spp. than that of *Stegastes* spp., while the opposite pattern held for the cyclopoid genera *Oncaea* and *Oithona*.

Some larval fish taxa exhibited distinct ontogenetic changes in diet, while others consistently consumed similar prey types throughout development (Fig. 4.2). Appendicularian-feeding lutjanines and acanthurids fed increasingly on appendicularians with ontogeny to the gradual exclusion of copepod nauplii and pteropods, respectively. *Stegastes* spp. consumed fewer cyclopoids and more calanoids with growth, as did *Halichoeres* spp. The other labrids *Xyrichtys* spp. and *Thalassoma bifasciatum* continued to consume similar proportions of the same copepod taxa throughout most of the larval period, and *Serranus* spp. exhibited consistent feeding upon calanoid copepods with ontogeny. The smaller sample sizes of other taxa (Epinephelinae, Etelinae, *Centropristis* spp. and *Chromis* spp.) were deemed insufficient for illustrating ontogenetic changes in diet.

Diet similarity among taxa

Cluster analysis identified distinct larval fish groupings based on the degree of diet similarity (Fig. 4.3a). Small acanthurids (group 1), consuming primarily copepod nauplii and *Limacina* pteropods, were grouped alone at the 55% similarity level. Lutjanines and larger acanthurids, which consumed high proportions of appendicularians, were grouped together (group 2). The distinct diets of the labrids (except larger *Halichoeres* spp.) yielded their own grouping (group 3), while the rest of the taxa (and their size and/or seasonal subdivisions) composed group 4. Within this group, there were 4 subgroups, including *Serranus* spp. (calanoid diet) and summer/fall-spawned epinephelines (calanoid and *Farranula* diet) that grouped separately. The two other subgroups exhibited diets that were more mixed; however, subgroup 4a comprised mainly consumers of nauplii, calanoid copepodites and moderate proportions of appendicularians. The two-dimensional NMDS plot (Fig. 4.3b) largely corroborated the results of the cluster analysis and yielded a low stress value of 0.12.

Prey consumption related to environmental and predator variables

The CCA for each of the five examined larval fish taxa revealed several significant environmental and larval explanatory variables (Fig. 4.4). Larval BL was a significant variable for all taxa since diets often changed with growth. The number of significant explanatory variables ranged from five (*Thalassoma bifasciatum*) to two (*Xyrichtys* spp.) out of the six that were tested. For mullid larvae, 20.6% of the variation in prey types was explained by the CCA, with 90% of this accounted for by the first two canonical axes (CCA-I&II). Acanthurid prey variability had 20.5% explained (95.6% by CCA-I&II), *Thalassoma bifasciatum* had 17.6% explained (82.4% by CCA-I&II), *Xyrichtys* spp. had 12.4% explained (all by CCA-I&II), and *Halichoeres* spp. had 17.3% explained (87.8% by CCA-I&II).

Several patterns can be drawn from the ordination diagrams of each larval taxon (Fig. 4.4). While changes in diet with growth were clear, the use of CCA helped discriminate how diet differed with other factors as well. Some examples include mullids consuming calanoid and *Farranula* copepods when exhibiting greater gut fullness; *Thalassoma bifasciatum* consuming *Farranula* more in the summer and *Oncaea* in the winter; and *Halichoeres* spp. feeding on *Farranula* when more full and calanoids when less full. Caution must be applied to some additional interpretations due to the correlations of the explanatory variables, though such correlations may also be informative. For example, fullness in mullids and *T. bifasciatum* increased with growth and daylight length (i.e. toward summer). For mullids, the lack of correlation between length and longitude suggests that the increase in gut fullness with longitude (i.e. toward the west) is real; for *T. bifasciatum*, the apparent increase in fullness toward the east is likely a result of inspected larvae from the east being slightly larger on average. It is worth noting for some taxa, since diets were often relatively consistent (temporally, spatially and often with ontogeny), that some distinctions observed in the CCA were for the less prevalent prey types, while the more abundant prey often occurred closer to the means of the explanatory variables (e.g. with *T. bifasciatum*).

Jaw morphology, prey size and trophic niche breadth

Many of the relationships of LJL and BL for larval fish taxa ($r^2 = 0.78$ to 0.96, mean 0.90) were significantly different (Fig. 4.5), but also generally formed two groups of taxa having similar slopes (i.e. relative growth rates of the jaw). Intuitively, the more slender (shallow bodied) taxa had relatively small jaws, with the exception being acanthurids. Despite these groupings, there appeared to be no relationship to diets and the degree of diet similarity between taxa of each group.

Mean prey sizes increased with LJL interval for most larval taxa (Fig. 4.6). Among taxa, prey sizes were similar, which occurred despite the large differences in prey types between many groups of larvae. For 7 of the 11 taxa, trophic niche breadth exhibited no significant change with growth. However, 4 taxa had significantly decreasing trophic niche breadths with increasing LJL.

Discussion

The diets of coral reef fish larvae in the SOF were often notably narrow, and there were clear taxon-specific distinctions among the several groups of larvae examined. While copepods were the dominant prey overall, there were clear differences in the stages and taxa of copepods consumed, not only among larval fish families but also among genera of the same families. Among the labrids, *Halichoeres* spp. larvae had a more mixed diet, consuming some calanoids and appendicularians, while *Thalassoma bifasciatum* and *Xyrichtys* spp., exhibiting very similar diets, excluded these prey and consistently consumed three non-calanoid taxa of copepods. Within the family Serranidae, there were clear differences among subfamilies, and also differences within subfamilies (including the temporal, and likely species, differences within Epinephelinae). Similarly, within Pomacentridae, the genera *Stegastes* and *Chromis* differed in the types of copepod prey consumed.

With regard to the stages of copepods consumed, some larval taxa, including *T. bifasciatum*, *Xyrichtys* spp., *Serranus* spp. and pomacentrids, had diets that largely excluded nauplii. In other taxa, nauplii constituted a substantial portion of the diet even into later stages (e.g. lutjanines and mullids). Contrary to work in higher latitudes (e.g. Economou 1991, Pepin & Penney 1997), there was no overall dominance of calanoid diets, as cyclopoids and even harpacticoids were common copepod prey. In addition to copepod diets, feeding upon appendicularians was exhibited by some families (e.g.

lutjanids, mullids and acanthurids). This particular strategy has been observed in other regions for certain taxa (Purcell et al. 2005), and within the SOF, by three genera of scombrids that consumed almost no crustacean prey (Llopiz et al. in prep). Although direct comparisons to environmental abundances of zooplankton prey were not performed, the typical relative abundances of zooplankton prey in the SOF (Llopiz and Cowen 2008; S. Smith unpublished data) and the clear distinctions in diets among larval taxa despite the temporal and spatial co-occurrence of the larvae, suggest feeding is highly selective in many of the groups examined.

Aside from prey-type differences, the degree to which ontogenetic diet shifts occurred also differed among larval taxa, illustrating an additional distinction in trophodynamic strategies. In mullids, lutjanines and acanthurids there were clear diet shifts with growth. Mullids switched from nauplii to copepodites and appendicularians, and lutjanines bypassed a copepodite-feeding period and shifted from nauplii to appendicularians. Acanthurids began feeding on pteropods and nauplii before consuming appendicularians later in the larval period. Such changes in diet over only a few millimeters in BL highlight the importance of developmental state when describing, classifying, or comparing the trophic roles of these organisms. Contrary to these ontogenetic diet shifts, the diets of *Serranus* spp., *Thalassoma bifasciatum*, and *Xyrichtys* spp. were generally consistent throughout development. This behavior has also been shown in other of the few studies in lower latitudes (Schmitt 1986, Ostergaard et al. 2005), including those on billfishes and tunas (Young and Davis 1990; Llopiz and Cowen 2008; Llopiz et al. in prep) in which diets were consistent with growth until a shift to piscivory. Such rigid and consistent diets throughout larval development may be more common toward the equator since there are few examples of this behavior in high-latitude larvae (but see Last 1978; Runge and Delafontaine 1996). Consuming the same prey types throughout larval ontogeny may be a strategy in the tropics and subtropics that allows larvae to maintain specific trophic niches among a high diversity of prey and potential competitors.

The analysis of several larval taxa, some of which did exhibit changes in diet with growth or season, was enhanced by the use of cluster analysis and NMDS to obtain quantitative measurements of diet overlap. These analyses confirmed some of the more qualitative conclusions drawn by describing the diets individually, and allowed for visualization of all the patterns of diet similarity. The groupings with the least similarity were a result of high reliance on non-copepod prey (e.g. by lutjanines and acanthurids), while other groupings appeared to generally follow patterns on whether appendicularians were consumed and the degree of nauplii and calanoid copepod consumption. A similar use of cluster analysis and NMDS has been employed for myctophid larvae (Conley & Hopkins 2004) and for a high diversity of shore-fish larvae in Australia (Sampey et al. 2007), including some coral reef fish taxa, albeit with low sample sizes. Within the present study, the extensive spatial and temporal coverage affords greater confidence that the observed among-taxa similarities and differences are likely representative of those occurring throughout the SOF and throughout the year.

The large scale sampling of this study inherently results in several potentially confounding variables, both environmental and larva-specific, that could mask the patterns occurring in the ecosystem. The use of CCA helped account for these factors and aided in the interpretation of how diets changed with the variables, in addition to illustrating how they did not change along some gradients. The influences of time, space, development, and several other variables could be examined concurrently to allow for interpreting their relations to prey type or each other individually. Diets were generally most associated with larval BL, but several other variables, which differed among larval taxa, were also significant. The result of seemingly low values for percent variance explained is generally expected for ecological research, and it is sometimes recommended these values be left unreported (ter Braak & Verdonschot 1995). However, they often are reported, and although no larval fish diet studies have employed CCA, the percentages of variance explained by our analyses were relatively high compared to some work on adult fishes (Garrison & Link 2000, Jaworski & Ragnarsson 2006).

Although simple in nature, feeding incidence is a useful parameter in larval fish studies for describing, at least qualitatively and for comparative purposes, the degree of feeding success. High feeding incidences (near 100%) were observed for nearly all taxa in this study with the exception being *Sparisoma* spp. While these parrotfish larvae may be extremely poor feeders, they often occurred at high abundances during the late larval stage suggesting previously successful feeding. Some possible explanations for the observed low feeding incidence are prey regurgitation upon capture due to a straight gut (Hay 1981), defecation upon capture (Canino & Bailey 1995), and feeding on items not observable by gut inspection (Pepin & Dower 2007).

In the literature, feeding incidences are quite variable among taxa in both high and low latitudes. Inshore of the SOF in Biscayne Bay, the average feeding incidence of several taxa was 50% (Houde & Lovdal 1984). Such values are substantially lower than the feeding incidences observed in this study for larvae that are presumably in a much poorer feeding environment. It has been shown that larvae in the SOF withstand an empty gut during most of the night since nighttime feeding does not occur and gut evacuation rates are rapid (Llopiz and Cowen 2008; Llopiz et al. in prep). These characteristics, coupled with nearly 100% feeding incidence, indicate that starvation mortality could be lower than expected, which would be counter to the presumed nutritional constraints of the warm and oligotrophic open ocean. Our results alone do not confirm starvation is not occurring, and considering the high temperatures of tropical and subtropical waters, some food in the gut may not be enough to meet the greater demands of growth and metabolism in lower latitudes (Houde 1989). As such, future work with techniques specifically addressing nutritional status would be necessary to support any inferences drawn here.

Supposing that the SOF are less nutritionally constraining for larval fish than otherwise presumed, this may be unique to the region and not typical of the tropical ocean. Although the open waters of the SOF are oceanic, the region may exhibit higher productivity than other low-latitude regions due to sub-mesoscale eddies (Lee et al. 1991) and a shoaling thermocline in the west that is driven by the physics of the system (Olson 2001). However, we still generally have a limited understanding of total secondary production in the oligotrophic tropical ocean, even though the role of microzooplankton (Landry & Calbet 2004), the microbial food web (Landry 2002), and primary production variability and patchiness (Marañon et al. 2003) as energy sources for the prey of larval fish has recently become better understood. Regardless, prey concentrations in the SOF are much lower than in higher latitudes (Llopiz and Cowen 2008). Additionally, *Thalassoma bifasciatum* has been observed to exhibit differing growth rates across the

SOF that were correlated to gut fullness (S. Sponaugle et al. unpublished data), suggesting the occurrence of growth-limiting prey conditions.

Another unknown aspect of the SOF that our results raise is the driving force behind the specific diets and selective feeding of larval fishes, which appear to be more prevalent and pronounced than in higher latitudes. If high larval diversity and low prey availability are important factors, this would imply that competitive exclusion has occurred and prey would be limiting if trophic niches did not exist. Yet, larvae can be rather dilute in relation to their prey (Cushing 1983, Dagg & Govoni 1996), which would make density dependent feeding success unlikely. Therefore, if a larva was experiencing prey at less than optimal abundances, there should be no advantage to feeding selectively and bypassing plenty of suitable prey. There is some supporting evidence, however, for the possibility of density dependent larval fish growth (Jenkins et al. 1991) and the potential depletion of resources if spatial and trophic niches did not exist (Llopiz et al. in prep). It is also evident from almost all studies that larvae are not always feeding optimally, regardless of prey presence in the gut. This raises questions regarding the likelihood of prey switching occurring if a larva's 'preferred' prey were absent but other types were present, and whether different larval fish taxa have intrinsic capacities to detect, strike, and capture some prey types with an inability to do so for others.

Among the high diversity of perciform fishes in low latitudes, there exists a wide variety of larval morphologies. The taxa of this study (all perciformes) exhibit a broad range of body shapes as larvae, and the allometric relationships of LJL and BL produced two general groupings of taxa with differing rates of jaw development. Because of these differences, and since mouth size rather than BL is likely to be more influential to prey consumption, LJL was used for comparisons of prey size as a function of growth. Mean prey sizes increased with LJL (except in *Halichoeres* spp.) as expected from most other larval feeding studies; however, most relationships were not very steep relative to the increase in LJL. This pattern, in part, contributed to the result of trophic niche breadth significantly decreasing with growth in four taxa (and trending negative in four others). This contradicts Pearre's (1986) general conclusion based on a meta-analysis of 45 data sets that trophic niche breadth remains constant with growth. Additionally, the observed decreases in our study are opposite to the findings of Pepin and Penney (1997), which largely rejected the generalization of Pearre (1986) by showing an increase in trophic niche breadth with size for a majority of species examined. If more prevalent in lower latitudes, a declining trophic niche breadth with growth (meaning a narrowing of the niche and a relative increase in prey size selectivity) is further support for the evidence of greater niche separation in these regions. However, generalizations regarding prey size, while convenient for modeling or synthesizing overarching patterns (Woodward et al. 2005), would largely be inappropriate for larval fishes in the SOF due to their distinct taxon-specific diets. Fish larvae in these waters clearly do not consume prey based solely on size.

The comparative approach utilized in this study has allowed for the observation of several distinctions among taxa, but comparisons to other work on coral reef fish larvae are generally not possible due to a lack of data. This study presents the first data for most of the taxa examined, while also incorporating thorough sampling over several broad scales. Although based on simple gut contents, these results illustrate that robust and novel empirical data can result from extensive temporal, spatial, ontogenetic, and taxonomic coverage. As a whole, the oceanic planktonic ecosystem remains relatively poorly understood, largely due to its enormity and myriad interactions of diverse organisms that differ in size by several orders of magnitude. Within these interactions, larval fishes are often regarded as minor and ephemeral components of the ecosystem; if they are not ignored completely, they are often grouped together as one link in the food web. With year-round or protracted spawning by a high diversity of fishes, tropical and subtropical fish larvae are essentially permanent members of the planktonic food web and, as shown here, they play various taxon- and size-specific roles. These results enhance our understanding of the many intricacies of the planktonic environment, while also raising other questions and adding complexity to often over-simplified processes.

Table 4.1. Larval coral reef fish taxa collected across the Straits of Florida and inspected for diet analyses. All taxa co-occurred throughout the year and the sampled transect. Feeding incidence is the proportion of larvae with prey present in the gut. *n*: larvae examined (total = 1266); BL: body length

Taxon	*n*	BL (mm)		Feeding incidence
		Range	Mean	
Serranidae				
Epinephelinae	61	2.8 – 12.8	5.7	0.98
Serraninae	140	2.9 – 10.4	5.1	0.97
Lutjanidae	107	2.9 – 9.4	4.8	0.98
Mullidae	153	2.7 – 22.8	7.6	1.00
Pomacentridae	95	2.4 – 8.8	3.9	1.00
Labridae				
Halichoeres spp.	71	3.3 – 9.8	5.9	1.00
Thalassoma bifasciatum	201	2.6 – 11.1	5.3	0.99
Xyrichtys spp.	139	3.4 – 13.5	6.8	0.94
Scaridae: *Sparisoma* spp.	156	2.8 – 10.9	7.0	0.04
Acanthuridae	143	2.1 – 8.9	3.8	0.99

Table 4.2. Percent indices of relative importance (%IRI; calculated as the product of numerical percentages and percent frequencies of occurrence in feeding larvae) for the dominant prey of 13 taxa of coral reef fish larvae collected in the Straits of Florida. Epinepheline larvae were further divided by time of year collected due to noted seasonal differences in species composition and diet. Some prey types with low %IRI (<0.4%) were grouped into the 'other' category, and included bivalve and gastropod larvae, cavolinid pteropods, small eggs, euphausiid calyptopes, tintinnids, radiolarians and foraminiferans. n_l = number of fish larvae examined; n_p = number of prey excised; rem.: remains

Table 4.2

	Serranidae						
	Serraninae		**Epinephelinae**		**Lutjanidae**		
	Serranus	***Centropristis***	**(wint./spr.)**	**(sum./fall)**	**Lutjaninae**	**Etelinae**	**Mullidae**
	(n_l = 102)	(n_l = 26)	(n_l = 40)[a]	(n_l = 19)	(n_l = 83)	(n_l = 20)	(n_l = 137)[b]
Prey category	(n_p = 710)	(n_p = 244)	(n_p = 742)	(n_p = 333)	(n_p = 759)	(n_p = 244)	(n_p = 3306)
Thecosomata: *Limacina*	-	0.1	4.5	0.7	-	-	-
Polychaete trochophore	-	-	-	-	-	-	-
Cladocera: *Evadne*	-	-	-	5.0	-	-	-
Copepoda							
Nauplius	1.7	9.7	19.2	8.4	28.3	20.6	38.9
Calanoida	96.7	45.8	53.7	38.2	1.2	35.6	34.5
Harpacticoida	-	0.8	0.2	-	-	-	-
Oithona	0.1	0.3	3.8	-	0.6	2.0	2.7
Oncaea	0.1	19.2	2.4	0.1	0.1	-	0.2
Corycaeus	-	1.4	0.3	-	-	-	0.6
Farranula	1.0	12.9	1.9	41.9	1.9	6.8	2.6
Unk./remains	-	1.5	1.0	0.1	0.1	2.0	0.3
Ostracoda	-	6.6	-	-	-	-	-
Chaetognatha	-	-	-	-	0.1	0.1	-
Appendicularia	-	-	-	-	58.3	14.6	11.2
Fish egg	-	-	-	-	-	-	0.1
Other	-	0.1	0.3	0.3	0.2	-	-
Unk. crust. rem.	0.5	1.5	12.5	5.3	4.3	17.1	8.4
Unk. item/soft rem.	-	-	0.2	-	5.1	1.1	0.3

[a] 41 larvae used for frequency of occurrence calculation

[b] 152 larvae used for frequency of occurrence calculation

Table 4.2 (cont.)

	Pomacentridae		**Labridae**			**Scaridae**	
	Chromis	***Stegastes***	***Halichoeres***	***Thalassoma***	***Xyrichtys***	***Sparisoma***	**Acanthuridae**
	($n_l = 36$)	($n_l = 52$)	($n_l = 71$)	($n_l = 198$)	($n_l = 131$)	($n_l = 7$)	($n_l = 142$)
Prey category	($n_p = 333$)	($n_p = 527$)	($n_p = 559$)	($n_p = 1293$)	($n_p = 523$)	($n_p = 8$)	($n_p = 1346$)
Thecosomata: *Limacina*	-	0.8	0.1	-	0.1	-	41.1
Polychaete trochophore	-	-	-	-	-	-	0.6
Cladocera: *Evadne*	-	-	-	-	-	-	-
Copepoda							
Nauplius	6.9	2.8	11.8	0.3	1.8	25.0	19.6
Calanoida	62.5	20.1	35.0	0.3	0.4	6.2	0.9
Harpacticoida	0.3	0.6	5.9	36.9	40.1	-	-
Oithona	3.0	14.6	0.1	-	-	6.2	-
Oncaea	2.1	29.0	12.7	16.6	38.3	-	1.3
Corycaeus	0.4	2.0	1.0	1.5	3.5	-	-
Farranula	19.9	24.2	9.1	44.0	14.5	56.2	-
Unk./remains	2.6	3.4	7.8	0.1	-	-	-
Ostracoda	-	-	-	0.1	0.7	-	-
Chaetognatha	-	-	-	-	-	-	-
Appendicularia	-	-	3.1	-	-	-	18.1
Fish egg	-	-	-	-	-	-	-
Other	-	-	0.5	0.1	0.1	-	1.0
Unk. crust. rem.	2.4	2.1	9.6	0.1	0.3	-	3.1
Unk. item/soft rem.	-	0.5	3.0	0.1	0.3	6.2	14.3

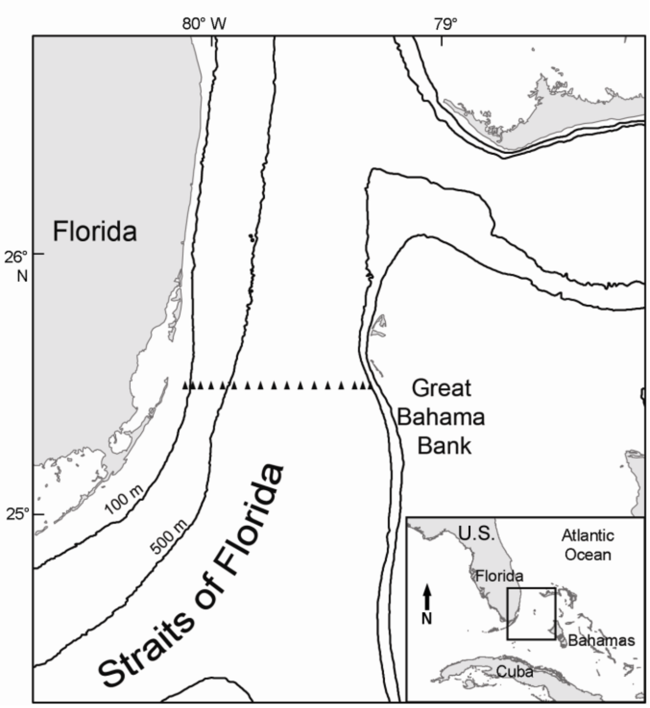
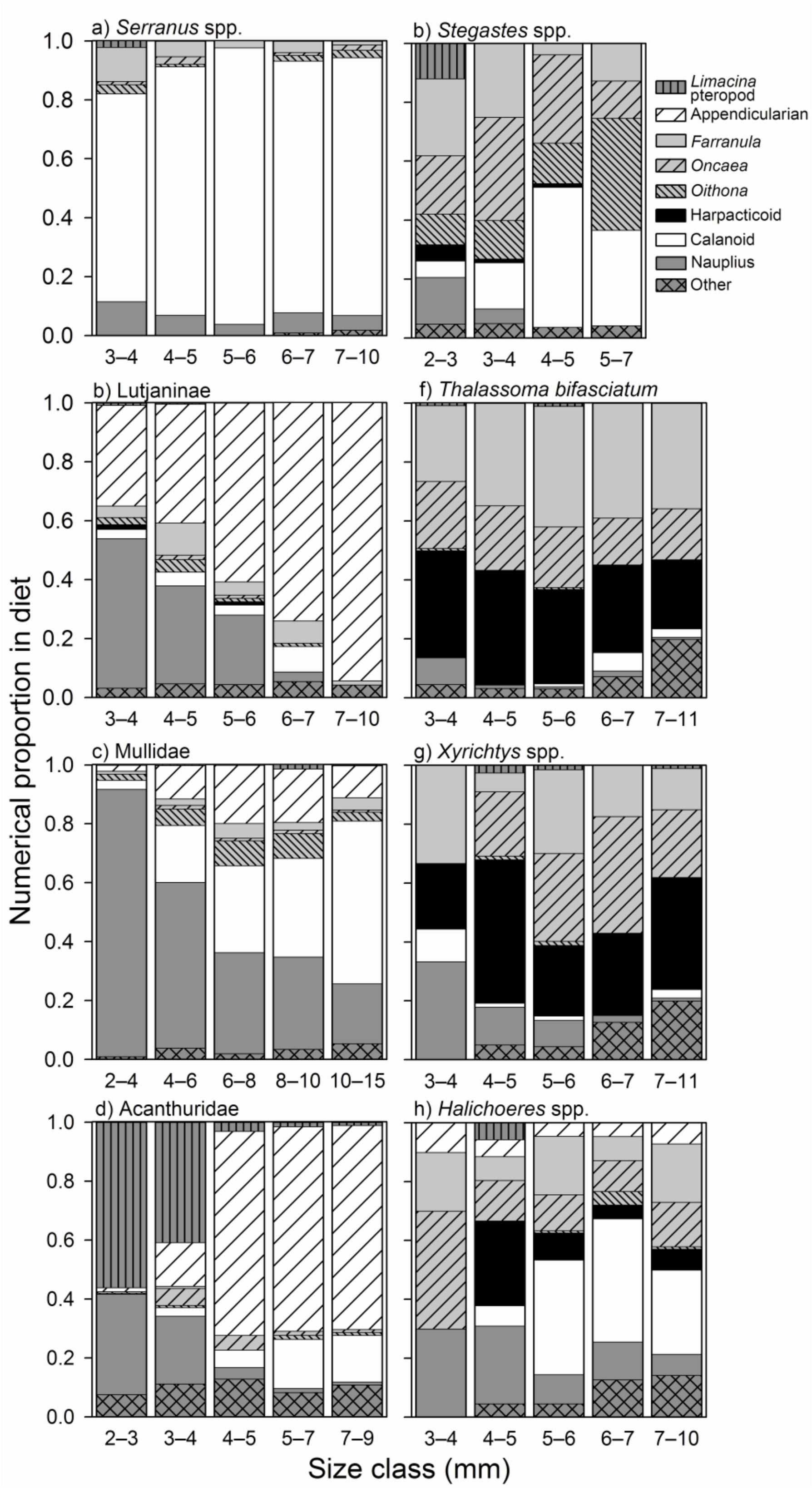


Figure 4.1. Straits of Florida region and the transect of 17 stations (triangles) sampled monthly in 2004 for ichthyoplankton.

Figure 4.2. Numerical proportions of consumed prey types by larval fish length class for 8 taxa of coral reef fish larvae collected in the Straits of Florida. Unidentifiable prey (see Table 4.1) were not included.

Fig. 4.2


a) *Serranus* spp.
b) *Stegastes* spp.
b) Lutjaninae
f) *Thalassoma bifasciatum*
c) Mullidae
g) *Xyrichtys* spp.
d) Acanthuridae
h) *Halichoeres* spp.
Limacina pteropod
Appendicularian
Farranula
Oncaea
Oithona
Harpacticoid
Calanoid
Nauplius
Other
Numerical proportion in diet
Size class (mm)
0.0
0.2
0.4
0.6
0.8
1.0
3–4
4–5
5–6
6–7
7–10
2–3
5–7
7–11
2–4
4–6
6–8
8–10
10–15
7–9

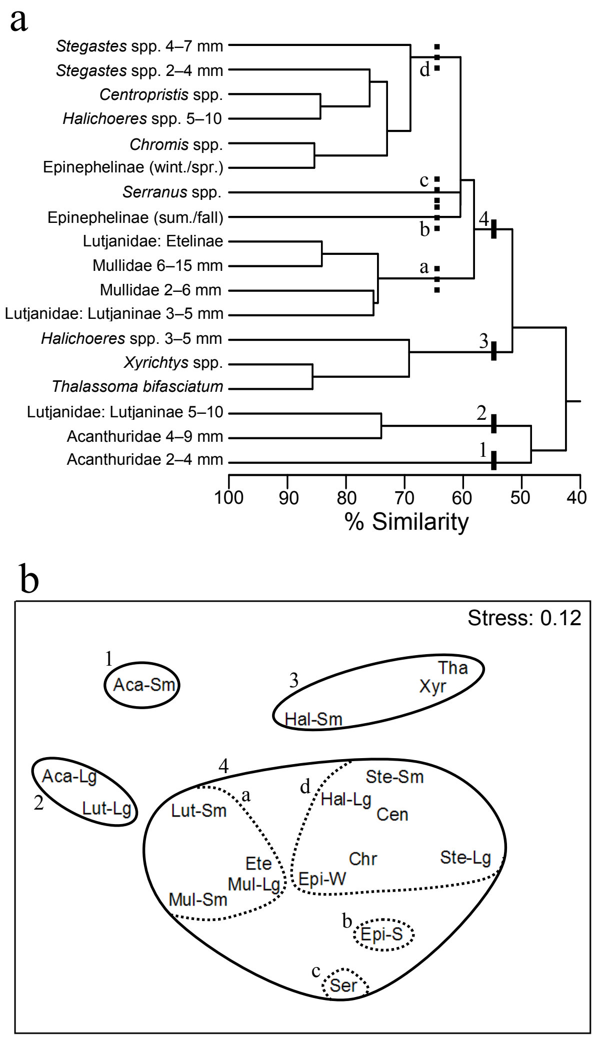
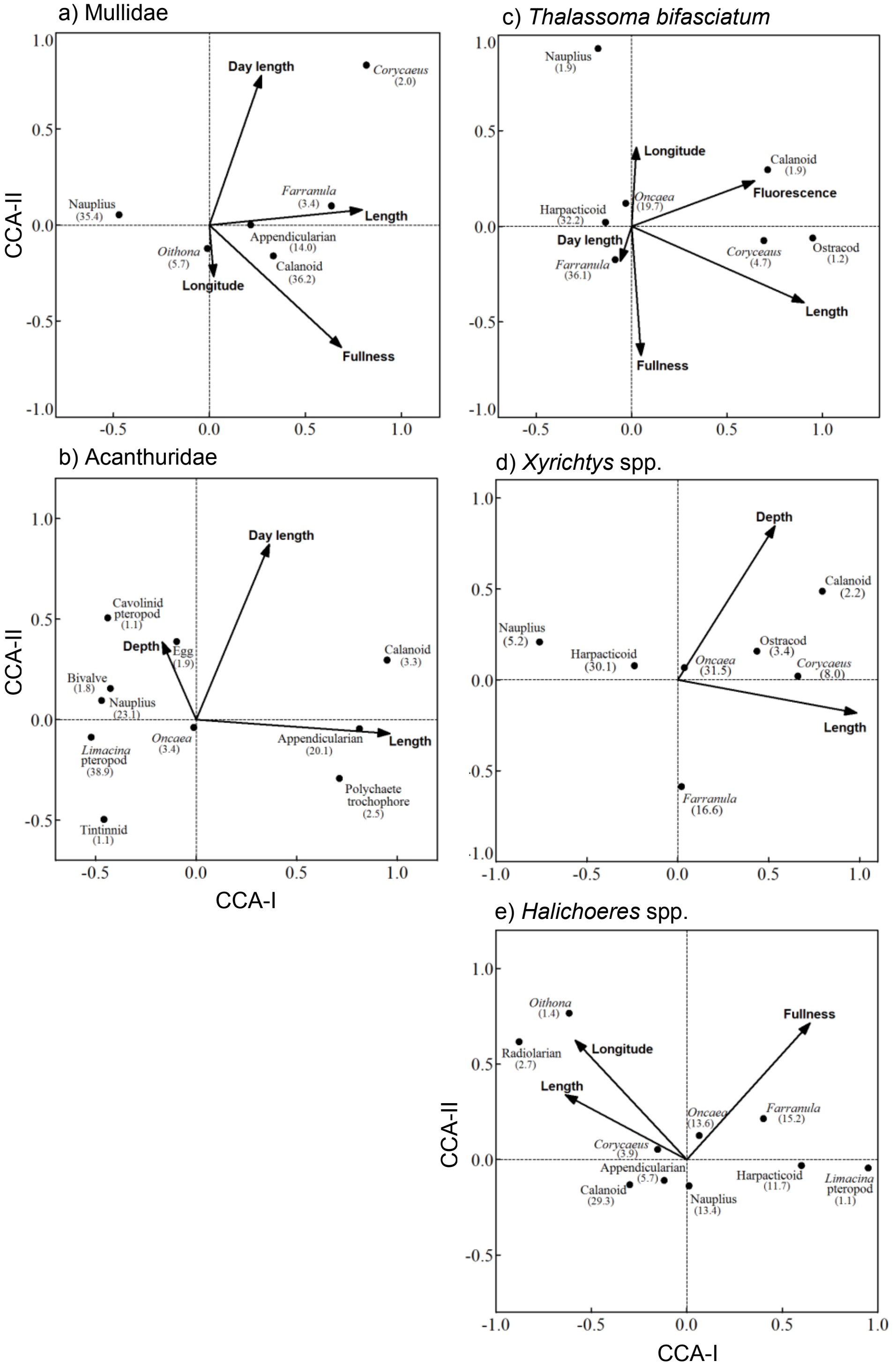


Figure 4.3. a) Cluster analysis and b) non-metric multidimensional scaling (NMDS) results assessing diet similarity among larval fish taxa and subdivisions of some taxa based on observed ontogenetic changes in diet (Fig. 4.2) or seasonal differences (Epinephelinae; Table 4.2). Main groups from the cluster analysis (55% similarity level and numbered) are circled with a solid line on the NMDS plot, and subgroups of group 4 (65% level and lettered) are circled with a dotted line. Labels in (b) are the first 3 letters of the taxon with ‘Sm’ representing the smaller of the BL classes in (a) and ‘Lg’ the larger. For Epinephelinae, ‘S’ is the summer/fall class and ‘W’ the winter/spring class.

Figure 4.4. Ordination biplots from the results of canonical correspondence analysis (CCA) of the diets of 5 taxa of coral reef fish larvae with the explanatory variables of body length, longitude, collection depth, day length, fluorescence, and gut fullness. Arrows represent the gradients (increasing in arrow direction) of explanatory variables that significantly accounted for the variability in diet. Numbers in parentheses are the numerical proportions of the prey type in the diet.

Fig. 4.4


a) Mullidae
Day length
Corycaeus (2.0)
Nauplius (35.4)
Farranula (3.4)
Length
Appendicularian (14.0)
Oithona (5.7)
Calanoid (36.2)
Longitude
Fullness
b) Acanthuridae
Day length
Cavolinid pteropod (1.1)
Depth
Egg (1.9)
Calanoid (3.3)
Bivalve (1.8)
Nauplius (23.1)
Oncaea (3.4)
Appendicularian (20.1)
Length
Limacina pteropod (38.9)
Polychaete trochophore (2.5)
Tintinnid (1.1)
c) Thalassoma bifasciatum
Nauplius (1.9)
Longitude
Calanoid (1.9)
Fluorescence
Harpacticoid (32.2)
Oncaea (19.7)
Day length
Farranula (36.1)
Coryceaus (4.7)
Ostracod (1.2)
Length
Fullness
d) Xyrichtys spp.
Depth
Calanoid (2.2)
Nauplius (5.2)
Harpacticoid (30.1)
Ostracod (3.4)
Oncaea (31.5)
Corycaeus (8.0)
Length
Farranula (16.6)
e) Halichoeres spp.
Oithona (1.4)
Fullness
Radiolarian (2.7)
Longitude
Length
Oncaea (13.6)
Farranula (15.2)
Corycaeus (3.9)
Appendicularian (5.7)
Calanoid (29.3)
Nauplius (13.4)
Harpacticoid (11.7)
Limacina pteropod (1.1)
CCA-I
CCA-II
1.0
0.5
0.0
-0.5
-1.0

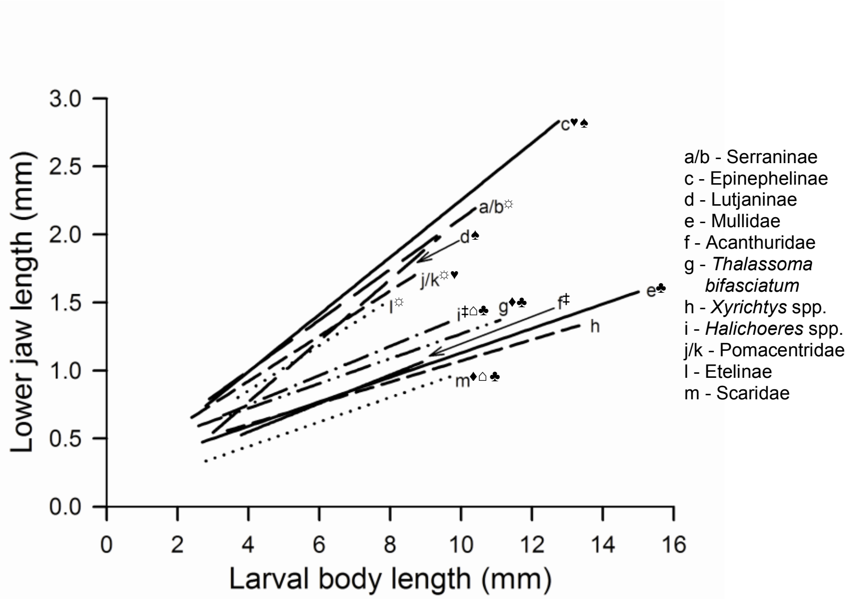


Figure 4.5. Relationships of lower jaw length and body length for 11 taxa of larval coral reef fishes. Letters denote taxon and also correspond to each taxon’s figure letter in Fig. 4.6 (if included). Relationships sharing the same symbol do not have significantly different slopes but do have significantly different intercepts (ANCOVA, α = 0.05, Bonferroni corrected).

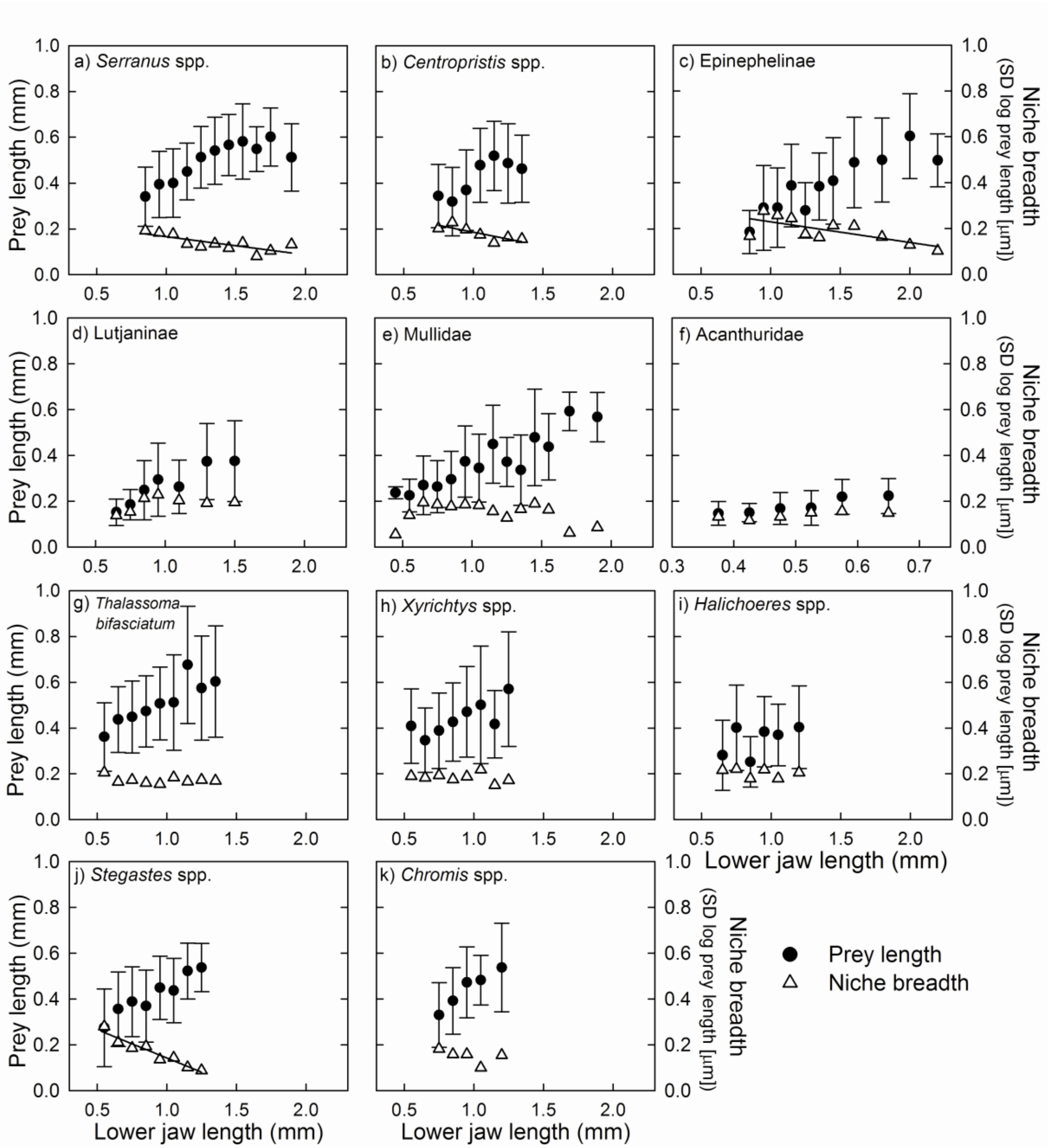


Figure 4.6. Relationships of mean prey length (±SD) within lower jaw length (LJL) intervals (filled circles), and tropic niche breadth (measured as the SD of the log-transformed prey lengths) within LJL intervals (open triangles), for 11 taxa of coral reef fish larvae. Regression analysis of trophic niche breadth values that yielded slopes significantly differing from zero have regression lines. For comparison, all axis scales are the same except for acanthurids (LJL axis).

Chapter 5. The Straits of Florida as larval fish feeding habitat: environmental characteristics, food webs, and latitudinal distinctions

Interest in the influence of feeding on larval fish survival and growth has resulted in a vast knowledge of the trophic ecologies of many species of marine fish larvae, especially in higher latitudes. However, in addition to our limited understanding in lower latitudes, ecosystem-level approaches to characterizing the feeding environment of fish larvae and elucidating the specific trophic pathways to a community of co-occurring larval fishes within the planktonic food web are largely absent from studies at all latitudes. Based on data collected monthly over two years across the Straits of Florida (SOF), we report on the physical and biological environment of planktonic larval fishes and synthesize the feeding ecologies of 21 taxa of fish larvae to illustrate, qualitatively and quantitatively, both the variety of trophodynamic strategies and the levels of community reliance upon specific zooplankton prey types. Physical and biological sampling revealed marked differences across the SOF, largely influenced by the Florida Current and its proximity to the Florida shelf break. The 20°C isotherm (proxy for thermocline depth) exhibited a mean vertical displacement of 148 m upward from the Great Bahama Bank to the Florida shelf. Fluorescence was highest at the western front of the Florida Current, and, similarly, total plankton and copepod nauplius abundances displayed a 2.5- to 3-fold increase from the central SOF to a peak at the edge of the Florida shelf break. A linkage web of 21 taxa of larval fishes and their dominant prey illustrated the highly variable and selective feeding strategies of the co-occurring larval taxa. Copepod nauplii had the most links (18), followed by calanoid copepods (14), the cyclopoids *Farranula* (14) and *Oncaea* (11), and appendicularians (12). A quantitative web of larval taxa and prey, which incorporated diet composition and larval abundances, more accurately illustrated the levels of larval community reliance upon each prey type. Appendicularians were most heavily relied upon, followed by calanoids, nauplii, and *Farranula*. To address the apparent differences in larval fish feeding ecologies between regions of high and low latitudes, 170 investigations on 130 larval fish taxa were reviewed. Distinctions between regions included higher feeding incidences, narrower diets, and less reliance upon calanoid copepods and nauplii in lower latitudes. These results, together with the detailed and novel investigation of the SOF larval fish subweb, highlight the substantial variability across environments in the functioning of planktonic ecosystems.

Background

The quintessential impetus for studying the feeding ecologies of larval fishes has been the potential for larval feeding and starvation to significantly impact survival to later (and exploitable) stages of life (e.g. Hjort 1914). The cascading effects of small changes in larval mortality (Houde 1987), and the role that feeding plays in a variety of processes other than starvation, including growth and predation avoidance (Anderson 1988), has resulted in the thorough documentation of the specific trophic roles of many taxa of fish larvae, and notably so in higher latitudes (e.g. Heath & Lough 2007). However, large-scale approaches highlighting broader ecological processes and community-level distinctions in the trophic pathways to co-occurring larval fishes are much more limited. Furthermore, while the physical and biological aspects of the environment of larval fishes may play a crucial role in community function, thorough temporal and spatial characterization of these aspects is difficult to achieve and often unavailable.

The oceanic plankton is composed of a high diversity of organisms with sizes that span several orders of magnitude. As such, the study of energy flow in planktonic environments necessarily requires a focus on specific components of the food web, while grouping or excluding others. This has often resulted in the grouping of larval fishes as one link, or fish larvae being disregarded altogether. This is despite evidence of species-specific and highly selective feeding by some fish larvae (e.g. Shelbourne 1957, Govoni et al. 1986b, Llopiz & Cowen 2008). Additionally, although larval fishes may generally have little impact on zooplankton prey (Dagg & Govoni 1996, Pepin & Penney 2000), some evidence indicates the possibility for depletion of prey resources and density-dependent larval growth (Jenkins et al. 1991, Llopiz et al. in prep). Even if consumption by larval fishes has negligible effects on prey abundances, understanding the specific spatial and dietary niches of co-occurring taxa of fish larvae, which necessarily requires a broad-scale investigation, may shed light on how larvae avoid substantially depleting prey levels, and thus minimize suboptimal feeding. Aside from ecosystem functioning, much remains unknown of the ecologies of many individual species of larval fish, and this information may be required for successful conservation efforts and future scientific applications. A broader approach to addressing these unknowns may bring us closer to these goals.

Although knowledge of larval fish feeding habits in lower latitudes generally lags behind that of higher latitudes, evidence suggests that some fundamental differences in the trophic ecologies of fish larvae from the two regions may exist (Sampey et al. 2007, Llopiz & Cowen 2008). Recent work in the Straits of Florida (SOF; Llopiz & Cowen 2008, Llopiz et al. unpublished data) has shown that larvae often exhibit narrow diets and highly selective feeding within a diverse spectrum of available prey. There is also the potential for higher feeding incidences and fewer taxa exhibiting ontogenetic diets shifts in lower latitudes. Despite these possibilities, a formal review addressing latitudinal distinctions in larval fish trophodynamics is not available.

It is clear from the high diversity of fishes in lower latitudes (Leis & Carson-Ewart 2000, Richards 2005) and the common migratory behavior of some species to utilize the tropics and subtropics as a spawning area (Bakun 1996) that the open ocean can be conducive to larval fish survival. However, the degree to which starvation mortality contributes to total larval mortality in lower latitudes is difficult to assess. Given the high temperatures and the resulting high energy demands (Houde 1989), in conjunction with the oligotrophy and low productivity of the low-latitude open ocean, it could be expected that starvation mortality in these regions is high. Our recent work in the SOF indicates that starvation mortality could be lower than presumed, but an explanation for the paradox is not apparent. Also unclear are many environmental aspects of the tropical/subtropical open ocean, including patterns of prey availability (spatial and seasonal) and the influence of the physical environment and primary productivity on prey levels. Therefore, addressing the driving forces behind the enigmatic aspects of low-latitude larval fish feeding (e.g. high feeding incidence, highly selective feeding on less-abundant prey) necessarily requires a better understanding of the environment itself.

Here we report on the physical and biological environment of the SOF, synthesize the observed patterns in larval fish trophodynamics in this region and relate these findings to work in high-latitude regions. Afforded by an extensive data set on the SOF planktonic ecosystem, including the trophic ecologies of numerous taxa of fish larvae, our three objectives are: (1) to describe the physical and biological characteristics of the SOF relevant to larval fish trophodynamics, including the temporal and spatial patterns of potential planktonic prey; (2) to synthesize the diets of 21 taxa of larval fishes in the SOF into qualitative and quantitative food subwebs that indicate levels of prey-type reliance by the larval fish community; and (3) to provide a thorough review of the larval fish literature to investigate the possibility for inherent latitudinal differences in the feeding of marine fish larvae.

Materials and methods

Field sampling and laboratory procedures

The Straits of Florida (SOF) region is a tropical/subtropical oceanic habitat between Florida and both Cuba and the Bahamas (Fig. 5.1). Within the SOF is the strongly flowing Florida Current that is fed either by the Loop Current of the Gulf of Mexico or, when the Loop Current is occasionally pinched off, directly by the waters exiting the Caribbean Sea through the Yucatan Channel. To the north, the Florida Current becomes a large portion of the Gulf Stream, contributing ca. one-third of the total transport off of Cape Hatteras (Leaman et al. 1989).

In 2003 and 2004, a transect of 17 stations (numbered west to east) across the SOF between the Florida shelf break south of Miami and Great Bahama Bank (25.5°N; Fig. 5.1) was sampled monthly for larval fishes, zooplankton, and several other biological and physical parameters (Llopiz & Cowen 2008, Richardson et al. in review). We utilized a coupled, asymmetrical multiple opening closing net and environmental sampling system (MOCNESS; Wiebe et al. 1985, Guigand et al. 2005) consisting of 4-m^2 (1-mm mesh) and 1-m^2 (150-μm mesh) openings. Discrete-depth sampling occurred in 25-m intervals from a depth of 100 m (50 m at the shallower, westernmost station). A paired neuston net (2x1 m, 1-mm mesh and 0.5x1 m, 150-μm mesh) sampled the sea surface to a depth of ca. 0.5 m. All nets were equipped with flowmeters for calculations of volume filtered, and plankton sampling was conducted during daylight hours. MOCNESS plankton samples were fixed in 95% ethanol and later drained and refilled with 70% ethanol. Larval fishes were sorted from all neuston, all 4-m^2 MOCNESS, and the 0 to 25 m 1-m^2 MOCNESS samples, and identified to varying levels of taxonomic resolution (at least family) following Richards (2005).

Water samples (20 l) were collected in 2004 for microzooplankton analyses from the surface waters of every station and at depth for a subset of stations using a CTD/rosette outfitted with 10 l Niskin bottles. CTD/rosette casts collected water from the midpoints of each of the nominal MOCNESS net intervals (i.e. 87, 62, 37 and 12 m). Water samples were filtered through 25μm-mesh with the remaining plankton transferred to a 20 ml vial and preserved in a 4% buffered formalin-seawater solution. For the thorough analysis of properties throughout the water column, CTD casts were performed during night hours at each station, measuring a variety of parameters that included temperature and fluorescence (a proxy for chlorophyll a). Continuous current speed and direction data were collected by a ship-mounted Teledyne RDI acoustic Doppler current profiler (ADCP; 150 and 600 kHz).

In the laboratory, samples were analyzed to investigate the horizontal, vertical and temporal patterns of plankton settled volumes and copepod nauplius abundances. The settled volumes of all subsurface (1-m^2 MOCNESS) plankton samples of the even-numbered stations and months in 2003 were measured by transferring each sample to a graduated cylinder and recording the volume of plankton after a settling time of 5 min. Nauplius abundances were estimated from the surface-water and CTD/rosette samples. At least 2 hr prior to examination, 2 drops of rose Bengal were added to the sample vials to stain nauplii and enhance their visibility. Nauplii were then enumerated under a Leica MZ16 stereomicroscope.

Data analysis

To describe the average current structure across the SOF, the velocities of the northward component of the current for each 8-m depth interval sampled by the ADCP (to 180 m) were used. For each cruise in 2004, a mean velocity within each 0.01° longitude interval was calculated (Richardson et al. in review), and means of these values from all cruises were grouped in 0.02° intervals. These 8-m, 0.02°-longitude interval mean velocities across the sampled transect were then plotted using bicubic interpolation (Matlab v 7.0, The Mathworks, Inc.). In the same manner, the average depth-specific fluorescence for 2004 was plotted using 1-m interval fluorescence values collected via CTD at each station and averaged over all cruises. A more thorough analysis of these fluorescence data, including spatio-temporal variability, primary production and the physical environment is presented elsewhere (Hitchcock et al. in prep). To illustrate the spatial variability in thermocline depth, the 20°C isotherm was used as a proxy for thermocline depth, as it was observed to occur in the main thermocline (consistent with other low-latitude studies [e.g. Kessler 1990, Houghton 1991]). The mean depth of the 20°C isotherm at each station was calculated from the CTD data collected in both 2003 and 2004 for winter/spring (Jan to Apr) and summer (Jun to Sep) periods separately to investigate any potential seasonal differences. Months in 2004 where weather conditions prevented the complete sampling of the transect with CTD (Feb and Nov) and ADCP (Jan and Nov) were excluded from the analyses.

Longitudinal, seasonal and vertical differences in nauplius abundances (ind. l^{-1}) and zooplankton standardized settled volumes (ml 1000 m^{-3} water sampled) were tested with ANOVA. For horizontal distributions, differences among stations were tested using surface-water nauplius abundances and the total standardized 0 to 100 m settled volumes. Based on these results, seasonal differences were tested within groups of stations having similar magnitudes. For vertical distributions, settled volumes and nauplius abundances were converted to relative values to account for the variability in magnitude across the transect. To meet the assumptions of independence, a single value of relative nauplius abundance or settled volume for each depth interval was calculated for the entire transect for each month sampled. These values were the means within each depth interval for each cruise. Vertical distribution analysis for nauplii was limited to the months of Feb to June.

The synthesis of larval fish feeding dynamics presented here incorporates some of the results of more focused reports on billfish larvae (Llopiz & Cowen 2008), tuna larvae (Llopiz et al. in prep) and coral reef fish larvae (Llopiz & Cowen in prep) to illustrate the dominant and distinctive trophic pathways to larval fishes in the SOF (also included are unreported data on wahoo *Acanthocybium*, king mackerel *Scomberomorus cavalla*, and Atlantic chub mackerel *Scomber colias*). In total, 2969 larvae were examined, from which over 23,000 prey were excised. In our qualitative and quantitative analyses of the larval fish component (or subweb) of the planktonic food web, the feeding data employed were limited to the numerical proportions of prey types consumed by each larval fish taxon. For the qualitative display of trophic linkages, a larval fish taxon was considered a consumer of a prey type if the type composed >1% of the consumer's diet.

To add to this analysis, a quantitative subweb of larval fish feeding was constructed by incorporating the proportions of prey types in the diet of each larval fish taxon and the relative abundances of the taxon within the SOF. Rather than separately reporting prey-type reliance by individual taxa, one of our objectives was to illustrate the degree to which the entire larval community may rely on each prey type in the subweb, which is dependent upon proportions of prey type consumption and larval abundances. To address this, a relative abundance was calculated from the two years of monthly collections for each of the 21 larval fish taxa, and then the numerical proportion of each prey type in the diet of a larval taxon was scaled by the taxon's relative abundance. The sum of these values for each prey type yielded an estimate of the degree of community reliance upon the prey type. This unique approach has the inherent limitation of being based upon numerical diet proportions rather than biomass or levels of consumption, which require in-depth knowledge of each larval taxon's daily ration. There are also ontogenetic changes in diet; however, assuming similar size-frequency distributions among the larval taxa, these should largely be accounted for since the size-frequency distributions of subsamples of inspected larvae were similar to those for collected larvae. The result of this approach should be a better estimate of the dominant energy pathways to larval fishes in the SOF when compared to the qualitative listing of shared prey types. Abundance calculations for each larval fish taxon are the sum of individuals m^{-2} sea surface area to the maximum depth sampled by the MOCNESS for all stations sampled in both 2003 and 2004. Regarding reference to prey types, only genera are reported when identified to the genus level, copepod orders follow Boxshall & Halsey (2004), and no distinction is made between the juvenile and adult copepodite stages of copepods.

Literature review

To investigate the potentially inherent latitudinal differences in larval fish feeding, we reviewed 63 published articles (and 2 yet-unpublished reports for the SOF). Though not exhaustive, especially for work conducted in higher latitudes, these reports yielded 170 separate investigations (taxon-specific data within a report) into the trophodynamics of 130 taxa of fish larvae (Appendix A). Included investigations were limited to those examining at least 50 larvae, and were grouped by latitude (low: 0 to 30°; mid: 30 to 45°; and high: >45°) and habitat type (estuarine/coastal and offshore). Aspects noted from each study included: (1) feeding incidence (proportion of examined larvae with food present in gut); (2) the two dominant prey types (occasionally three when a third was consumed at similar levels or distinct ontogenetic shifts were exhibited); (3) whether a clear ontogenetic diet shift was displayed during the larval stage; (4) whether feeding was highly selective with diets generally narrow; and (5) whether trophic niche breadth (Pearre 1986, Pepin & Penney 1997) significantly changed with larval growth. Results or conclusiveness for all of these aspects within each study was rare, however. It is also worth noting that the degrees to which diets were narrow or an ontogenetic diet shift occurred are somewhat subjective, but should complement the other quantitative characteristics.

Results

The physical and biological environment of the Straits of Florida

Cross-sections of the SOF with depth illustrated distinct spatial variability (both horizontally and vertically) in current structure and thermocline depth (Figs. 5.2a & 5.2b). The average northward velocity in the core of the Florida Current was ca. 1.7 m s^{-1}, occurring ca. 21 km from the Florida shelf. These values are averages, however, and month-to-month variability in the location and velocity of the meandering Florida Current core was high. Maximum velocities were often near 2.3 m s^{-1} with the greatest observed difference between horizontal locations of the core being 30 km (not shown). The depth of the 20°C isotherm exhibited a mean vertical displacement of 148 m across the SOF, rising from ca. 230 m near Great Bahama Bank to ca. 80 m at the edge of the Florida shelf break. Seasonal differences in thermocline depth were small, with winter depths in the western SOF averaging only 10 m deeper than summer values.

Biologically, the deep chlorophyll maximum was a clear feature in the distribution of fluorescence across the SOF (Fig. 5.2c), generally averaging a depth of 75 to 100 m. Additionally, fluorescence levels in the western SOF were distinctly higher and there was a shoaling of the deep chlorophyll maximum. Similarly, total plankton and copepod nauplius abundances (Fig. 5.2d) were significantly greater in the western SOF (settled vol.: $F = 4.1$, $p = 0.002$; nauplii: $F = 4.9$, $p < 0.001$), and both measures exhibited a 2.5- to 3-fold increase toward the west relative to the lowest levels observed in the eastern-central SOF.

There were significant differences between months in total plankton (Fig. 5.3a; west: $F = 10.3$, $p = 0.001$; cent/east: $F = 5.4$, $p = 0.004$). The pattern of significantly higher levels in Feb than in all other months (Tukey hsd, $p = 0.002$ to 0.035) was apparent in both the western and central/eastern regions of the SOF. Seasonal variability in nauplius abundance (Fig. 5.3b) was also significant within the different regions (west: $F = 3.7$, $p = 0.001$; cent: $F = 8.9$, $p < 0.001$; east: $F = 9.8$, $p < 0.001$). However, in the central and eastern SOF, nauplius abundances were low in the summer months, while in the western SOF abundances were generally highest in the summer.

Vertically in the water column, the relative abundances of both total plankton and nauplii were significantly different with depth (Fig. 5.3c; settled vol.: $F = 22.5$, $p < 0.001$; nauplii: $F = 6.0$, $p = 0.003$). Nauplius abundance increased with depth, while total plankton was lowest in the deepest interval (75 to 100 m).

Patterns of prey consumption and reliance

The trophic linkage web (Fig. 5.4) of 21 taxa of larval fishes and their 20 dominant prey types from the SOF illustrates the variability in larval fish diets and highlights some common patterns of prey consumption. Based on linkage numbers, the most diverse diet was exhibited by acanthurid (surgeonfish) larvae with 11 prey types. The most shared prey type was copepod nauplii (18 links), followed by calanoid copepodites and the cyclopoid *Farranula* (14 links each). The cyclopoids *Oncaea*, *Corycaeus* and *Oithona* were also commonly consumed, while *Evadne* cladocerans, highly consumed by billfish and *Thunnus* spp. larvae, were infrequently consumed by coral reef fish larvae. The narrowest diets were exhibited by scombrids, of which nearly all consumed appendicularians (also highly shared with 12 links) and other larval fish. Eggs (2 links) were not commonly consumed by larvae in the SOF.

By accounting for taxon-specific larval abundances and proportions of consumed prey types (Table 5.1), the quantitative web of larval fishes and their dominant prey (Fig. 5.5) better illustrates the relative reliance upon each prey type by this subset of the larval fish community. Relative reliance was greatest for appendicularians due to the high abundances of acanthurids (highest relative abundance) and scombrids, the latter of which often fed upon appendicularians almost exclusively. Calanoid copepods had the second greatest level of community reliance, with ca. half of it being accounted for by the abundant *Serranus* spp. (seabasses) larvae. The reliance upon copepod nauplii was the third highest, and this was largely accounted for by *Thunnus* spp. tunas and acanthurids. Acanthurid feeding also constituted nearly all of the community reliance upon *Limacina* pteropods. The community reliance upon harpacticoid copepods was almost completely due to the labrids (wrasses), especially *Thalassoma bifasciatum* and *Xyrichtys* spp.

Literature review: larval fish trophodynamics with latitude

The review of 170 investigations on the feeding of larval fishes (Appendix A) revealed several distinctions among latitudinal regions (Table 5.2). In offshore studies, feeding incidences were significantly higher in low latitudes than in high latitudes (Mann-Whitney, $p = 0.005$). Additionally, within low latitudes feeding incidences were significantly lower for larvae in coastal and estuarine environments than for larvae occurring offshore (Mann-Whitney, $p = 0.001$). Nauplii and calanoid copepodites constituted 46% and 29%, respectively, of the dominant prey types in high-latitude studies. In low latitudes, these values were 22% (nauplii) and 15% (calanoids). A smaller proportion of taxa in lower latitudes exhibited large ontogenetic diet shifts (60% vs. 93% in high latitudes), and a greater proportion of taxa in lower latitudes displayed what were classified as highly narrow and specific diets (69% vs. 12% in high latitudes). One taxon in high latitudes was piscivorous (*Scomber scombrus*), while 15 piscivorous taxa occurred in lower latitudes (all scombroids). The relationship of trophic niche breadth with larval growth increased in several high-latitude studies (44%) and not in any low-latitude studies. Contrary to this, trophic nice breadth declined with growth in some low-latitude taxa (36%), but not in taxa within other regions.

Discussion

The Straits of Florida as larval fish feeding habitat

The planktonic ecosystem of the Straits of Florida displayed marked spatial and temporal variability in its physical and biological characteristics. The rapid and dynamic Florida Current is the dominant feature of this system, and while its current structure and other physical attributes have been extensively studied (e.g. Brooks & Niiler 1977, Molinari et al. 1985, Johns & Schott 1987, Leaman et al. 1987, Leaman et al. 1989, Wang & Mooers 1998), linkages to the biological environment are less common. The pattern of the vertical displacement of the thermocline (and isopycnals) with the resulting upwelling near the shelf break (Leaman et al. 1987, Csanady 1989, Olson 2001) differs from classical wind-driven upwelling in that it is due to the dissipation of the western boundary current's high energy to eddies. This results in eddy mass transport along the inclined isopycnals that are a result, themselves, of the rapid, northerly current maintaining geostophic balance (e.g. Csanady 1989). In addition to western boundary current upwelling, the dynamic nature of the western front of the Florida Current can yield mesoscale and submesoscale eddies that also result in upwelling and significantly enhance levels of primary productivity (Hitchcock et al. 1987, Lee et al. 1991). There have been a limited number of studies investigating the primary producers of the region, especially regarding horizontal variability (Alexander et al. 1961, Alexander & Corcoran 1963, Vargo 1968). Since this is the focus of a more-detailed report (Hitchcock et al. in prep), we include the limited data on the physical environment and distribution of fluorescence to illustrate the linkages in the system from the physical to the biological and across trophic levels. Most relevant to larval fishes, however, is the distribution of zooplankton, and detailed data on the patterns of cross-straits distributions of zooplankton and, specifically, nauplii in the SOF have been previously unavailable.

The abundances of total plankton and copepod nauplii declined markedly across the SOF from maximum levels near the western front of the Florida Current (where fluorescence was highest) to minima that occurred in the eastern portion of the SOF. A similar pattern of decreasing plankton biomass across the Gulf Stream has been observed to the north off of Cape Hatteras (Allison & Wishner 1986). Peak nauplius abundances in the western SOF (7 to 10 ind. l^{-1}) were in the same range as those observed on the shoreward edge of the Florida Current off of the lower Florida Keys (Lane et al. 2003). When these values are compared to copepod nauplius abundances in higher latitudes, however, there is a range of differences. Due to distinct bloom periods in higher latitudes in both primary and secondary productivity, nauplius abundances during these periods are generally near 20 to 40 ind. l^{-1} and can be over 100 ind. l^{-1}, while in non-bloom periods levels can be comparable to those observed in the SOF (e.g. Nielsen & Richardson 1989, Incze & Ainaire 1994). In the Kuroshio off Japan, an ecosystem similar to the SOF, notable nauplius abundances of >100 ind. l^{-1} were observed near the western front of the current (Nakata 1990). When making comparisons, however, it is difficult to account for inconsistent sampling techniques (e.g. mesh size; see Dagg et al. 1988) and the latitudinal differences in the taxonomic distributions of copepods, specifically the prevalence of small cyclopoids, and thus small nauplii, in low-latitude offshore environments (e.g. Turner 2004). In addition to the zooplankton and nauplius maxima on the western edge of the SOF, our data for appendicularian and total larval fish abundance exhibited a similar pattern, with larval fishes increasing 3.5-fold from the eastern-central SOF to the westernmost station (Llopiz et al. in prep). The observed trends in prey abundance highlight distinct differences in the feeding environment of larval fishes over relatively small spatial scales. Although the implications of such differences have yet to be thoroughly explored, larval bluehead wrasse (*Thalassoma bifasciatum*) have been shown to exhibit variable growth rates that correlate with proximity to the Florida shelf break and levels of gut fullness (Sponaugle et al. in prep).

The seasonal patterns of nauplius abundances in the SOF varied with region. In the western SOF, largely encompassing all of the Florida Current, abundances were generally variable, but the highest levels occurred in late spring and summer. The central and eastern regions displayed a different pattern of higher abundances occurring in the winter and early spring. While there were clear differences in all regions (only 4 to 10 ind. l^{-1} in magnitude but increases of a factor of 2 to 4), large and distinct seasonal peaks were generally absent. The more coarsely resolved seasonal distributions of total plankton displayed a peak in Feb within the three regions of the SOF, while levels remained quite consistent during the rest of the year. Our observations differed from those of the only other study in the SOF to examine temporal patterns of plankton abundance (at one station near the Great Bahama Bank), which displayed a peak from March through June (Bsharah 1957). The absence of data from multiple years and the dearth of studies in the SOF highlight the need for further work in this ecosystem. Without several years of data, true seasonality to naupliar or zooplankton patterns cannot be inferred since the distinct possibility of a lack of seasonality exists. Other work in Barbados and Bermuda has generally found no seasonal trends in total zooplankton when examined over several years (Herman & Beers 1969, Moore & Sander 1977).

In characterizing the prey environment of larval fishes, examining only total plankton and nauplii is a limitation considering the narrow and selective feeding exhibited by several taxa of larvae in the SOF. With a narrow diet of only one or two types of prey, relative feeding conditions for a particular taxon can only be inferred from broad prey-availability indices if the ‘preferred’ prey follow such indices. Furthermore, levels of prey availability may only be influential to growth and survival if they are below a certain threshold (Houde 1978, Puvanendran & Brown 1999). Determining this threshold, in addition to the translating effects on growth and survival if below the threshold, is a major challenge for establishing applicability of feeding-related data. The knowledge of how specific prey types follow general indices (e.g. NPZD models) and to what degree and at what point there are significant effects on larval survival, is critical for predicting mortality rates and, thus, also to the accurate modeling of population connectivity and successful larval transport (e.g. Cowen et al. 2006, Paris et al. 2007).

The role of larval fishes in the planktonic food web

The low-latitude planktonic ecosystem of the SOF is larval fish habitat for a high diversity of larval fishes, especially perciformes (Richards 2005). Such a diversity of fish larvae and possible zooplankton prey inherently results in the potential for trophodynamic complexity, which, in turn, presents challenges to capturing processes relevant to those likely occurring at the ecosystem scale. The analysis of 21 larval fish taxa, many over broad temporal, spatial and ontogenetic scales, allowed for unique and detailed results on a complex web of fish larvae and their planktonic prey. The basic and qualitative linkage web illustrated clear distinctions among the often specific and narrow diets of fish larvae in the SOF. Relatively common prey were nauplii, appendicularians, and calanoid and cyclopoid copepodites. However, many taxa did not feed at all on some of these prey types, and considering the general spatial and temporal overlap of the larvae and the high relative abundances of these prey (Llopiz & Cowen 2008, S. Smith et al. unpublished data), varying degrees of trophic niche separation clearly exist for many of these larval fish taxa due to prey selectivity.

Although many feeding patterns among taxa are evident within the qualitative subweb of fish larvae and prey, the novel application of a quantitative web allowed for a more detailed investigation of energy flow to larval fishes and provided quantitative insight into the reliance upon each prey type by a large subset of the larval fish community. This approach (modified from work on an insect-parasitoid web by Lewis et al. (2002)) incorporated the percent composition of the diet of each larval fish taxon and the taxon’s relative abundance in the plankton across the SOF throughout two years of monthly samples (>61,000 ind.). With the 21 larval fish taxa representing a community of consumers, an index of relative community ‘reliance’ was calculated for each prey type. The prey type with the highest level of reliance was appendicularians (28%), largely due to the high abundances of acanthurid (surgeonfish) larvae (which fed predominantly upon appendicularians during the middle to late larval period) and the high abundances of the four taxa of tuna larvae that occur in the SOF. Prior to piscivory, three of these taxa of tunas (*Euthynnus alletteratus*, *Katsuwonus pelamis* and *Auxis* spp.) displayed nearly exclusive feeding upon appendicularians (Table 5.1; Llopiz et al. in prep), while *Thunnus* spp. exhibited a mixed diet that included appendicularians, *Evadne* cladocerans, and nauplii. Consumption by *Thunnus* spp. accounted for nearly 40% of the relative community reliance upon copepod nauplii. Although nauplii had the greatest number of links in the qualitative linkage web, which could be another indicator of reliance, they had the third highest level of relative community reliance in the quantitative web (16%), with calanoid copepods having a slightly higher value (17.5%).

There are limitations to our quantitative analysis of this larval fish subweb in the SOF. One is the use of numerical proportions of prey types. While the relative numbers of prey being removed by a taxon or community of larval fish is informative, the size, weight, and carbon content differences among prey types does not allow for quantitative estimates of actual levels of energy flow. The greatest hurdles to estimating biomass are the small sizes of zooplankters, the inability to accurately measure soft prey types (e.g. appendicularians), and the high diversity of zooplankton prey consumed. Considering the size differences of prey types in this study, a biomass approach would likely yield even greater community reliance upon appendicularians due to their relatively large size, and a lower level of reliance upon nauplii, which are the smallest of the prey types. The reliance upon larval fishes as prey by the community would be an underestimate due to the large size and biomass in one larval fish and the resulting low numerical proportions of fish larvae in the diets of piscivorous taxa. Also contributing to lower numerical proportions of larval fish prey is the shift to piscivory by larvae at larger sizes that, due to mortality, are less abundant than smaller individuals. In addition to utilizing biomass or carbon content, the most accurate approach to estimating energy flow would have to include values of daily rations for each larval taxon. However, obtaining estimates of daily rations is laborious for a single larval taxon, and they can be highly variable due to model choice alone (Llopiz & Cowen 2008). Although open to improvement, the scale and novel approach of this work in the SOF, with the inclusion of 21 larval taxa and large sample sizes of collected and inspected larvae, remains informative and sheds light on some ecosystem-relevant processes occurring in the plankton of the open ocean that have otherwise been difficult to elucidate.

Latitudinal distinctions in larval fish trophodynamics

The limited number of larval fish trophic studies in lower latitudes has precluded, until recently, a review of potential regional differences in the feeding of marine fish larvae. In one of the only general reviews on larval fish feeding ecologies, Hunter (1981) only discussed larval piscivory occurring in several species (without reference to their prevalence in lower latitudes) and mentioned the relative lack of data from tropical and subtropical regions. We have compiled the results on several general feeding descriptors from 170 investigations and 130 larval fish taxa to examine the possibility for regional differences in feeding success, diet composition, prey selectivity, and patterns of trophic niche breadth relationships. All known studies in lower latitudes with suitable sample sizes were included (16 of 46 investigations are from our work in the SOF), but a substantial portion of high latitude studies were excluded while attempting to retain high taxonomic diversity (see Heath and Lough (2007) for a review on the diets of only larval cod that included 29 published studies).

A potential indicator of larval fish feeding success is the incidence of feeding by a sample of fish larvae. Feeding incidences for taxa in offshore environments were significantly higher in lower latitudes. Given the high temperatures in these regions and the corresponding increase in metabolic rates and energy demands (Houde 1989), the significant but not extreme difference (0.14) between high and low latitude regions could be expected if levels of starvation between the two regions were similar; larvae in cooler waters should simply be able to withstand an empty gut for a longer period. A caveat to making comparisons of feeding incidences between low and high latitudes is the distinct difference in the productivity cycles of the regions, with high latitudes exhibiting narrow periods of high productivity. The sampling strategy of high-latitude studies could influence feeding incidences (since values will depend upon the levels of prey abundances during the period of sampling), as could the temporal span of the study. Contrary to high latitudes, the tropical and subtropical open ocean maintains lower and more stable levels of productivity (Raymont 1983, Longhurst & Pauly 1987). Accordingly, fishes in these regions exhibit protracted or year-round spawning. Although the influence of small-scale temporal and spatial patchiness of larval fish prey in low latitudes is unknown, broad-scale sampling is necessary for inferring the relevance of observed larval feeding incidences in these environments.

The consistently high feeding incidences in the low-latitude offshore environment are somewhat paradoxical considering the oligotrophy of the habitat, which should result in low prey availability. It is generally hypothesized that this environment offers reduced predation mortality (Bakun & Broad 2003) with the corollary being the existence of a nutritional tradeoff. While such high feeding incidences certainly call into question the prevalence of high levels of starvation mortality in lower latitudes, further research specifically addressing this possibility is needed. Another surprising trend was the considerably lower feeding incidences of taxa from coastal and estuarine habitats. The median feeding incidence of these larvae was less than half that of offshore larvae despite the much greater levels of productivity nearer the coast and within estuaries.

Clear distinctions in the dominant prey types among high and low latitudes were also evident. The prevalence of both nauplii and calanoid copepodites as dominant prey in higher latitudes was twice that in lower latitudes. Other dominant prey types in lower latitudes were several genera of cyclopoid copepods (notably *Farranula* and *Oncaea*), *Evadne* cladocerans, *Limacina* pteropods, and appendicularians. This supports the likelihood that the greater diversity of zooplankton in lower latitudes (van der Spoel & Pierrot-Bults 1979, Hillebrand 2004) allows for a greater number of trophic niches to be exploited by the higher diversity of larval fishes that also occurs in the tropics and subtropics. Also supporting this possibility were the proportions of taxa within high and low latitudes that generally displayed very narrow diets. Despite the greater opportunity in lower latitudes to have a broad diet (due to the high diversity of prey), 69% of the taxa examined from this region exhibited highly specific diets compared to a value of 12% for high latitudes. Greater niche separation in the tropics was also indicated by more taxa in these regions having a generally consistent diet with growth rather than changing diets (and thus niches) with ontogeny. This behavior could result in a declining relationship of trophic niche breadth with growth, which was observed in some low-latitude taxa. Other than an instance of a dome-shaped relationship at mid-latitudes (Morote et al. 2008), trophic niche breadth was only observed to remain stable or increase with growth in middle and high latitudes, while either not changing or decreasing with growth in lower latitudes.

One of the clearest distinctions among regions is the difference in the number of piscivorous larval taxa. Among the studies reviewed, only one species in high latitudes (*Scomber scombrus*) consumed other fish larvae, while at least 15 species in low latitudes displayed piscivory. Based on our observations in the SOF, the number of piscivorous species in lower latitudes is substantially higher than this. Strong larval piscivory appears to be limited to the scombroids (e.g. tunas, mackerels, istiophorid billfishes, swordfish, snake mackerels and barracudas), and, although not all scombroids are piscivorous as larvae, at least 29 species in the SOF appear to be larval piscivores.

The synthesis of larval fish trophodynamics in the SOF in conjunction with a thorough review of studies across regions and ecosystems highlights intrinsic and evolved distinctions in the feeding of marine fish larvae. Though these differences are informative, our understanding of the potential evolutionary mechanisms that have yielded these differences is extremely limited. For example, one of the most notable behaviors of low-latitude fish larvae is their taxon-specific feeding on a small number of available prey types. While relatively easy to document, the evolutionary advantage of this strategy is largely unknown. Additionally, such behaviors contradict the assumptions of larval fishes experiencing high levels of starvation mortality and growth-limiting prey abundances. Considering the scale of these unknowns, no single study is likely to offer a thorough explanation. However, since that until recently such questions of larval fishes in low-latitude environments were not even asked, a substantially greater understanding of the tropical and subtropical planktonic ecosystem by way of an increasing focus and number of studies appears to be imminent.

Table 5.1. Numerical percentages of prey types in the diets of 21 taxa of fish larvae collected in the Straits of Florida (SOF) used for constructing a quantitative subweb (Fig. 5.5). These values were scaled by the relative abundances of the larval taxa in the SOF (column in bold) and the sums of these values across larval taxa for each prey type yielded an index of community reliance, which was then expressed as a relative value (row in bold). Values in bold correspond to respective bar widths in Fig. 5.5. Genera without further information are cyclopoid copepods. Append.: appendicularian; Harpact: harpacticoid copepod

			Numerical percentage in diet										
		Rel. comm. reliance	Append.	Calanoid	Nauplius	*Farranula*	*Oncaea*	*Limacina* pteropod	Harpact.	*Oithona*	*Corycaeus*	*Evadne* cladoceran	Larval fish
Larval taxon	Common name	**Rel. larval abund.**	**27.6**	**17.5**	**16.1**	**9.0**	**7.8**	**6.5**	**6.2**	**1.9**	**1.9**	**1.6**	**1.0**
Acanthuridae	surgeonfishes	**15.2**	20.2	3.3	23.1	0.4	3.4	38.9	-	0.5	0.1	0.1	-
Xyrichtys spp.	razorfishes (wrasses)	**9.9**	-	2.2	5.2	16.6	31.5	0.8	30.1	0.4	8.0	-	-
Serranus spp.	seabasses	**9.6**	-	86.5	6.1	3.9	1.2	0.3	-	1.5	0.1	-	-
Thunnus spp.	oceanic tunas	**9.5**	12.1	7.2	64.8	3.1	0.1	-	-	-	-	11.2	1.1
Katsuwonus pelamis	skipjack tuna	**9.2**	92.6	-	3.1	-	-	-	-	-	-	-	4.3
Thalassoma bifasciatum	bluehead wrasse	**7.6**	-	1.9	1.9	36.1	19.7	0.3	32.2	0.2	4.7	-	-
Euthynnus alletteratus	little tunny	**6.8**	92.1	-	2.3	-	0.1	-	-	-	-	-	5.3
Stegastes spp.	damselfishes	**5.0**	-	23.2	6.0	19.1	24.9	3.2	2.2	15.7	4.5	-	-
Lutjaninae	snappers	**4.9**	52.9	4.2	27.3	7.1	0.8	0.3	0.5	2.5	0.5	0.8	-
Auxis spp.	bullet/frigate mackerels	**4.6**	95.9	0.8	2.0	-	-	0.1	-	-	-	0.1	0.2
Halichoeres spp.	wrasses	**3.7**	5.7	29.3	13.4	15.2	13.6	1.1	11.4	1.4	3.9	-	-
Chromis spp.	chromises/ damselfishes	**3.5**	-	48.8	13.5	21.2	4.4	0.7	2.0	7.7	1.7	-	-
Mullidae	goatfishes	**3.2**	13.4	36.4	33.1	6.5	0.9	0.4	-	5.5	2.4	0.5	-
Centropristis spp.	seabasses	**2.5**	-	35.6	11.6	13.3	18.7	0.9	3.1	1.8	3.6	-	-
Epinephelinae	groupers	**1.8**	-	46.7	17.2	14.5	3.4	7.3	0.6	4.2	0.9	2.0	-
Etelinae	snappers	**1.2**	18.9	35.3	23.2	12.6	0.5	-	0.5	6.8	-	-	-
Scomber colias	Atl. chub mack.	**0.5**	62.9	22.6	10.1	-	0.6	-	-	-	-	-	0.6
Istiophorus platypterus	sailfish	**0.4**	-	0.3	0.2	32.5	0.1	2.9	-	-	7.7	54.1	2.0
Makaira nigricans	blue marlin	**0.3**	-	-	-	52.1	-	0.8	-	-	2.1	42.8	2.1
Scomberomorus cavalla	king mackerel	**0.3**	80.0	-	8.9	-	-	-	-	-	-	-	11.1
Acanthocybium solandri	wahoo	**0.2**	68.9	1.0	-	-	-	-	-	-	-	-	30.1

Table 5.2. Results of a review of 65 studies (170 investigations, 130 taxa) on the trophodynamics of larval fishes from different latitudinal regions.

		Latitude		
	Total	High	Mid.	Low
Articles/reports	65	27	22	16
Separate investigations	170	73	47	50
Taxa	130	44	40	46
Median feeding incidence (*n* taxa)				
Offshore		0.76 (28)	0.78 (14)	0.90 (31)
Coastal/estuarine		0.58 (8)	0.82 (15)	0.43 (14)
Predominant prey				
Eggs		0.09	0.07	0.03
Nauplii		0.46	0.39	0.22
Calanoids		0.29	0.20	0.15
n (prey types)		87	70	88
Exhibiting ontogenetic diet shifts (*n* taxa)		0.93(40)	0.90 (30)	0.60 (28)
Exhibiting narrow/specific diets				
Highly		0.12	0.14	0.69
Moderate		0.08	0.05	0.16
n (taxa)		26	22	32
Taxa piscivorous as larvae		1	3	15
Trophic niche breadth with growth				
Nonsignificant		0.56	1.00	0.64
Increasing		0.44	-	-
Decreasing		-	-	0.36
n (investigations)		16	13	14

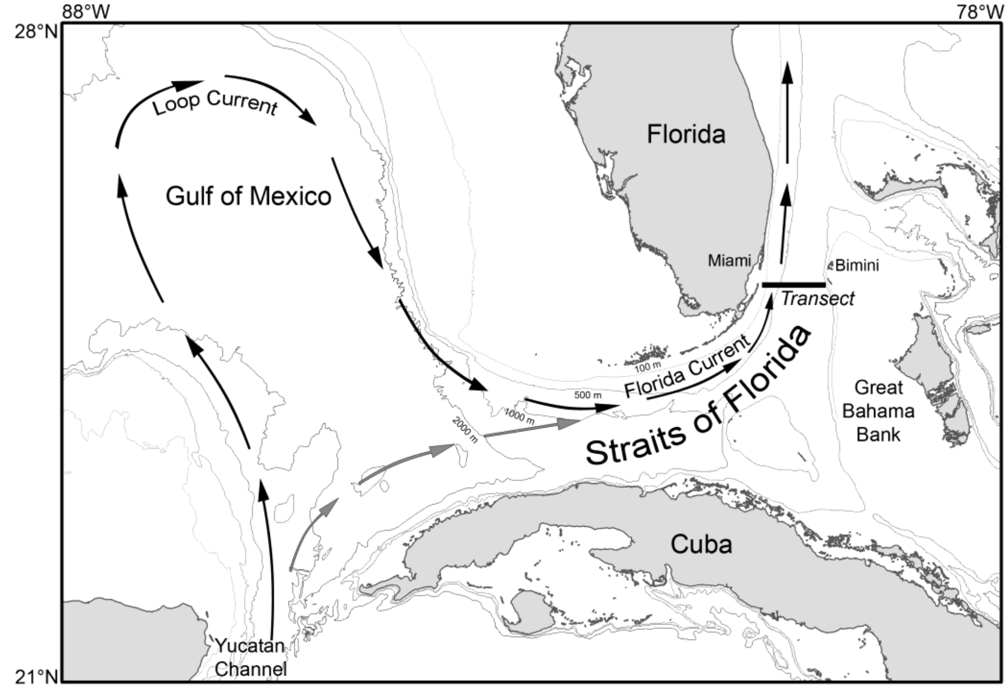
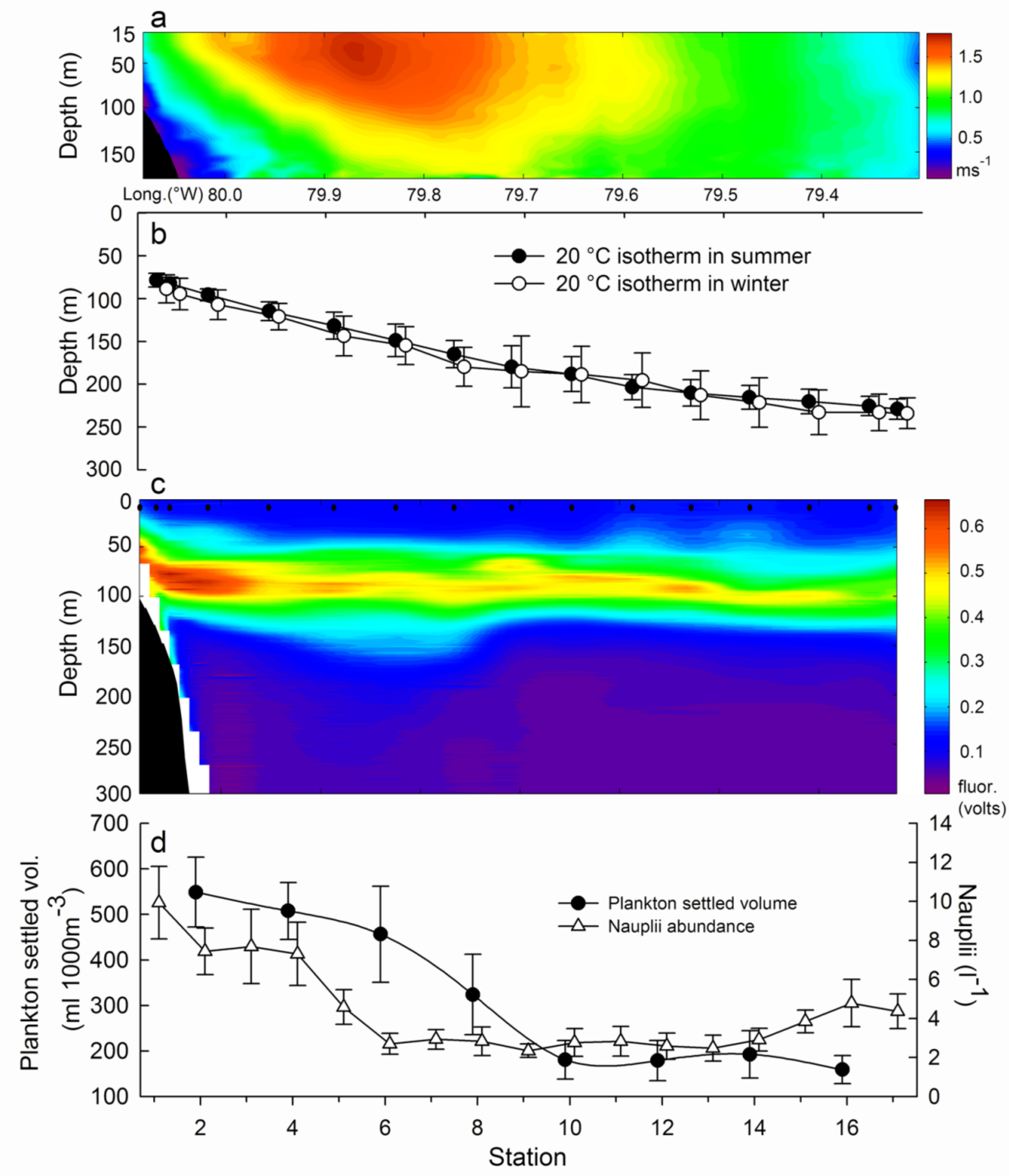


Figure 5.1. Map of the Straits of Florida and upstream regions of the Gulf of Mexico and northern Caribbean Sea. In 2003 and 2004, a transect of 17 stations between the Florida shelf break and Great Bahama Bank was sampled monthly for larval fishes, other zooplankton and several physical parameters. Upstream of the Straits of Florida, the Loop Current in the Gulf of Mexico is most often the source for the Florida Current, but can pinch off resulting in Caribbean waters flowing directly into the Straits of Florida (indicated by gray arrows).

Figure 5.2. Horizontal distributions across the Straits of Florida of (a) mean northward current velocity with depth, (b) mean (±SD) depth of the 20°C isotherm in summer and winter, (c) mean fluorescence (proxy for chlorophyll) with depth, and (d) mean (±SE) of total plankton (settled volume) and copepod nauplius abundance. Total plankton and nauplius abundances differed significantly across the Straits of Florida ($p = 0.002$ and $p < 0.001$, respectively). Current velocity resolution is 8 m depth and 0.02° longitude, and fluorescence resolution is 1 m depth with interpolation between the sampled stations (indicated by ● in c). Data points in b correspond to longitude (but offset for clarity) and exclude the westernmost station (where depth was often insufficient for the presence of the 20°C isotherm) and the easternmost station (not sampled with CTD). Data in c also exclude easternmost station. Data points in d do not correspond to longitude but station number (west to east) across the transect.

Fig. 5.2


a
Depth (m)
15
50
100
150
1.5
1.0
0.5
ms^{-1}
Long.(°W) 80.0
79.9
79.8
79.7
79.6
79.5
79.4
b
Depth (m)
0
50
100
150
200
250
300
20 °C isotherm in summer
20 °C isotherm in winter
c
Depth (m)
0
50
100
150
200
250
300
0.6
0.5
0.4
0.3
0.2
0.1
fluor. (volts)
d
Plankton settled vol. (ml 1000m^{-3})
700
600
500
400
300
200
100
Nauplii (l^{-1})
14
12
10
8
6
4
2
0
Plankton settled volume
Nauplii abundance
2
4
6
8
10
12
14
16
Station

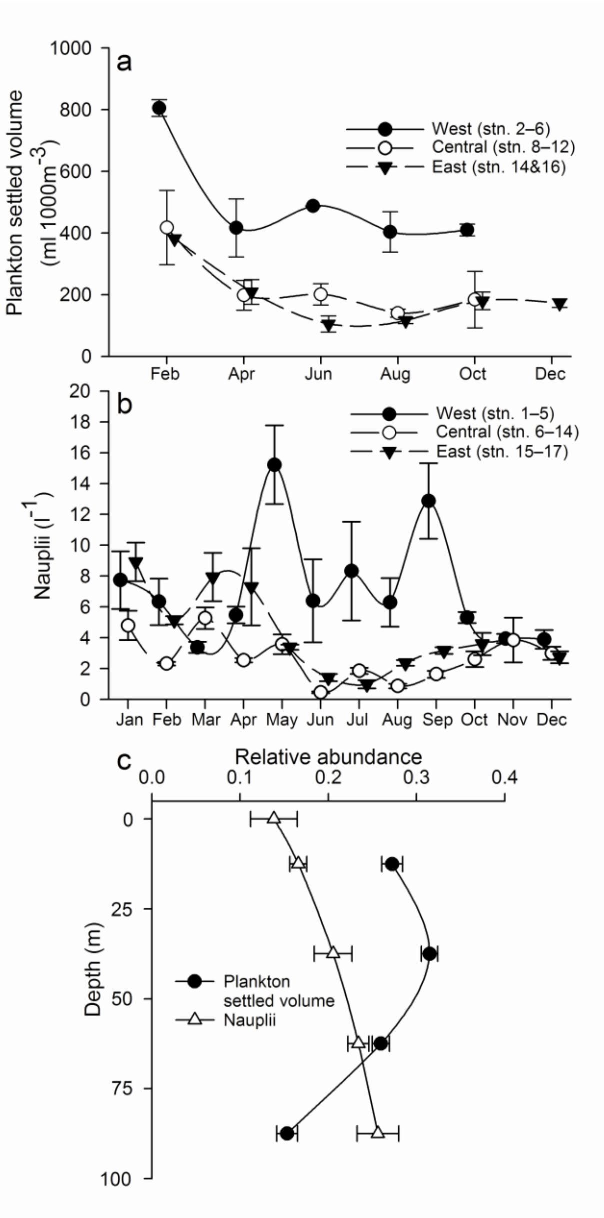


Figure 5.3. Season patterns of mean (±SE) (a) total plankton and (b) copepod nauplius abundance, and (c) the vertical distributions of mean (±SE) relative abundances of each. Regional divisions in a and b were based on the observed differences in abundances across the Straits of Florida (Fig 2d). All seasonal differences within regions were significantly different (all $p \leq 0.004$), and both relative total plankton and nauplius abundance differed significantly with depth ($p < 0.001$ and $p = 0.004$, respectively).

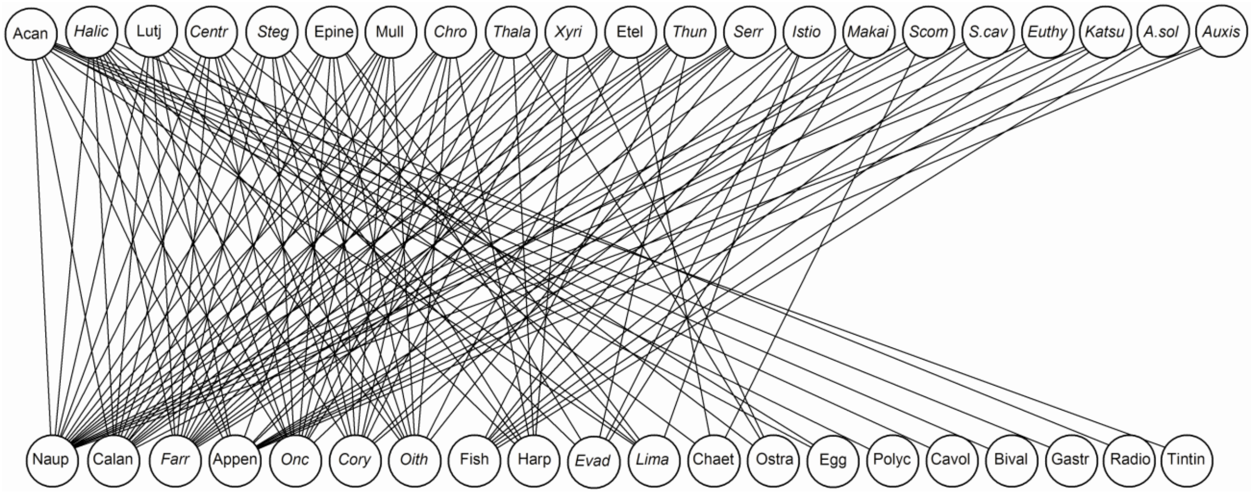
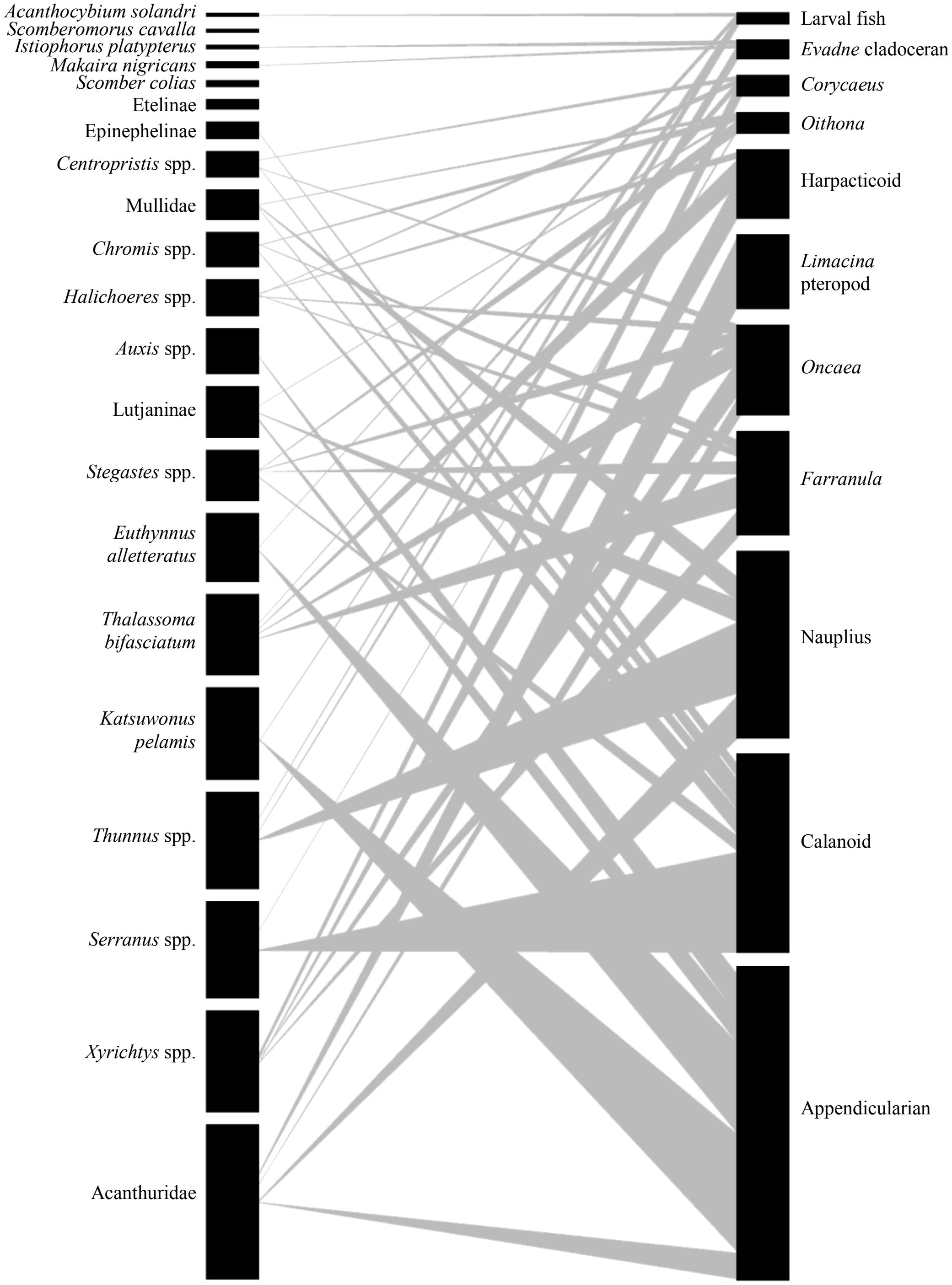


Figure 5.4. Linkage web of 21 taxa of larval fishes (top) and their predominant prey (bottom) from the Straits of Florida. Links are present between larval taxa and the prey types that numerically composed at least 1% of the diet. Abbreviations of larval taxa and prey types are the first few letters of the names in Table 5.1 or Fig. 5.5, with the exception of '*S. cav*' (*Scomberomorus cavalla*) and '*A. sol*' (*Acanthocybium solandri*).

Figure 5.5. Quantitative web of the larval fish taxa and prey in Fig. 5.4 and Table 5.1. Bar heights of the larval fish taxa (left) correspond to their relative abundance in the plankton (Table 5.1) over two years of monthly sampling (> 61, 000 larvae). Bar heights of the prey (right) correspond to the relative level of community reliance upon the prey type by the 21 taxa of fish larvae examined. The width of each larval taxon's linking triangle, relative to the bar height of the prey type, corresponds to the contribution to each prey type's index of reliance. The percent composition of prey types in the diets of each larval taxon is given in Table 5.1. Linkages contributing <5% of a prey type's level of reliance were excluded for clarity.

Fig. 5.5


Acanthocybium solandri
Scomberomorus cavalla
Istiophorus platypterus
Makaira nigricans
Scomber colias
Etelinae
Epinephelinae
Centropristis spp.
Mullidae
Chromis spp.
Halichoeres spp.
Auxis spp.
Lutjaninae
Stegastes spp.
Euthynnus alletteratus
Thalassoma bifasciatum
Katsuwonus pelamis
Thunnus spp.
Serranus spp.
Xyrichtys spp.
Acanthuridae
Larval fish
Evadne cladoceran
Corycaeus
Oithona
Harpacticoid
Limacina pteropod
Oncaea
Farranula
Nauplius
Calanoid
Appendicularian

Chapter 6. Summary and conclusions

While the planktonic larval fish remains enigmatic, it is perhaps less so with this contribution on the trophic ecologies of several low-latitude taxa. The results presented here are generally the product of basic ecological data collected in a rather simple manner—tow a net through the water, pick out the fish larvae, and cut them open. However, given the unprecedented temporal and spatial scale of the study, some notable advances have been made that should serve to enhance our understanding of processes occurring in the oceanic plankton, including some at the ecosystem level.

In chapter 2, several unique characteristics of larval billfish feeding ecologies emerged. Perhaps most noteworthy was the degree to which feeding was narrow and selective. Larvae almost exclusively consumed either *Farranula* copepods or *Evadne* cladocerans despite higher abundances of other prey types. Furthermore, these prey were consumed from the first-feeding stage up to and after a very distinct ontogenetic shift to piscivory.

The dominance of *Farranula* and *Evadne* naturally raised the question of 'preference' for one over the other. In each analysis of prey selectivity, *Evadne* was always consumed in proportions greater than available in the environment, while the opposite held for *Farranula*. Though we cannot say that larvae are actively passing on *Farranula* to get the next *Evadne*, one significant result that can be inferred is that *Evadne* was often unavailable to billfish larvae as evidenced by the frequent absence of *Evadne* in the guts of larval billfishes, which occurred more often in the western Straits of Florida (SOF). It could be hypothesized that selection for *Evadne* is the result of a conferred evolutionary advantage for such a behavior, and if so, the unavailability of

Evadne may be manifested in reduced growth rates and, ultimately, lower total survival. Similarly, several large blue marlin larvae that were collected in the central SOF had only consumed crustacean prey, but were clearly capable of piscivory. This suggested the potential for growth-limiting levels of available larval fish prey. However, despite substantial growth variability in blue marlin larvae (Sponaugle et al. 2005), a link to prey availability has yet to be established.

The four abundant taxa of tuna larvae in the SOF were the focus of chapter 3. Similar to billfishes, tuna larvae exhibited ontogenetic shifts to piscivory; however, prior to piscivory, diets were markedly different from billfishes. Three taxa (skipjack, little tunny and *Auxis* spp.) displayed highly selective feeding upon appendicularians to the near exclusion of any other prey, whereas oceanic tunas (*Thunnus* spp.) exhibited one of the most diverse diets observed in the SOF (with appendicularians contributing substantially). These taxon-specific diets are particularly interesting in light of the fact that all taxa are nearly morphologically identical.

The horizontal distributions of tuna larvae were also taxon-specific—a characteristic directly related to the spawning by adults upstream. Skipjack and *Thunnus* spp. were distributed quite evenly across the SOF, but little tunny and *Auxis* spp. were largely limited to the western SOF within the Florida Current. The co-occurrence of all four taxa in one region of the SOF, together with the high abundances of these larvae and their almost exclusive reliance upon appendicularians, raises questions regarding the distribution of available appendicularians. The result of this work indicated a precipitous decline from west to east in appendicularian abundance, with the western edge of the Florida Current exhibiting abundances nearly four-fold higher than abundances in the eastern-central SOF. Furthermore, skipjack and *Thunnus* spp., the two taxa present throughout the SOF and, therefore, within the regions of much lower prey availability, displayed significantly different vertical distributions. The mixed feeding of *Thunnus* spp. and the reduced spatial overlap in the vertical dimension between *Thunnus* spp. and skipjack illustrate separate dietary and spatial niches within the plankton. However, whether the driving force for these evolved specializations is related to prey availability and competition avoidance is a difficult question to address.

One approach to at least supporting the possible influence of prey availability on larval tuna distributions is to estimate the consumption of the larvae, and thus the capacity to substantially impact prey levels. With the specific objective of obtaining daily ration estimates, periodic sampling after sunset allowed for the determination of gut evacuation rates (since most larvae do not feeding during the night), which were then used in conjunction with the diel cycle of gut fullness to yield a size-specific daily ration in numbers of appendicularians. Since every larval tuna collected over the two-year study was measured (courtesy of Dave Richardson), a daily ration could be assigned to each collected larva. Daily rations were then related to the abundances of the larvae (m^{-3}) to calculate a removal rate of appendicularians (m^{-3} d^{-1}). These removal rates were applied to the environmental abundances of appendicularian to obtain estimates of percent-removal rates of appendicularians. The high abundances of tuna larvae in the western SOF resulted in high removal rates, but due to the high abundances of appendicularians, percent removal rates were not excessive. However, if the low levels of appendicularians in the east were exposed to the commonly observed high removal rates of the west, percent removal rates could be very large and potentially result in competition among and within tuna taxa. The relevance of these estimates is contingent upon the population growth rates of appendicularians (which are poorly understood in the oligotrophic ocean), but it is nonetheless noteworthy that this potential scenario is avoided by the co-occurrence of all four taxa only where prey availability is highest (in the western SOF).

The investigation into the feeding of larval coral reef fishes (chapter 4) was generally limited to the analysis of diets and diet variability. However, the inclusion of 13 taxa and the examination of 1266 individuals yielded one of the largest and most diverse studies on larval fish trophodynamics in any region to date. Rather than simply documenting the separate diets of each larval taxon, multivariate techniques were employed to carry out a quantitative analysis of diet overlap in several co-occurring fish larvae, and to address the influence of several variables on diet variability within taxa. The most interesting aspects of the findings were the distinct differences in diet composition and the clear separation in feeding niches among these organisms, which are only ephemerally associated with the planktonic ecosystem (a mere 2 to 6 weeks out of a sometimes decades-long lifespan) and appear to be extremely dilute relative to prey abundance.

The taxon-specific feeding behaviors of coral reef fishes were defined both by diets and by whether diet changed with ontogeny. For example, diets of *Serranus* spp. seabasses were almost exclusively composed of calanoid copepods, and this behavior was consistent with growth. Diets of the wrasses *Thalassoma bifasciatum* and *Halichoeres* spp. also changed little with growth, but completely excluded calanoids and largely consisted of harpacticoid copepods and the cyclopoids *Oncaea* and *Farranula*. While most taxa consumed copepods, four taxa relied on appendicularians, though to varying degrees. Most notably, lutjanine snappers consumed either copepod nauplii or appendicularians, with appendicularians becoming the near-exclusive prey type in the late larval stage. Clearly, the absence of copepodites in the diets of snappers is unrelated to capability or availability—these larvae, as well as others, simply appear to have an intrinsic ‘preference’ for specific prey.

One of the three goals of chapter 5 was to synthesize some of the above results into a broader investigation of patterns of energy flow in the plankton. The approach taken was to construct both a qualitative and quantitative web of larval taxa and their dominant prey. The qualitative linkage web illustrates larval feeding patterns in a simplistic manner. Larval taxa had a certain number of prey, and prey had a certain number of consumers. Though informative, this web inherently disregarded the degree to which each prey type contributed to the diets of each larval consumer. Additionally, to get at the larger question of community-level importance of prey types, the abundances of the larvae must be considered. To this end, the quantitative web incorporated the consumed prey-type proportions of each larval taxon and the abundances of the larval taxon in the plankton to elucidate the relative importance of each prey type, or their degree of reliance by the larval fish community as a whole. Inspired by a quantitative web of insects and parasitoids (Lewis et al. 2002), this is a completely unique approach to understanding the relative magnitude of specific trophic pathways to larval fishes.

Another objective of chapter 5 was to shed light on the variability in the physical and biological environment of the SOF and how it may relate to prey availability for larval fishes. Over the narrow SOF, substantial differences in thermocline depth, fluorescence, and total plankton and copepod nauplius abundances were observed, all of which were associated with the Florida Current and the variability in current structure across the SOF. The Florida Current generally occurs just offshore of the Florida Shelf break, exhibiting current speeds often near 2.5 m s^{-1}. Distribution patterns, from fluorescence to zooplankton to larval fishes, consistently showed significant declines toward the east. This illustrates the likelihood for distinct differences in the trophic functioning of this ecosystem over a very narrow region of oceanic waters.

Much of the data presented here has provided new perspectives on the specific trophic roles of larval fishes in the low-latitude planktonic food web. Many of the characteristics exhibited by the larvae appeared to differ from those of higher latitudes, but an in-depth review specifically addressing the possible differences was not previously available. This was the last goal of chapter 5, and was met by compiling the results of 65 studies (170 data sets on 130 taxa) to illustrate some potentially inherent latitudinal distinctions in larval fish prey consumption. Several notable differences were observed, including higher feeding incidences in lower latitudes, in addition to narrower diets and less reliance on eggs, nauplii and calanoid copepods in these regions. One of the clearest differences was the number of piscivorous larval taxa occurring in the two regions. Only one species in high latitudes (*Scomber scombrus*) exhibited larval piscivory, while 15 species in the low-latitude studies were piscivorous. Within the SOF, the number of piscivorous taxa is likely near 30, and throughout the world's lower latitudes, the number should be even greater.

Remaining questions and opportunities for future research

Several dominant themes related to the feeding ecologies of larval fishes have emerged from this work. One of the most striking patterns is the prevalence of narrow diets and highly selective feeding. This begs questions regarding the mechanism behind these behaviors. According to ecological theory, narrow diets and specialization should be the result of forces that minimize competition. Though this was supported for tuna larvae with the additional component of space, it is inherently difficult to elucidate thoroughly the adaptive pressures that have yielded currently observed behaviors. Additional studies along these lines are certainly merited.

In addition to feeding selectively, fish larvae in the SOF appeared to be feeding rather successfully. This is largely inferred from the extremely high feeding incidences, the rapid digestion in these warm waters that was shown for billfishes and tunas, and the nightly 10 to 14 hr period in which feeding does not occur. The rapid gut evacuation (~3 hrs) displayed by billfishes and tunas clearly shows that larvae can withstand an empty gut for 7 to 10 hours every day. Yet, during daylight hours, almost all larvae had at least some food present and well over half of them had guts qualitatively described as greater than half full. All evidence indicates that levels of larval starvation mortality may be substantially lower than expected based on temperature, primary production and prey availability. Future work using techniques to unambiguously support or refute this possibility could make a significant contribution to our understanding of larval fish survival in the open ocean.

If starvation levels are indeed low, given that the ocean is not overflowing with trillions of adult billfishes, tunas and reef fishes, the dominant mechanism resulting in the high mortality rates of larval fishes is likely to be predation. Predation mortality is one of the most poorly understood aspects of larval fish ecology, and any results from an investigation into sources and rates of larval predation mortality are likely to be significant.

In lower latitudes, there is still much to be learned about the cascading effects of feeding-related processes to larval growth rates. The relationship between larval growth and feeding may be influenced by large-scale patterns in prey levels and prey-type availability (e.g. *Farranula* vs. *Evadne* for billfishes), or small-scale patchiness (e.g. availability of fish larvae for piscivores). Even general investigations into associations between feeding success (e.g. gut fullness) and growth are largely unavailable from low-latitude waters.

These are only some of the many questions that have come to me in the course of this work. If pursued, some of these avenues for future research should substantially advance our knowledge of the early life stages of fishes and the functioning of planktonic ecosystems. Perhaps such work will build upon a strong base of information presented here.

Appendix A. Literature review information for Chapter 5 on 170 investigations (65 reports, 130 taxa) on the feeding of larval fishes within various regions and environments. See ‘Materials and methods’ for information regarding criteria and classification. Lat: latitudinal division; FI: feeding incidence, calculated from daytime only (D), nighttime only (N), or all larvae (T) if indeterminable, and estimated when indicated (~); TNB: trophic niche breadth relationship, either nonsignificant (ns) or significantly increasing or decreasing; Ref: reference in list following table; (-) indicates insufficient or lack of data.

Taxon	**Common name**	**Region**	**Lat.**	**Env.**	**FI**	**Predominant prey**	**Ontogenetic diet shift**	**Specific, narrow diet**	**TNB with size**	**Ref.**
Ammodytes marinus	lesser sand-eel	North Sea	high	offshore	~0.5(D)	tintinnids, nauplii	yes	-	-	32
Ammodytes marinus	lesser sand-eel	North Sea	high	offshore	-	eggs, nauplii, *Oithona*	yes	not	-	10
Ammodytes sp.	(sand-eel)	SW Greenland	high	offshore	0.85(D)	‘all copepod stages'	-	-	ns	56
Anoplopoma fimbria	sablefish	Bering Sea	high	offshore	1.0(T)	nauplii, calanoids	yes	-	-	20
Arnoglossus laterna	scaldfish	North Sea	high	offshore	~0.4(D)	appendicularians	yes	highly	-	32
Boreogadus saida	Arctic cod	NE Greenland	high	offshore	0.76(D)	egg, nauplii	no	-	-	39
Buglossideum luteum	solenette	North Sea	high	offshore	~0.6(D)	nauplii, harpacticoids, polychaete larvae	-	-	-	32
Callionymus lyra	dragonet	North Sea	high	offshore	~0.95(D)	nauplii, calanoids	no	-	-	32
Clupea harengus	Atlantic herring	North Sea	high	offshore	~0.35(D)	nauplii, *Oithona*, calanoids	-	-	-	32
Echiichthys vipera	lesser weever	North Sea	high	offshore	~0.9(D)	nauplii, eggs	yes	-	-	32
Gadus morhua	cod	Baltic Sea	high	offshore	~0.6(D)	nauplii, calanoids	yes	-	ns	62
Gadus morhua	cod	North Sea	high	offshore	~0.70(D)	nauplii, calanoids	yes	-	-	31
Gadus morhua	cod	Nova Scotia	high	offshore	-	nauplii, calanoids	-	not	-	37
Gadus morhua	cod	Nova Scotia	high	offshore	-	nauplii, calanoids, *Oithona*	-	-	-	38
Gadus morhua	cod	Irish Sea	high	offshore	-	nauplii, calanoids	-	-	-	59
Gadus morhua	cod	North Sea	high	offshore	~0.7(D)	tintinnids, nauplii	yes	-	-	32
Gadus morhua	cod	North Sea	high	offshore	-	nauplii, calanoids	yes	not	-	10

Taxon	Common name	Region	Lat.	Env.	FI	Predominant prey	Ontogenetic diet shift	Specific, narrow diet	TNB with size	Ref.
Gaidropsarus vulgaris	three-bearded rockling	North Sea	high	offshore	~0.8(D)	nauplii, *Oithona*	yes	-	-	32
Glyptocephalus cynoglossus	witch flounder	North Sea	high	offshore	0.49(T)	appendicularians	-	highly	-	32
Gobius spp.	gobies	North Sea	high	offshore	~0.8(D)	nauplii, calanoids	yes	-	-	32
Hippoglossoides platessoides	American plaice	North Sea	high	offshore	-	nauplii, calanoids	yes	not	-	10
Hyperoplus lanceolatus	greater sand-eel	North Sea	high	offshore	~0.6(D)	nauplii, calanoids	yes	-	-	32
Limanda limanda	dab	North Sea	high	offshore	~0.6(D)	nauplii, calanoids	yes	-	-	30
Limanda limanda	dab	North Sea	high	offshore	~0.65(D)	nauplii, calanoids	yes	-	-	32
Liparis liparis	sea snail	North Sea	high	offshore	~0.85(D)	nauplii, calanoids	yes	-	-	32
Melanogrammus aeglefinus	haddock	North Sea	high	offshore	-	nauplii, *Oithona*	yes	not	-	10
Merlangius merlangus	whiting	North Sea	high	offshore	~0.75(D)	nauplii, calanoids	yes	-	-	31
Merlangius merlangus	whiting	North Sea	high	offshore	~0.8(D)	nauplii, calanoids	yes	-	-	32
Merlangius merlangus	whiting	North Sea	high	offshore	-	nauplii, calanoids	yes	not	-	10
Micromesistius poutassou	blue whiting	W Ireland	high	offshore	0.92(D)	eggs, nauplii	yes	-	-	22
Micromesistius poutassou	blue whiting	W Ireland	high	offshore	0.8(T)	nauplii, eggs	yes	-	-	21
Microstomus kitt	lemon sole	North Sea	high	offshore	~0.8(D)	nauplii, appendicularians	yes	-	-	32
Pholis gunnellis	rock gunnel	North Sea	high	offshore	0.78(T)	nauplii, calanoids	-	-	-	32
Platichthys flesus	flounder	North Sea	high	offshore	~0.5(D)	dinoflagellates, appendicularians	yes	-	-	30
Pleuronectes platessa	plaice	North Sea	high	offshore	~0.5(D)	appendicularians	no	-	-	30

Taxon	**Common name**	**Region**	**Lat.**	**Env.**	**FI**	**Predominant prey**	**Ontogenetic diet shift**	**Specific, narrow diet**	**TNB with size**	**Ref.**
Pleuronectes platessa	plaice	North Sea	high	offshore	0.52(N)	appendicularians	no	highly	-	55
Pleuronectes platessa	plaice	North Sea	high	offshore	~0.5(D)	nauplii, appendicularians	yes	-	-	32
Pollachius virens	saithe	North Sea	high	offshore	-	nauplii, calanoids	yes	not	-	10
Reinharditius hippoglossoides	Greenland halibut	SW Greenland	high	offshore	0.97(D)	‘all copepod stages'	-	-	ns	56
Scomber scombrus	Atlantic mackerel	Celtic Sea	high	offshore	0.65(D)	nauplii, fish larvae	yes	-	-	23
Scomber scombrus	Atlantic mackerel	Nova Scotia	high	offshore	0.75(T)	nauplii,'copepods', fish larvae	yes	moderate	-	13
Scomber scombrus	Atlantic mackerel	S Ireland	high	offshore	0.9(D)	nauplii, 'copepods', fish larvae	yes	-	-	7
Scomber scombrus	Atlantic mackerel	North Sea	high	offshore	0.79(T)	nauplii, cladocerans	yes	-	-	32
Solea solea	sole	North Sea	high	offshore	~0.75(D)	nauplii, polychaete larvae	yes	-	-	30
Sprattus sprattus	sprat	Baltic Sea	high	offshore	~0.8(D)	nauplii, calanoids	yes	-	ns	62
Sprattus sprattus	sprat	North Sea	high	offshore	~0.35(D)	nauplii, calanoids	-	-	-	32
Sprattus sprattus	sprat	Baltic Sea	high	offshore	~0.4(D)	nauplii, calanoids	yes	not	increasing	9
Theragra chalcogramma	walleye pollock	Gulf of Alaska	high	offshore	-	nauplii, calanoids	yes	not	-	29
Theragra chalcogramma	walleye pollock	Gulf of Alaska	high	offshore	0.95(T)	nauplii, eggs	-	-	-	3
Trachurus trachurus	Atlantic horse mackerel	North Sea	high	offshore	1.0(T)	nauplii, calanoids	yes	-	-	32
Trisopterus esmarkii	Norway pout	North Sea	high	offshore	-	nauplii, calanoids	yes	not	-	10
Trisopterus luscus	bib	North Sea	high	offshore	~0.75(D)	nauplii, calanoids	yes	-	-	31
Sebastes spp.	redfish	Newfoundland	high	offshore	-	eggs, nauplii, *Oithona*	-	not	-	1

Taxon	Common name	Region	Lat.	Env.	FI	Predominant prey	Ontogenetic diet shift	Specific, narrow diet	TNB with size	Ref.
Ammodytes sp.	(sand lance)	Hudson Bay, Canada	high	coastal	~0.18(D)	nauplii, tintinnids	-	-	-	12
Boreogadus saida	Arctic cod	Hudson Bay, Canada	high	coastal	~0.45(D)	nauplii, eggs	-	-	-	12
Callionymus lyra	dragonet	English channel	high	coastal	0.56(T)	nauplii, 'copepods'	yes	-	-	11
Clupea harengus	Atlantic herring	Conception Bay, Newfoundland	high	coastal	-	nauplii, calanoids	yes	not	ns	44
Gadus morhua	cod	Conception Bay, Newfoundland	high	coastal	-	nauplii, calanoids	yes	not	increasing	44
Gadus morhua	cod	Iceland	high	coastal	-	euphausiid nauplii, calanoids	yes	-	-	60
Glyptocephalus cynoglossus	witch flounder	Conception Bay, Newfoundland	high	coastal	-	nauplii, calanoids	yes	not	increasing	44
Hippoglossoides platessoides	American plaice	Conception Bay, Newfoundland	high	coastal	-	nauplii, calanoids	yes	not	increasing	44
Liparis sp.	snailfish	Conception Bay, Newfoundland	high	coastal	-	nauplii, calanoids	yes	not	ns	44
Mallotus villosus	capelin	Conception Bay, Newfoundland	high	coastal	-	nauplii, calanoids	yes	not	increasing	44
Merlangius merlangus	whiting	English channel	high	coastal	0.49(T)	nauplii, 'copepods'	yes	-	-	11
Microchirus variegatus	thickback sole	English channel	high	coastal	0.59(T)	eggs, *Evadne*, polychaete larvae	yes	moderate	-	11
Nototheniops larseni	Antarctic fish	Antarctica	high	coastal	~0.95(D)	*Oncaea*, eggs	-	-	-	28
Phrynorhombus norvegicus	Norwegian topknot	English channel	high	coastal	0.76(T)	nauplii, 'copepods'	yes	-	-	11
Pleuronectes americanus	winter flounder	Conception Bay, Newfoundland	high	coastal	-	nauplii, bivalve larvae	yes	not	increasing	44
Pleuronectes ferrugineus	yellowtail flounder	Conception Bay, Newfoundland	high	coastal	-	nauplii, calanoids	yes	not	ns	44
Stichaeus punctatus	Arctic shanny	Conception Bay, Newfoundland	high	coastal	-	nauplii, calanoids	yes	not	ns	44

Taxon	Common name	Region	Lat.	Env.	FI	Predominant prey	Ontogenetic diet shift	Specific, narrow diet	TNB with size	Ref.
Tautogolabrus adspersus	cunner	Conception Bay, Newfoundland	high	coastal	-	nauplii, calanoids	yes	not	ns	44
Ulvaria subbifurcata	radiated shanny	Conception Bay, Newfoundland	high	coastal	-	nauplii, calanoids	yes	not	increasing	44
Clupea harengus	Atlantic herring	North Sea estuary	high	estuarine	~0.75(D)	nauplii, 'copepods'	yes	not	-	14
Anoplopoma fimbria	sablefish	Oregon/Washington	med	offshore	-	nauplii, 'copepods'	yes	-	-	19
Auxis rochei	bullet tuna	Mediterranean Sea	med	offshore	0.88(D)	nauplii, *Evadne*	yes	moderate	dome-shaped	41
Benthosema glaciale	glacier lanternfish	Mediterranean Sea	med	offshore	~0.25(D)	nauplii, calanoids	yes	-	-	48
Benthosema glaciale	glacier lanternfish	Mediterranean Sea	med	offshore	-	-	-	-	ns	49
Ceratoscopelus maderensis	Madeira lanternfish	Mediterranean Sea	med	offshore	-	-	-	-	ns	49
Diaphus garmani	(lanternfish)	E Japan	med	offshore	0.71(D)	nauplii, appendicularians	one distinct	highly	ns	53
Engraulis mordax	northern anchovy	California Current	med	offshore	~0.15(D)	nauplii	yes	-	-	2
Gadus morhua	cod	Georges Bank	med	offshore	0.99(T)	nauplii, calanoids	yes	not	-	27
Hygophum benoiti	Benoit's lanternfish	Mediterranean Sea	med	offshore	-	-	-	-	ns	49
Isopsetta isolepis	butter sole	Oregon	med	offshore	~0.85(D)	nauplii, calanoids	yes	not	-	15
Lampanyctus crocodilus	Jewel lanternfish	Mediterranean Sea	med	offshore	-	-	-	-	ns	49
Melanogrammus aeglefinus	haddock	Georges Bank	med	offshore	1.0(T)	nauplii, calanoids	yes	not	-	27
Merluccius productus	Pacific hake	S California	med	offshore	0.80(D)	eggs, calanoids	-	-	-	75

Taxon	Common name	Region	Lat.	Env.	FI	Predominant prey	Ontogenetic diet shift	Specific, narrow diet	TNB with size	Ref.
Merluccius productus	Pacific hake	S California	med	offshore	~0.95(D)	nauplii, calanoids	yes	not	-	57
Myctophum asperum	prickly lanternfish	E Japan	med	offshore	0.68(D)	ostracods, polychaete larvae	no	highly	ns	53
Myctophum punctatum	spotted lanternfish	Mediterranean Sea	med	offshore	~0.25(D)	eggs, calanoids	no	-	-	48
Myctophum punctatum	spotted lanternfish	Mediterranean Sea	med	offshore	-	-	-	-	ns	49
Notolepis rissoi	ribbon barracudina	Mediterranean Sea	med	offshore	-	-	-	-	ns	49
Parophrys vetulus	English sole	Oregon	med	offshore	~0.85(D)	appendicularians	no	highly	-	15
Sardinops sagax	Pacific sardine	California Current	med	offshore	~0.15(D)	eggs, nauplii	yes	-	-	2
Thunnus alalunga	albacore	Mediterranean Sea	med	offshore	1.0(D)	calanoids, *Evadne*	yes	not	ns	5
Trachurus symmetricus	jack mackerel	California Current	med	offshore	~0.6(T)	harpacticoids, calanoids	yes	-	-	2
Ammodytes americanus	American sand lance	Long Island Sound	med	coastal	0.96(D)	nauplii, calanoids	yes	not	-	40
Atherinopsis californiensis	jacksmelt	S California	med	coastal	0.47(N)	nauplii, harpacticoids	yes	-	-	63
Boops boops	bogue	Mediterranean Sea	med	coastal	0.54(D)	eggs, nauplii	yes	not	-	52
Diplodus sargus	white sea bream	Mediterranean Sea	med	coastal	0.52(D)	eggs, nauplii	yes	not	-	52
Engraulis encrasicolus	European anchovy	Mediterranean Sea	med	coastal	0.4(D)	nauplii, Oithona	-	not	-	8
Gadus macrocephalus	Pacific cod	Mutsu Bay, Japan	med	coastal	0.96(D)	nauplii, calanoids	yes	not	-	58
Genyonemus lineatus	white croaker	S California	med	coastal	0.95(N)	harpacticoids, calanoids	yes	-	-	63
Kyphosus spp.	chubs	SE Australia	med	coastal	-	nauplii, calanoids	-	-	-	46
Leuresthes tenuis	grunion	S California	med	coastal	0.36(N)	nauplii, harpacticoids	-	-	-	63

Taxon	Common name	Region	Lat.	Env.	FI	Predominant prey	Ontogenetic diet shift	Specific, narrow diet	TNB with size	Ref.
Liza argentea	flat-tail mullet	SE Australia	med	coastal	-	nauplii, calanoids	-	-	-	46
Paralabrax spp.	kelp/sand bass	S California	med	coastal	0.68(D)	nauplii, bivalve larvae	-	-	-	63
Paralichthys californicus	California halibut	S California	med	coastal	0.38(D)	tintinnids	-	-	-	63
Scomber scombrus	Atlantic mackerel	Long Island Sound	med	coastal	0.52(D)	nauplii, calanoids	yes	not	-	45
Seriphus politus	queenfish	S California	med	coastal	0.82(D)	harpacticoids, calanoids	yes	-	-	63
Trachurus declivis	jack mackerel	Tasmania	med	coastal	0.78(D)	harpacticoids, oithona	yes	-	-	65
Afurcagobius suppositus	long-headed goby	SW Australian estuary	med	estuarine	-	nauplii, harpacticoids	yes	not	-	16
Ammodytes personatus	Pacific sandeel	Japanese estuary	med	estuarine	0.96(D)	nauplii, 'copepodites'	yes	-	-	42
Ammotretis rostratus	long-snouted flounder	SE Australian estuary	med	estuarine	1.0(D)	bivalves, calanoids	yes	not	ns	25
Favonigobius lateralis	(goby)	SW Australian estuary	med	estuarine	-	nauplii, bivalve larvae	yes	not	-	16
Hexagrammos spp.	greenling	Japanese estuary	med	estuarine	1.0(D)	nauplii, 'copepodites'	yes	-	-	42
Parablennius tasmanianus	Tasmanian blenny	SW Australian estuary	med	estuarine	-	nauplii, Oithona	yes	not	-	16
Pseudogobius olorum	blue-spot goby	SW Australian estuary	med	estuarine	-	nauplii, Oithona	yes	not	-	16
Rhombosolea tapirina	greenback flounder	SE Australian estuary	med	estuarine	1.0(D)	bivalves, Evadne	yes	not	ns	25
Sebastiscus marmoratus	(scorpionfish)	Japanese estuary	med	estuarine	1.0(D)	nauplii, 'copepodites'	yes	-	-	42
Urocampus carinirostris	hairy pipefish	SW Australian estuary	med	estuarine	-	nauplii, Oithona	yes	not	-	16

Taxon	Common name	Region	Lat.	Env.	FI	Predominant prey	Ontogenetic diet shift	Specific, narrow diet	TNB with size	Ref.
Acanthocepola sp.	bandfish	Andaman Sea	low	offshore	1.0(D)	calanoids, *Oncaea*	no	-	ns	43
Acanthuridae	surgeonfishes	Straits of Florida	low	offshore	0.99(D)	*Limacina*, nauplii, appendicularians	yes	highly	ns	35
Auxis spp.	bullet/frigate tuna	Gulf of California	low	offshore	~0.5(D)	nauplii, eggs	no	moderate		51
Auxis spp.	bullet/frigate tuna	Straits of Florida	low	offshore	0.99(D)	appendicularians	no	highly	-	36
Benthosema suborbitale	smallfin lanternfish	Gulf of Mexico	low	offshore	~0.9(D)	ostracods, calanoids	-	highly	-	6
Carangoides sp.	trevally	Andaman Sea	low	offshore	~0.98(D)	*Oncaea*, corycaeids	no	-	ns	43
Ceratoscopelus townsendi	dogtooth lampfish	Gulf of Mexico	low	offshore	~0.6(D)	salps, calanoids	-	highly	-	6
Diogenichthys laternatus	Diogenes lanternfish	N Chile	low	offshore	0.27(D)	eggs, ostracods	-	moderate	-	47
Epinephelinae	groupers	Straits of Florida	low	offshore	0.98(D)	calanoids, *Farranula*	-	moderate	decreasing	35
Euthynnus alletteratus	little tunny	Straits of Florida	low	offshore	0.99(D)	appendicularians	one distinct (piscivory)	highly	-	36
Euthynnus lineatus	black skipjack	Gulf of California	low	offshore	~0.6(D)	appendicularians, nauplii	yes	not	-	51
Gempylus serpens	snake mackerel	Tropical Indian & Pacific	low	offshore	0.88(D)	*Farranula*, calanoids, larval fish	one distinct (piscivory)	moderate	-	33
Halichoeres spp.	wrasses	Straits of Florida	low	offshore	1.0(D)	nauplii, calanoids, *Oncaea*	yes	not	ns	35
Hygophum taaningi	(lanternfish)	Gulf of Mexico	low	offshore	~0.9(D)	salps	-	highly	-	6
Istiophorus platypterus	sailfish	Straits of Florida	low	offshore	0.90(D)	*Farranula*, *Evadne*, fish larvae	one distinct (piscivory)	highly	decreasing (<8mm)	34
Katsuwonus pelamis	skipjack	NW Australia	low	offshore	0.42(D)	appendicularians, fish larvae	one distinct (piscivory)	highly	-	64

Taxon	Common name	Region	Lat.	Env.	FI	Predominant prey	Ontogenetic diet shift	Specific, narrow diet	TNB with size	Ref.
Katsuwonus pelamis	skipjack	Straits of Florida	low	offshore	0.99(D)	appendicularians, larval fish	one distinct (piscivory)	highly	-	36
Lutjaninae	snappers	Straits of Florida	low	offshore	1.0(D)	nauplii, appendicularians	yes	highly	ns	35
Makaira nigricans	Indo-Pacific blue marlin	Tropical Indian & Pacific	low	offshore	0.94(T)	*Corycaeus*, *Evadne*, fish larvae	one distinct (piscivory)	highly	-	61
Makaira nigricans	Atlantic blue marlin	Straits of Florida	low	offshore	0.98(D)	*Farranula*, *Evadne*, fish larvae	one distinct (piscivory)	highly	decreasing (<8mm)	34
Mullidae	goatfishes	Straits of Florida	low	offshore	1.0(D)	nauplii, calanoids, appendicularians	yes	not	ns	35
Myctophum affine	metallic lanternfish	Gulf of Mexico	low	offshore	~0.9(D)	ostracods	-	highly	-	6
Myctophum selenops	Wisner's lanternfish	Gulf of Mexico	low	offshore	~0.9(D)	ostracods, *Oncaea*	-	highly	-	6
Notolychnus valdivae	topside lampfish	Gulf of Mexico	low	offshore	~0.9(D)	calanoids, nauplii	-	not	-	6
Scomberomorus spp.	Spanish mackerels	Great Barrier Reef	low	offshore	0.86(T)	fish larvae, appendicularians	no	highly	-	26
Scorpaenodes sp.	scorpionfish	Andaman Sea	low	offshore	1.0(D)	calanoids, *Oncaea*	yes	-	ns	43
Serranus spp.	seabasses	Straits of Florida	low	offshore	0.96(D)	calanoids	no	highly	decreasing	35
Sparisoma spp.	parrotfishes	Straits of Florida	low	offshore	0.04(D)	-	-	-	-	35
Stegastes spp.	damselfishes	Straits of Florida	low	offshore	1.0(D)	*Oncaea*, *Farranula*, calanoids	no	not	decreasing	35
Tetrapturus angustirostris	shortbill spearfish	Tropical Indian & Pacific	low	offshore	~0.9(T)	*Corycaeus*, fish larvae	one distinct (piscivory)	highly	-	61
Thalassoma bifasciatum	bluehead wrasse	Straits of Florida	low	offshore	0.99(D)	*Farranula*, harpacticoids	no	highly	ns	35
Thunnus spp.	bluefin/ albacore tunas	NW Australia	low	offshore	0.54(D)	nauplii, calanoids, cyclopoids	yes	not	-	64
Thunnus spp.	oceanic tunas	Straits of Florida	low	offshore	0.98(D)	nauplii, *Evadne*, appendicularians	yes	moderate	-	36

Taxon	**Common name**	**Region**	**Lat.**	**Env.**	**FI**	**Predominant prey**	**Ontogenetic diet shift**	**Specific, narrow diet**	**TNB with size**	**Ref.**
Triphoturus mexicanus oculeus	(lanternfish)	N Chile	low	offshore	0.18(D)	nauplii, ostracods	-	moderate	-	47
Xiphias gladius	swordfish	W Atlantic	low	offshore	-	*Farranula*, fish larvae	one distinct (piscivory)	highly	-	18
Xyrichtys spp.	razorfish wrasses	Straits of Florida	low	offshore	0.94(D)	*Oncaea*, harpacticoids	no	highly	ns	35
Brevoortia patronus	gulf menhaden	Gulf of Mexico	low	coastal	~0.4(D)	dinoflagellates, bivalve larvae	yes	moderate	-	17
Chloroscombrus chrysurus	bumper	Gulf of Mexico	low	coastal	0.8(D)	*Penilia*, 'copepods'	-	-	-	50
Hypoatherina tropicalis	Whitley's silverside	Great Barrier Reef	low	coastal	0.99(D)	nauplii, 'copepods'	no	-	-	54
Leiostomus xanthurus	spot	Gulf of Mexico	low	coastal	~0.75(D)	*Limacina*, *Oncaea*	yes	highly	-	17
Micropogonias undulatus	Atlantic croaker	Gulf of Mexico	low	coastal	~0.6(D)	eggs, calanoids	no	not	-	17
Anchoa mitchilli	bay anchovy	Biscayne Bay, FL	low	estuarine	0.38(D)	nauplii, 'copepods'	-	-	-	24
Archosargus rhomboidalis	W Atlantic seabream	Biscayne Bay, FL	low	estuarine	0.42(D)	nauplii, 'copepods'	-	-	-	24
Blenniidae	blennies	Biscayne Bay, FL	low	estuarine	0.42(D)	nauplii, 'copepods'	-	-	-	24
Callionymus pauciradiatus	spotted dragonet	Biscayne Bay, FL	low	estuarine	0.66(D)	nauplii, 'copepods'	-	-	-	24
Cynoscion nebulosus	spotted seatrout	Biscayne Bay, FL	low	estuarine	0.78(D)	nauplii, 'copepods'	-	-	-	24
Gobiidae	gobies	Biscayne Bay, FL	low	estuarine	0.33(D)	nauplii, tintinnids	-	-	-	24
Harengula jaguana	scaled sardine	Biscayne Bay, FL	low	estuarine	0.35(D)	nauplii, 'copepods'	-	-	-	24
Opisthonema oglinum	thread herring	Biscayne Bay, FL	low	estuarine	0.43(D)	nauplii, 'copepods'	-	-	-	24
Orthopristis chrysoptera	pigfish	Biscayne Bay, FL	low	estuarine	0.43(D)	nauplii, 'copepods'	-	-	-	24

References associated with Appendix A

(1) Anderson JT (1994) Feeding ecology and condition of larval and pelagic juvenile redfish *Sebastes* spp. Mar Ecol Prog Ser 104:211-226

(2) Arthur DK (1976) Food and feeding of larvae of three fishes occurring in the California Current, *Sardinops sagax, Engraulis mordax,* and *Trachurus symetricus*. Fish Bull 74:517-530

(3) Canino MF, Bailey KM, Incze LS (1991) Temporal and geographic differences in feeding and nutritional condition of walleye pollock larvae *Theragra chalcogramma* in Shelikof Strait, Gulf of Alaska. Mar Ecol Prog Ser 79:27-35

(4) Cass-Calay SL (2003) The feeding ecology of larval Pacific hake (*Merluccius productus*) in the California Current region: an updated approach using a combined OPC/MOCNESS to estimate prey biovolume. Fish Oceanogr 12:34-48

(5) Catalan IA, Alemany F, Morillas A, Morales-Nin B (2007) Diet of larval albacore *Thunnus alalunga* (Bonnaterre, 1788) off Mallorca Island (NW Mediterranean). Sci Mar 71:347-354

(6) Conley WJ, Hopkins TL (2004) Feeding ecology of lanternfish (Pisces: Myctophidae) larvae: prey preferences as a reflection of morphology. Bull Mar Sci 75:361-379

(7) Conway DVP, Coombs SH, Lindley JA, Llewellyn CA (1999) Diet of mackerel (*Scomber scombrus*) larvae at the shelf-edge to the south-west of the British Isles and the incidence of piscivory and coprophagy. Vie Et Milieu-Life and Environment 49:213-220

(8) Conway DVP, Coombs SH, Smith C (1998) Feeding of anchovy *Engraulis encrasicolus* larvae in the northwestern Adriatic Sea in response to changing hydrobiological conditions. Mar Ecol Prog Ser 175:35-49

(9) Dickmann M, Mollmann C, Voss R (2007) Feeding ecology of Central Baltic sprat *Sprattus sprattus* larvae in relation to zooplankton dynamics: implications for survival. Mar Ecol Prog Ser 342:277-289

(10) Economou AN (1991) Food and feeding ecology of five gadoid larvae in the northern North Sea. ICES J Mar Sci 47:339-351

(11) Fortier L, Harris RP (1989) Optimal foraging and density-dependent competition in marine fish larvae. Mar Ecol Prog Ser 51:19-33

(12) Fortier L, Ponton D, Gilbert M (1995) The match/mismatch hypothesis and the feeding success of fish larvae in ice-covered southeastern Hudson Bay. Mar Ecol Prog Ser 120:11-27

(13) Fortier L, Villeneuve A (1996) Cannibalism and predation on fish larvae by larvae of Atlantic mackerel, *Scomber scombrus*: trophodynamics and potential impact on recruitment. Fish Bull 94:268-281

(14) Fox CJ, Harrop R, Wimpenny A (1999) Feeding ecology of herring (*Clupea harengus*) larvae in the turbid Blackwater Estuary. Mar Biol 134:353-365

(15) Gadomski DM, Boehlert GW (1984) Feeding ecology of pelagic larvae of english sole *Parophrys vetulus* and butter sole *Isopsetta isolepis* off the Oregon coast. Mar Ecol Prog Ser 20:1-12

(16) Gaughan DJ, Potter IC (1997) Analysis of diet and feeding strategies within an assemblage of estuarine larval fish and an objective assessment of dietary niche overlap. Fish Bull 95:722-731

(17) Govoni JJ, Hoss DE, Chester AJ (1983) Comparative feeding of three species of larval fishes in the Northern Gulf of Mexico: *Brevoortia patronus, Leiostomus xanthurus,* and *Micropogonias undulatus*. Mar Ecol Prog Ser 13:189-199

(18) Govoni JJ, Laban EH, Hare JA (2003) The early life history of swordfish (*Xiphias gladius*) in the western North Atlantic. Fish Bull 101:778-789

(19) Grover JJ, Olla BL (1987) Effects of an El Niño event on the food habits of larval sablefish, *Anoplopoma fimbria*, off Oregon and Washington. Fish Bull 85:71-79

(20) Grover JJ, Olla BL (1990) Food habits of larval sablefish *Anoplopoma fimbria* from the Bering Sea. Fish Bull 88:811-814

(21) Hillgruber N, Kloppmann M (1999) Distribution and feeding of blue whiting *Micromesistius poutassou* larvae in relation to different water masses in the Porcupine Bank area, west of Ireland. Mar Ecol Prog Ser 187:213-225

(22) Hillgruber N, Kloppmann M (2000) Vertical distribution and feeding of larval blue whiting in turbulent waters above Porcupine Bank. J Fish Biol 57:1290-1311

(23) Hillgruber N, Kloppmann M (2001) Small-scale patterns in distribution and feeding of Atlantic mackerel (*Scomber scombrus* L.) larvae in the Celtic Sea with special regard to intra-cohort cannibalism. Helgoland Marine Research 55:135-149

(24) Houde ED, Lovdal JA (1984) Seasonality of occurrence, foods and food preferences of ichthyoplankton in Biscayne Bay, Florida. Estuarine Coastal and Shelf Science 18:403-419

(25) Jenkins GP (1987) Comparative diets, prey selection, and predatory impact of co-occurring larvae of two flounder species. J Exp Mar Biol Ecol 110:147-170

(26) Jenkins GP, Milward NE, Hartwick RF (1984) Food of larvae of Spanish mackerels, genus *Scomberomorus* (Teleostei, Scombridae), in shelf waters of the Great Barrier Reef. Aust J Mar Freshw Res 35:477-482

(27) Kane J (1984) The feeding habits of co-occurring cod and haddock larvae from Georges Bank. Mar Ecol Prog Ser 16:9-20

(28) Kellermann A (1990) Food and feeding dynamics of the larval Antarctic fish *Nototheniops larseni*. Mar Biol 106:159-167

(29) Kendall AW, Clarke ME, Yoklavich MM, Boehlert GW (1987) Distribution, feeding, and growth of larval walleye pollock, *Theragra chalcogramma*, from Shelikof Strait, Gulf of Alaska. Fish Bull 85:499-521

(30) Last JM (1978a) The food of four species of pleuronectiform larvae in the eastern English Channel and southern North Sea. Mar Biol 45:359-368

(31) Last JM (1978b) The food of three species of gadoid larvae in the eastern English Channel and southern North Sea. Mar Biol 48:377-386

(32) Last JM (1980) The food of twenty species of fish larvae in the west-central North Sea. Fish Res Tech Rep Dir Fish Res (GB) 60:1-44

(33) Lipskaya NY, Gorbunova NN (1980) Feeding of the larvae of the snake mackerel *Gempylus serpens*. Oceanology 20:204-208

(34) Llopiz JK, Cowen RK (2008) Precocious, selective and successful feeding of larval billfishes in the oceanic Straits of Florida. Mar Ecol Prog Ser 358:231-244

(35) Llopiz JK, Cowen RK Variable trophodynamic strategies among larval coral reef fishes in the oceanic plankton. Unsubmitted manuscript.

(36) Llopiz JK, Richardson DE, Crompton EM, Cowen RK Spatial and dietary niche separation among planktonic larval tunas in the subtropical ocean. Unsubmitted manuscript.

(37) McLaren IA, Avendano P (1995) Prey field and diet of larval cod on Western-Bank, Scotian Shelf. Can J Fish Aquat Sci 52:448-463

(38) McLaren IA, Avendano P, Taggart CT, Lochmann SE (1997) Feeding by larval cod in different water-masses on Western Bank, Scotian Shelf. Fish Oceanogr 6:250-265

(39) Michaud J, Fortier L, Rowe P, Ramseier R (1996) Feeding success and survivorship of Arctic cod larvae, *Boreogadus saida*, in the northeast water polynya (Greenland sea). Fish Oceanogr 5:120-135

(40) Monteleone DM, Peterson WT (1986) Feeding ecology of American sand lance *Ammodytes americanus* larvae from Long Island Sound. Mar Ecol Prog Ser 30:133-143

(41) Morote E, Olivarl MP, Pankhurst PM, Villate F, Uriarte M (2008) Trophic ecology of bullet tuna *Auxis rochei* larvae and ontogeny of feeding-related organs. Mar Ecol Prog Ser 353:243-254

(42) Nagano N, Iwatsuki Y, Okazaki Y, Nakata H (2001) Feeding strategy of Japanese sand lance larvae in relation to ciliated protozoa in the vicinity of a thermohaline front. J Oceanogr 57:155-163

(43) Ostergaard P, Munk P, Janekarn V (2005) Contrasting feeding patterns among species of fish larvae from the tropical Andaman Sea. Mar Biol 146:595-606

(44) Pepin P, Penney RW (1997) Patterns of prey size and taxonomic composition in larval fish: are there general size-dependent models? J Fish Biol 51:84-100

(45) Peterson WT, Ausubel SJ (1984) Diets and selective feeding by larvae of Atlantic mackerel *Scomber scombrus* on zooplankton. Mar Ecol Prog Ser 17:65-75

(46) Rissik D, Suthers IM (1996) Feeding in a larval fish assemblage: The nutritional significance of an estuarine plume front. Mar Biol 125:233-240

(47) Rodriguez-Grana L, Castro L, Loureiro M, Gonzalez HE, Calliari D (2005) Feeding ecology of dominant larval myctophids in an upwelling area of the Humboldt Current. Mar Ecol Prog Ser 290:119-134

(48) Sabates A, Bozzano A, Vallvey I (2003) Feeding pattern and the visual light environment in myctophid fish larvae. J Fish Biol 63:1476-1490

(49) Sabates A, Saiz E (2000) Intra- and interspecific variability in prey size and niche breadth of myctophiform fish larvae. Mar Ecol Prog Ser 201:261-271

(50) Sanchez-Ramirez M (2003) Diet composition and feeding habits of Atlantic bumper, *Chloroscombrus chrysurus* (Pisces: Carangidae), larvae in the southern Gulf of Mexico. Bull Mar Sci 72:675-683

(51) Sanchez-Velasco L, Contreras-Arredondo I, Esqueda-Escarcega G (1999) Diet composition of *Euthynnus lineatus* and *Auxis* sp. larvae (Pisces: Scombridae) in the Gulf of California. Bull Mar Sci 65:687-698

(52) Sanchez-Velasco L, Norbis W (1997) Comparative diets and feeding habits of *Boops boops* and *Diplodus sargus* larvae, two sparid fishes co-occurring in the northwestern Mediterranean (May 1992). Bull Mar Sci 61:821-835

(53) Sassa C, Kawaguchi K (2004) Larval feeding habits of *Diaphus garmani* and *Myctophum asperum* (Pisces: Myctophidae) in the transition region of the western North Pacific. Mar Ecol Prog Ser 278:279-290

(54) Schmitt PD (1986) Feeding by larvae of *Hypoatherina tropicalis* (Pisces: Atherinidae) and its relation to prey availability in One Tree Lagoon, Great Barrier Reef, Australia. Environ Biol Fish 16:79-94

(55) Shelbourne JE (1957) The feeding and condition of plaice larvae in good and bad plankton patches. J Mar Biol Ass U K 36:539-&

(56) Simonsen CS, Munk P, Folkvord A, Pedersen SA (2006) Feeding ecology of Greenland halibut and sandeel larvae off West Greenland. Mar Biol 149:937-952

(57) Sumida BY, Moser HG (1980) Food and feeding of Pacific hake larvae, *Merluccius productus*, off southern California and northern Baja California. California Cooperative Oceanic Fisheries Investigations Report 21:161-166

(58) Takatsu T, Nakatani T, Miyamoto T, Kooka K, Takahashi T (2002) Spatial distribution and feeding habits of Pacific cod (*Gadus macrocephalus*) larvae in Mutsu Bay, Japan. Fish Oceanogr 11:90-101

(59) Thompson AB, Harrop RT (1991) Feeding dynamics of fish larvae on Copepoda in the western Irish Sea, with particular reference to cod *Gadus morhua*. Mar Ecol Prog Ser 68:213-223

(60) Thorisson K (1989) The food of larvae and pelagic juveniles of cod (*Gadus morhua* L.) in the coastal waters west of Iceland. Rapp P-v Reun Cons int Explor Mer 191:264-272

(61) Uotani I, Ueyanagi S (1997) Feeding habits of Indo-Pacific blue marlin and shortbill spearfish larvae. Journal of the School of Marine Science and Technology, Tokai University 43:107-116

(62) Voss R, Koster FW, Dickmann M (2003) Comparing the feeding habits of co-occurring sprat (*Sprattus sprattus*) and cod (*Gadus morhua*) larvae in the Bornholm Basin, Baltic Sea. Fish Res 63:97-111

(63) Watson W, Davis RL (1989) Larval fish diets in shallow coastal waters off San Onofre, California. Fish Bull 87:569-591

(64) Young JW, Davis TLO (1990) Feeding ecology of larvae of southern bluefin, albacore and skipjack tunas (Pisces: Scombridae) in the eastern Indian Ocean. Mar Ecol Prog Ser 61:17-29

(65) Young JW, Davis TLO (1992) Feeding ecology and interannual variations in diet of larval jack mackerel, *Trachurus declivis* (Pisces: Carangidae), from coastal waters of eastern Tasmania. Mar Biol 113:11-20

LITERATURE CITED

Alexander JE, Corcoran EF (1963) Distribution of chlorophyll in the Straits of Florida. Limnol Oceanogr 8:294-297

Alexander JE, Steele JH, Corcoran EF (1961) The seasonal cycle of chlorophyll in the Florida Straits. Proceedings of the Gulf and Caribbean Fisheries Institute 14:63-67

Alldredge AL (1981) The impact of appendicularian grazing on natural food concentrations in situ. Limnol Oceanogr 26:247-257

Allison SK, Wishner KF (1986) Spatial and temporal patterns of zooplankton biomass across the Gulf Stream. Mar Ecol Prog Ser 31:233-244

Andersen NG (1998) The effect of meal size on gastric evacuation in whiting. J Fish Biol 52:743-755

Anderson JT (1988) A review of size dependent survival during pre-recruit stages of fishes in relation to recruitment. J Northwest Atl Fish Soc 8:55-66

Anderson JT (1994) Feeding ecology and condition of larval and pelagic juvenile redfish *Sebastes* spp. Mar Ecol Prog Ser 104:211-226

Bailey KM, Houde ED (1989) Predation on eggs and larvae of marine fishes and the recruitment problem. Adv Mar Biol 25:1-83

Bajkov AD (1935) How to estimate the daily food consumption of fish under natural conditions. Trans Am Fish Soc 65:288-289

Bakun A (1996) Patterns in the ocean: ocean processes and marine population dynamics. University of California Sea Grant, San Diego, in cooperation with Centro de Investigaciones Biológicas de Noroeste, La Paz, Baja California Sur, Mexico

Bakun A, Broad K (2003) Environmental 'loopholes' and fish population dynamics: comparative pattern recognition with focus on El Nino effects in the Pacific. Fish Oceanogr 12:458-473

Block BA, Dewar H, Blackwell SB, Williams TD, Prince ED, Farwell CJ, Boustany A, Teo SLH, Seitz A, Walli A, Fudge D (2001) Migratory movements, depth preferences, and thermal biology of Atlantic bluefin tuna. Science 293:1310-1314

Bochdansky AB, Deibel D (2001) Consequences of model specification for the determination of gut evacuation rates: redefining the linear model. Can J Fish Aquat Sci 58:1032-1042

Boxshall GA, Halsey SH (2004) An introduction to copepod diversity. The Ray Society, London

Brooks IH, Niiler PP (1977) Energetics of the Florida Current. J Mar Res 35:163-191

Bsharah L (1957) Plankton of the Florida Current V. Environmental conditions, standing crop, seasonal and diurnal changes at a station forty miles east of Miami. Bulletin of Marine Science of the Gulf and Caribbean 7:201-251

Buckley LJ, Lough RG (1987) Recent growth, biochemical composition, and prey field of larval haddock (*Melanogrammus aeglefinus*) and Atlantic cod (*Gadus morhua*) on Georges Bank. Can J Fish Aquat Sci 44:14-25

Canino MF, Bailey KM (1995) Gut evacuation of walleye pollock larvae in response to feeding conditions. J Fish Biol 46:389-403

Canino MF, Bailey KM, Incze LS (1991) Temporal and geographic differences in feeding and nutritional condition of walleye pollock larvae *Theragra chalcogramma* in Shelikof Strait, Gulf of Alaska. Mar Ecol Prog Ser 79:27-35

Chesson J (1978) Measuring preference in selective predation. Ecology 59:211-215

Chisholm LA, Roff JC (1990) Size-weight relationships and biomass of tropical neritic copepods off Kingston, Jamaica. Mar Biol 106:71-77

Collette BB, Potthoff T, Richards WJ, Ueyanagi S, Russo JL, Nishikawa Y (1984) Scombroidei: development and relationships. In: Moser HG (ed) Ontogeny and systematics of fishes, American Society of Ichthyologists and Herpetologists Special Publication No 1, p 591-620

Collette BB, Reeb C, Block BA (2001) Systematics of the tunas and mackerels (Scombridae). In: Block BA, Stevens ED (eds) Tuna: physiology, ecology and evolution. Academic Press, San Diego, p 1-33

Conley WJ, Hopkins TL (2004) Feeding ecology of lanternfish (Pisces: Myctophidae) larvae: prey preferences as a reflection of morphology. Bull Mar Sci 75:361-379

Conway DVP, Coombs SH, Lindley JA, Llewellyn CA (1999) Diet of mackerel (*Scomber scombrus*) larvae at the shelf-edge to the south-west of the British Isles and the incidence of piscivory and coprophagy. Vie Et Milieu-Life and Environment 49:213-220

Cowen RK (2002) Larval dispersal and retention and consequences for population connectivity. In: Sale PF (ed) Coral reef fishes: dynamics and diversity in a complex ecosystem. Academic Press, San Diego, p 149-170

Cowen RK, Paris CB, Srinivasan A (2006) Scaling of connectivity in marine populations. Science 311:522-527

Cowen RK, Sponaugle S (1997) Relationships between early life history traits and recruitment among coral reef fishes. In: Chambers RC, Trippel EA (eds) Early life history and recruitment in marine fish populations. Chapman & Hall, London, p 423-449

Csanady GT (1989) Energy dissipation and upwelling in a western boundary current. J Phys Oceanogr 19:462-473

Cushing DH (1975) Marine ecology and fisheries. Cambridge University Press, Cambridge

Cushing DH (1983) Are fish larvae too dilute to affect the density of their food organisms? J Plankton Res 5:847-854

Cushing DH (1990) Plankton production and year-class strength in fish populations: an update of the match/mismatch hypothesis. Adv Mar Biol 26:249-293

Dagg MJ, Govoni JJ (1996) Is ichthyoplankton predation an important source of copepod mortality in subtropical coastal waters? Mar Freshw Res 47:137-144

Dagg MJ, Ortner PB, Alyamani F (1988) Winter-time distribution and abundance of copepod nauplii in the northern Gulf of Mexico. Fish Bull 86:319-330

Deibel D, Lee SH (1992) Retention efficiency of sub-micrometer particles by the pharyngeal filter of the pelagic tunicate *Oikopleura vanhoeffeni*. Mar Ecol Prog Ser 81:25-30

den Boer PJ (1968) Spreading of risk and stabilization of animal numbers. Acta Biotheoretica 18:165-194

Economou AN (1991) Food and feeding ecology of five gadoid larvae in the northern North Sea. ICES J Mar Sci 47:339-351

Eggers DM (1979) Comment on some recent methods for estimating food consumption by fish. J Fish Res Board Can 36:1018-1019

Elgar MA (1990) Evolutionary compromise between a few large and many small eggs: comparative evidence in teleost fish. Oikos 59:283-287

Elliott JM, Persson L (1978) The estimation of daily rates of food consumption for fish. Journal of Animal Ecology 47:977-991

Fenaux R (1976) Cycle vital d'un appendiculaire: *Oikopleura dioca* Fol, 1872. Description et chronologie. Annales de l'Institut Oceanographique, Paris 52:89-107

Field JG, Clarke KR, Warwick RM (1982) A practical strategy for analyzing multispecies distribution patterns. Mar Ecol Prog Ser 8:37-52

Fortier L, Leggett WC (1983) Vertical migrations and transport of larval fish in a partially mixed estuary. Can J Fish Aquat Sci 40:1543-1555

Fortier L, Villeneuve A (1996) Cannibalism and predation on fish larvae by larvae of Atlantic mackerel, *Scomber scombrus*: trophodynamics and potential impact on recruitment. Fish Bull 94:268-281

Garrison LP, Link JS (2000) Diets of five hake species in the northeast United States continental shelf ecosystem. Mar Ecol Prog Ser 204:243-255

Gehringer JW (1956) Observations on the development of the Atlantic sailfish *Istiophorus americanus* (Cuvier) with notes on an unidentified species of istiophorid. Fish Bull 57:139-171

Gorbunova NN, Lipskaya NY (1975) Feeding of larvae of the blue marlin, *Makaira nigricans* (Pisces, Istiophoridae). J Ichthyol 15:109-116

Govoni JJ, Boehlert GW, Watanabe Y (1986a) The physiology of digestion in fish larvae. Environ Biol Fish 16:59-77

Govoni JJ, Hoss DE, Chester AJ (1983) Comparative feeding of three species of larval fishes in the Northern Gulf of Mexico: *Brevoortia patronus, Leiostomus xanthurus,* and *Micropogonias undulatus*. Mar Ecol Prog Ser 13:189-199

Govoni JJ, Laban EH, Hare JA (2003) The early life history of swordfish (*Xiphias gladius*) in the western North Atlantic. Fish Bull 101:778-789

Govoni JJ, Ortner PB, Alyamani F, Hill LC (1986b) Selective feeding of spot, *Leiostomus xanthurus*, and Atlantic croaker, *Micropogonias undulatus*, larvae in the northern Gulf of Mexico. Mar Ecol Prog Ser 28:175-183

Guigand CM, Cowen RK, Llopiz JK, Richardson DE (2005) A coupled asymmetrical multiple opening closing net with environmental sampling system. Mar Technol Soc J 39:22-24

Hare JA, Cowen RK (1991) Expatriation of *Xyrichtys novacula* (Pisces, Labridae) larvae: evidence of rapid cross-slope exchange. J Mar Res 49:801-823

Hay DE (1981) Effects of capture and fixation on gut content and body size of Pacific herring larvae. Rapp Cons int Explor Mer 178:395-400

Heath MR, Lough RG (2007) A synthesis of large-scale patterns in the planktonic prey of larval and juvenile cod (*Gadus morhua*). Fish Oceanogr 16:169-185

Herman SS, Beers JR (1969) Ecology of inshore plankton populations in Bermuda. Part II. Seasonal abundance and composition of zooplankton. Bull Mar Sci 19:483-503

Hillebrand H (2004) Strength, slope and variability of marine latitudinal gradients. Mar Ecol Prog Ser 273:251-267

Hillgruber N, Haldorson LJ, Paul AJ (1995) Feeding selectivity of larval walleye pollock *Theragra chalcogramma* in the oceanic domain of the Bering Sea. Mar Ecol Prog Ser 120:1-10

Hillgruber N, Kloppmann M (2001) Small-scale patterns in distribution and feeding of Atlantic mackerel (*Scomber scombrus* L.) larvae in the Celtic Sea with special regard to intra-cohort cannibalism. Helgoland Marine Research 55:135-149

Hitchcock GL, Langdon C, Smayda TJ (1987) Short-Term Changes in the Biology of a Gulf-Stream Warm-Core Ring - Phytoplankton Biomass and Productivity. Limnol Oceanogr 32:919-928

Hjort J (1914) Fluctuations in the great fisheries of northern Europe viewed in the light of biological research. Rapp P-v Reun Cons int Explor Mer 20:1-228

Hopcroft RR, Roff JC (1995) Zooplankton growth rates: extraordinary production by the larvacean *Oikopleura dioica* in tropical waters. J Plankton Res 17:205-220

Houde E (1987) Fish early life dynamics and recruitment variability. In: Hoyt RD (ed) American Fisheries Society Symposium 2. American Fisheries Society, Bethesda, MD, p 17-29

Houde ED (1978) Critical food concentrations for larvae of three species of subtropical marine fishes. Bull Mar Sci 28:395-411

Houde ED (1989) Comparative growth, mortality, and energetics of marine fish larvae: temperature and implied latitudinal effects. Fish Bull 87:471-495

Houde ED, Lovdal JA (1984) Seasonality of occurrence, foods and food preferences of ichthyoplankton in Biscayne Bay, Florida. Estuarine Coastal and Shelf Science 18:403-419

Houde ED, Schekter RC (1981) Growth rates, rations and cohort consumption of marine fish larvae in relation to prey concentrations. Rapp P-v Reun Cons int Explor Mer 178:441-453

Houghton RW (1991) The relationship of sea surface temperature to thermocline depth at annual and interannual time scales in the tropical Atlantic Ocean. Journal of Geophysical Research 96:15173-15185

Hughes TP, Baird AH, Bellwood DR, Card M, Connolly SR, Folke C, Grosberg R, Hoegh-Guldberg O, Jackson JBC, Kleypas J, Lough JM, Marshall P, Nystrom M, Palumbi SR, Pandolfi JM, Rosen B, Roughgarden J (2003) Climate change, human impacts, and the resilience of coral reefs. Science 301:929-933

Hunter JR (1981) Feeding ecology and predation in marine fish larvae. In: Lasker R (ed) Marine Fish Larvae. Washington Sea Grant Program, Seattle, p 33-77

Iles TD, Sinclair M (1982) Atlantic herring: stock discreteness and abundance. Science 215:627-633

Incze LS, Ainaire T (1994) Distribution and abundance of copepod nauplii and other small (40-300 µm) zooplankton during spring in Shelikof Strait, Alaska. Fish Bull 92:67-78

Jaworski A, Ragnarsson SA (2006) Feeding habits of demersal fish in Icelandic waters: a multivariate approach. ICES J Mar Sci 63:1682-1694

Jenkins GP, Milward NE, Hartwick RF (1984) Food of larvae of Spanish mackerels, genus *Scomberomorus* (Teleostei, Scombridae), in shelf waters of the Great Barrier Reef. Aust J Mar Freshw Res 35:477-482

Jenkins GP, Young JW, Davis TLO (1991) Density dependence of larval growth of a marine fish, the southern bluefin tuna, *Thunnus maccoyii*. Can J Fish Aquat Sci 48:1358-1363

Jennings S, Kaiser MJ, Reynolds JD (2001) Marine Fisheries Ecology. Blackwell Science, Oxford

Jobling M (1981) Mathematical models of gastric emptying and the estimation of daily rates of food consumption for fish. J Fish Biol 19:245-257

Johannes RE (1978) Reproductive strategies of coastal marine fishes in the tropics. Environ Biol Fish 3:65-84

Johns WE, Schott F (1987) Meandering and transport variations of the Florida Current. J Phys Oceanogr 17:1128-1147

Kessler WS (1990) Observations of long Rossby waves in the northern tropical Pacific. Journal of Geophysical Research 95:5183-5217

King KR, Hollibaugh JT, Azam F (1980) Predator-prey interactions between the larvacean *Oikopleura dioica* and bacterioplankton in enclosed water columns. Mar Biol 56:49-57

Landry MR (2002) Integrating classical and microbial food web concepts: evolving views from the open-ocean tropical Pacific. Hydrobiologia 480:29-39

Landry MR, Calbet A (2004) Microzooplankton production in the oceans. ICES J Mar Sci 61:501-507

Lane PVZ, Smith SL, Graber HC, Hitchcock GL (2003) Mesoscale circulation and the surface distribution of copepods near the south Florida Keys. Bull Mar Sci 72:1-18

Last JM (1978) The food of four species of pleuronectiform larvae in the eastern English Channel and southern North Sea. Mar Biol 45:359-368

Leaman KD, Johns E, Rossby T (1989) The average distribution of volume transport and potential vorticity with temperature at three sections across the Gulf Stream. J Phys Oceanogr 19:36-51

Leaman KD, Molinari RL, Vertes PS (1987) Structure and variability of the Florida Current at 27°N: April 1982–July 1984. J Phys Oceanogr 17:565-583

Lechowicz MJ (1982) The sampling characteristics of electivity indices. Oecologia 52:22-32

Lee TN, Yoder JA, Atkinson LP (1991) Gulf Stream frontal eddy influence on productivity of the Southeast United States continental shelf. Journal of Geophysical Research 96:22191-22205

Legendre P, Legendre L (1998) Numerical Ecology. Elsevier, Amsterdam

Leis JM, Carson-Ewart BM (eds) (2000) The larvae of Indo-Pacific coastal fishes: an identification guide to marine fish larvae, Brill, Leiden

Leis JM, Carson-Ewart BM (2003) Orientation of pelagic larvae of coral-reef fishes in the ocean. Mar Ecol Prog Ser 252:239-253

Lewis OT, Memmott J, Lasalle J, Lyal CHC, Whitefoord C, Godfray HCJ (2002) Structure of a diverse tropical forest insect-parasitoid community. Journal of Animal Ecology 71:855-873

Lipskaya NY, Gorbunova NN (1977) Feeding of sailfish larvae. Oceanology 17:517-523

Llopiz JK, Cowen RK (2008) Precocious, selective and successful feeding of larval billfishes in the oceanic Straits of Florida. Mar Ecol Prog Ser 358:231-244

Lo E (2005) Gaussian error propagation applied to ecological data: Post-ice-storm-downed woody biomass. Ecol Monogr 75:451-466

Longhurst AR, Pauly D (1987) Ecology of tropical oceans. Academic Press, San Diego

Lough RG, Broughton EA (2007) Development of micro-scale frequency distributions of plankton for inclusion in foraging models of larval fish, results from a Video Plankton Recorder. J Plankton Res 29:7-17

Luthy SA, Cowen RK, Serafy JE, McDowell JR (2005a) Toward identification of larval sailfish (*Istiophorus platypterus*), white marlin (*Tetrapturus albidus*), and blue marlin (*Makaira nigricans*) in the western North Atlantic Ocean. Fish Bull 103:588-600

Luthy SA, Serafy JE, Cowen RK, Denit KL, Sponaugle S (2005b) Age and growth of larval Atlantic sailfish, *Istiophorus platypterus*. Mar Freshw Res 56:1027-1035

Manly BFJ, McDonald LL, Thomas DL, McDonald TL, Erickson WP (2002) Resource selection by animals: statistical design and analysis for field studies, 2nd edn. Kluwer Academic Publishers, Dordrecht

Marañon E, Behrenfeld MJ, González N, Mouriño B, Zubkov MV (2003) High variability of primary production in oligotrophic waters of the Atlantic Ocean: uncoupling from phytoplankton biomass and size structure. Mar Ecol Prog Ser 257:1-11

Margulies D (1993) Assessment of the nutritional condition of larval and early juvenile tuna and Spanish mackerel (Pisces, Scombridae) in the Panama Bight. Mar Biol 115:317-330

McGowan JA, Walker PW (1979) Structure in the copepod community of the North Pacific central gyre. Ecol Monogr 49:195-226

Molinari RL, Wilson WD, Leaman K (1985) Volume and heat transports of the Florida Current: April 1982 through August 1983. Science 227:295-297

Moore E, Sander F (1977) A study of the offshore zooplankton of the tropical western atlantic near Barbados. Ophelia 16:77-96

Morote E, Olivarl MP, Pankhurst PM, Villate F, Uriarte M (2008) Trophic ecology of bullet tuna *Auxis rochei* larvae and ontogeny of feeding-related organs. Mar Ecol Prog Ser 353:243-254

Mullin MM, Onbe T (1992) Diel reproduction and vertical distributions of the marine cladocerans, *Evadne tergestina* and *Penilia avirostris*, in contrasting coastal environments. J Plankton Res 14:41-59

Munk P, Kiorboe T (1985) Feeding behavior and swimming activity of larval herring (*Clupea harengus*) in relation to density of copepod nauplii. Mar Ecol Prog Ser 24:15-21

Nakata K (1990) Abundance of nauplii and protein synthesis activity of adult female copepods in the Kuroshio front during the Japanese sardine spawning season. J Oceanogr Soc Japan 46:219-229

Neter J, Kutner MH, Nachtsheim CJ, Wassermann W (1996) Applied linear statistical models. McGraw-Hill, Boston

Nielsen TG, Richardson K (1989) Food chain structure of the North Sea plankton communities: seasonal variations of the role of the microbial loop. Mar Ecol Prog Ser 56:75-87

Novales Flamarique I, Browman HI (2001) Foraging and prey-search behaviour of small juvenile rainbow trout (*Oncorhynchus mykiss*) under polarized light. J Exp Biol 204:2415-2422

Olson DB (2001) Biophysical dynamics of western transition zones: a preliminary synthesis. Fish Oceanogr 10:133-150

Ostergaard P, Munk P, Janekarn V (2005) Contrasting feeding patterns among species of fish larvae from the tropical Andaman Sea. Mar Biol 146:595-606

Paffenhofer GA, Mazzocchi MG (2003) Vertical distribution of subtropical epiplanktonic copepods. J Plankton Res 25:1139-1156

Pandolfi JM, Bradbury RH, Sala E, Hughes TP, Bjorndal KA, Cooke RG, McArdle D, McClenachan L, Newman MJH, Paredes G, Warner RR, Jackson JBC (2003) Global trajectories of the long-term decline of coral reef ecosystems. Science 301:955-958

Paris CB, Cherubin LM, Cowen RK (2007) Surfing, spinning, or diving from reef to reef: effects on population connectivity. Mar Ecol Prog Ser 347:285-300

Pearre S (1986) Ratio-based trophic niche breadths of fish, the Sheldon spectrum, and the size-efficiency hypothesis. Mar Ecol Prog Ser 27:299-314

Pennington M (1985) Estimating the average food consumption by fish in the field from stomach contents data. Dana 5:81-86

Pepin P (1991) Effect of temperature and size on development, mortality, and survival rates of the pelagic early life-history stages of marine fish. Can J Fish Aquat Sci 48:503-518

Pepin P, Dower JE (2007) Variability in the trophic position of larval fish in a coastal pelagic ecosystem based on stable isotope analysis. J Plankton Res 29:727-737

Pepin P, Pearre S, Koslow JA (1987) Predation on larval fish by Atlantic mackerel, *Scomber scombrus*, with a comparison of predation by zooplankton. Can J Fish Aquat Sci 44:2012-2018

Pepin P, Penney R (2000) Feeding by a larval fish community: impact on zooplankton. Mar Ecol Prog Ser 204:199-212

Pepin P, Penney RW (1997) Patterns of prey size and taxonomic composition in larval fish: are there general size-dependent models? J Fish Biol 51:84-100

Persson L (1986) Patterns of food evacuation in fishes: a critical review. Environ Biol Fish 16:51-58

Post JT, Serafy JE, Ault JS, Capo TR, deSylva DP (1997) Field and laboratory observations on larval Atlantic sailfish (*Istiophorus platypterus*) and swordfish (*Xiphias gladius*). Bull Mar Sci 60:1026-1034

Postel L, Fock H, Hagen W (2000) Biomass and abundance. In: Harris RP, Wiebe PH, Lenz J, Skjoldal HR, Huntley M (eds) ICES zooplankton methodology manual. Academic Press, San Diego, p 83-192

Prince ED, Cowen RK, Orbesen ES, Luthy SA, Llopiz JK, Richardson DE, Serafy JE (2005) Movements and spawning of white marlin (*Tetrapturus albidus*) and blue marlin (*Makaira nigricans*) off Punta Cana, Dominican Republic. Fish Bull 103:659-669

Purcell JE, Sturdevant MV, Galt CP (2005) A review of appendicularians as prey of invertebrate and fish predators. In: Gorsky G, Youngbluth MJ, Deibel D (eds) Response of marine ecosystems to global change: ecological impacts of appendicularians. Contemporary Publishing International, Paris, p 359-435

Puvanendran V, Brown JA (1999) Foraging, growth and survival of Atlantic cod larvae reared in different prey concentrations. Aquaculture 175:77-92

Raymont JEG (1983) Plankton and productivity in the oceans. Pergamon Press, Oxford

Remsen A, Hopkins TL, Samson S (2004) What you see is not what you catch: a comparison of concurrently collected net, Optical Plankton Counter, and Shadowed Image Particle Profiling Evaluation Recorder data from the northeast Gulf of Mexico. Deep-Sea Research Part I 51:129-151

Richards WJ (ed) (2005) Guide to the early life history stages of fishes of the western central North Atlantic, Vol. CRC Press, Miami

Richards WJ, Leming T, McGowan MF, Lamkin JT, Kelley-Fraga S (1989) Distribution of fish larvae in relation to hydrographic features of the Loop Current boundary in the Gulf of Mexico. Rapp P-v Reun Cons int Explor Mer 191:169-176

Richardson DE, VanWye JD, Exum AM, Cowen RK, Crawford DL (2007) High-throughput species identification: from DNA isolation to bioinformatics. Mol Ecol Notes 7:199-207

Robertson DR (1991) The role of adult biology in the timing of spawning of tropical reef fishes. In: Sale PF (ed) The ecology of fishes on coral reefs. Academic Press Inc, San Diego, p 356-386

Röpke A (1993) Do larvae of mesopelagic fishes in the Arabian Sea adjust their vertical distribution to physical and biological gradients? Mar Ecol Prog Ser 101:223-235

Runge JA, DeLafontaine Y (1996) Characterization of the pelagic ecosystem in surface waters of the northern Gulf of St. Lawrence in early summer: the larval redfish-*Calanus*-microplankton interaction. Fish Oceanogr 5:21-37

Sabates A, Saiz E (2000) Intra- and interspecific variability in prey size and niche breadth of myctophiform fish larvae. Mar Ecol Prog Ser 201:261-271

Sampey A, McKinnon AD, Meekan MG, McCormick MI (2007) Glimpse into guts: overview of the feeding of larvae of tropical shorefishes. Mar Ecol Prog Ser 339:243-257

Sanchez-Velasco L, Contreras-Arredondo I, Esqueda-Escarcega G (1999) Diet composition of *Euthynnus lineatus* and *Auxis* sp. larvae (Pisces: Scombridae) in the Gulf of California. Bull Mar Sci 65:687-698

SAS Institute Inc. (1999) SAS/STAT User's Guide, Version 8. SAS Institute Inc., Cary, NC

Schekter RC (1971) Food habits of some larval and juvenile fishes from the Florida Current near Miami, Florida. M.Sc., University of Miami

Schmitt PD (1986) Feeding by larvae of *Hypoatherina tropicalis* (Pisces: Atherinidae) and its relation to prey availability in One Tree Lagoon, Great Barrier Reef, Australia. Environ Biol Fish 16:79-94

Shelbourne JE (1957) The feeding and condition of plaice larvae in good and bad plankton patches. J Mar Biol Ass U K 36:539-&

Shoji J, Kishida T, Tanaka M (1997) Piscivorous habits of Spanish mackerel larvae in the Seto Inland Sea. Fish Sci 63:388-392

Shoji J, Maehara T, Aoyama M, Fujimoto H, Iwamoto A, Tanaka M (2001) Daily ration of Japanese Spanish mackerel *Scomberomorus niphonius* larvae. Fish Sci 67:238-245

Shoji J, Tanaka M (2006) Growth-selective survival in piscivorous larvae of Japanese Spanish mackerel *Scomberomorus niphonius*: early selection and significance of ichthyoplankton prey supply. Mar Ecol Prog Ser 321:245-254

Sponaugle S, Denit KL, Luthy SA, Serafy JE, Cowen RK (2005) Growth variation in larval *Makaira nigricans*. J Fish Biol 66:822-835

Stephens DW, Krebs JR (1986) Foraging theory. Princeton University Press, Princeton

Systat Software Inc. (2004) SYSTAT for windows, version 11, Richmond, CA

Tanaka M, Kaji T, Nakamura Y, Takahashi M (1996) Developmental strategy of scombrid larvae: high growth potential related to food habits and precocious digestive system development. In: Watanabe Y, Yamashitsa Y, Oozeki Y (eds) Survival strategies in early life stages of marine resources. A.A. Balkema, Rotterdam, p 125-139

ter Braak CJF (1986) Canonical correspondence analysis: a new eigenvector technique for multivariate direct gradient analysis. Ecology 67:1167-1179

ter Braak CJF, Simlauer P (2002) Canoco for Windows, version 4.5. Center for Biometry, Wageningin, The Netherlands, and Microcomputer Power, Ithaca, New York, USA

ter Braak CJF, Verdonschot PFM (1995) Canonical correspondence analysis and related multivariate methods in aquatic ecology. Aquat Sci 57:255-289

Troedsson C, Bouquet JM, Aksnes DL, Thompson EM (2002) Resource allocation between somatic growth and reproductive output in the pelagic chordate *Oikopleura dioica* allows opportunistic response to nutritional variation. Mar Ecol Prog Ser 243:83-91

Turner JT (2004) The importance of small planktonic copepods and their roles in pelagic marine food webs. Zool Stud 43:255-266

Uotani I, Ueyanagi S (1997) Feeding habits of Indo-Pacific blue marlin and shortbill spearfish larvae. Journal of the School of Marine Science and Technology, Tokai University 43:107-116

van der Spoel S, Pierrot-Bults AC (eds) (1979) Zoogeography and diversity of plankton, Vol. Bunge Scientific Publishers, Utrecht

Vargo G (1968) Studies of phytoplankton ecology in tropical and subtropical environments of the atlantic ocean. Part 2. Quantitative studies of phytoplankton distribution in the Straits of Florida and its relation to physical factors. Bull Mar Sci 18:5-60

Venrick EL (1990) Phytoplankton in an oligotrophic ocean: species structure and interannual variability. Ecology 71:1547-1563

Voss GL (1953) A contribution to the life history and biology of the sailfish, *Istiophorus americanus* Cuv. and Val., in Florida Waters. Bulletin of Marine Science of the Gulf and Caribbean 3:206-240

Wang J, Mooers CNK (1998) Three-dimensional perspectives of the Florida Current: transport, potential vorticity, and related dynamical properties. Dyn Atmos Oceans 27:135-149

Webber MK, Roff JC (1995) Annual structure of the copepod community and its associated pelagic environment off Discovery Bay, Jamaica. Mar Biol 123:467-479

Whelan CJ, Brown JS (2005) Optimal foraging and gut constraints: reconciling two schools of thought. Oikos 110:481-496

Wiebe PH, Morton AW, Bradley AM, Backus RH, Craddock JE, Barber V, Cowles TJ, Flierl GR (1985) New developments in the MOCNESS, an apparatus for sampling zooplankton and micronekton. Mar Biol 87:313-323

Winemiller KO, Rose KA (1993) Why do most fish produce so many tiny offspring? Am Nat 142:585-603

Woodward G, Ebenman B, Emmerson M, Montoya JM, Olesen JM, Valido A, Warren PH (2005) Body size in ecological networks. Trends Ecol Evol 20:402-409

Wuenschel MJ, Werner RG (2004) Consumption and gut evacuation rate of laboratory-reared spotted seatrout (Sciaenidae) larvae and juveniles. J Fish Biol 65:723-743

Young JW, Davis TLO (1990) Feeding ecology of larvae of southern bluefin, albacore and skipjack tunas (Pisces: Scombridae) in the eastern Indian Ocean. Mar Ecol Prog Ser 61:17-29