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A global comparative analysis of the feeding dynamics and environmental conditions of larval tunas, mackerels, and billfishes

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ABSTRACT

Scombroid fishes, including tunas, mackerels, and billfishes, constitute some of the most important fisheries in lower latitudes around the world. Though the early life stages of these taxa are relatively well-studied, worldwide patterns in larval feeding dynamics and how such patterns relate to environmental conditions are poorly resolved. We present a synthesis of feeding success (i.e. feeding incidences) and diets of larval scombroids from around the world, and relate these results to water column and sea surface properties for the several regions in which larval feeding studies have been conducted. Feeding success of larval tunas was shown to be distinctly different among regions. In some locations (the Straits of Florida and the Mediterranean Sea), nearly no larvae had empty guts, whereas in other locations (the Gulf of California and off NW Australia) ~40–60% of larvae were empty. Diets were consistently narrow in each region (dominated by cyclopoid copepods, appendicularians, nauplii, and other fish larvae), and were usually, but not always, similar for a given scombroid taxon among regions (though diets differed among taxa). Larval habitat conditions were often similar among the 9 regions examined, but some clear differences included low levels of eddy kinetic energy and cooler waters (at the surface and at depth) in the Mediterranean, and lower chlorophyll concentrations around the Nansei Islands, Japan and off NW Australia where feeding success was low. When observed zooplankton abundances are also taken into account, the compiled results on feeding and environmental conditions indicate a bottom-up influence on feeding success. Moreover, the variability among regions highlights the potential for region-specific mechanisms regulating larval survival and, ultimately, levels of adult recruitment.

1. Introduction

Among the most important commercial and recreational fisheries in tropical and subtropical waters are the tunas, mackerels, and billfishes of the suborder Scombroidei (Juan-Jordá et al., 2011; Majkowski, 2007; Sibert et al., 2006). Given their economic and cultural significance, these taxa are well-studied when compared to other fishes in low-latitude oceanic and shelf waters, and early life history research makes up a substantial proportion of the work in this field. Scientists' and managers' interest in understanding the biology and ecology of the larval stages of scombroids stems from the large influence that larval survival can have on adult recruitment levels (Houde, 1987). Of the many studies on scombroid larvae, several (especially those investigating the tunas) have focused on diets and feeding success (e.g. Catalán et al., 2011; Llopiz et al., 2010; Morote et al., 2008; Young and Davis, 1990). This is unsurprising considering the importance of feeding success, not only in determining levels of starvation mortality (Margulies, 1993; Tanaka et al., 2008), but also in regulating predation mortality via growth-rate and size-at-age influences (e.g. Anderson, 1988; Cushing, 1975; Houde, 1987; Leggett and Deblois, 1994; Ware, 1975) as well as the interaction of feeding and condition with predator-avoidance capabilities (Fuiman and Magurran, 1994; Takasuka et al., 2003).

Some common themes are evident in the feeding studies on scombroid early life stages. In general, tuna and billfish larvae have very narrow diets and, when compared to available zooplankton prey, are highly selective in their feeding habits (Catalán et al., 2011; Llopiz and Cowen, 2008; Young and Davis, 1990). These larvae frequently rely heavily upon appendicularians (Jenkins et al., 1984; Llopiz et al., 2010; Young and Davis, 1990), cladocerans (Catalán et al., 2011; Llopiz and Cowen, 2008; Morote et al., 2008; Uotani et al., 1981), and cyclopoid copepods in the genera *Farranula* and *Corycaeus* (Govoni et al., 2003; Llopiz and Cowen, 2008; Uotani and Ueyanagi, 1997; Young and Davis, 1990), while rarely consuming calanoid copepods. Additionally, of the scombroid taxa examined, nearly all have been observed to be piscivorous during the larval stage (i.e. they consume other fish larvae), with *Scomberomorus* often displaying piscivory at first-feeding

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(Finucane et al., 1990; Shoji and Tanaka, 2001). A piscivorous feeding behavior is likely necessary for larvae to fuel their rapid growth rates and high metabolic demands in the warm waters in which they occur (Govoni et al., 2003; Sponaugle et al., 2010; Tanaka et al., 1996).

Feeding success of scombroid larvae, as indicated by the proportions of larvae examined with empty guts, appears to be variable among taxa and regions, ranging from nearly all larvae containing food (e.g. in the Straits of Florida; Llopiz et al., 2010; Llopiz and Cowen, 2008) to only 40–50% of daytime-collected larvae showing evidence of feeding (e.g. in the waters off NW Australia; Young and Davis, 1990). However, our understanding of the potential environmental factors that might contribute to regional differences in larval feeding success and diets is rather limited. While several studies have examined the environmental conditions of larval tuna habitat, most of the work in this vein has investigated Atlantic bluefin tuna and co-occurring species in the Mediterranean (Alemany et al., 2010; Druon et al., 2011; García et al., 2005, 2003, 2013; Kocheda et al., 2013), and, to a lesser degree, the Gulf of Mexico (Muhling et al., 2010; Teo et al., 2007). Of late, two studies have taken a comparative approach to thoroughly illustrating distinctions among spawning habitats of Atlantic bluefin tuna (Muhling et al., 2013) and all 3 bluefin tuna species that occur in different regions of the world (MacKenzie and Mariani, 2012). These works found clear regional differences and similarities, but were limited in either the number of regions examined or in the number of parameters examined, especially those most relevant to larval feeding.

Considering that scombroid genera (and often species) are widely distributed around the world, the evolution of the same or closely related species utilizing spawning habitats in distinctly different geographical regions offers an opportunity to compare how environmental conditions vary among locations used for spawning and larval development, and to investigate how larval feeding dynamics might relate to regional environmental conditions. A comparison of larval feeding dynamics and larval feeding habitat may elucidate taxon-, region-, and stage-specific processes and conditions that are critical to the survival of the early stages of these important species.

Our goals for the present work are twofold, and in line with those of the Climate Impacts on Oceanic Top Predators (CLIOTOP) program of taking a comparative approach to better understanding the structure and function of open ocean ecosystems (Lehodey and Maury, 2010). First, we present a synthesis of published results on the feeding dynamics of larval scombroids, specifically larval tunas (tribe Thunnini), Spanish mackerels, istiophorid billfishes, and swordfish occurring worldwide. Second, we complement the synthesis on larval feeding success and diets with a characterization of the environments (i.e. water column structure and sea surface properties) in which most larval scombroid research has been conducted, thereby elucidating any relationships between environmental factors and observed patterns in feeding success or prey consumption. Since the published investigations on larval scombroid feeding success and diets compose a small sample size and often (but not always) occurred over short durations, our goal in highlighting environmental differences among spawning and larval nursery areas is not to formally test for causative factors determining feeding differences, but to highlight potential environmental influences that could lead to future hypotheses and facilitate research that will better elucidate environmental influences on larval scombroid feeding and survival.

2. Methods

2.1. Literature synthesis

Peer-reviewed, published results on diets and feeding success of field-collected larval scombroids were gathered by thoroughly searching the Aquatic Sciences and Fisheries Abstracts database and Google Scholar using several search terms related to feeding (e.g. 'food', 'feeding', 'diets'), the larval stage ('larva*'), and scombroid taxa (e.g. 'tuna', 'scombrid*', specific genera, etc.). Additionally, we cross-referenced all references within the publications discovered to find papers not emerging from the database searches. In total, 15 journal articles reported unique data for one or more scombroid taxa. Since articles often reported on more than one taxon, the total number of article-taxon combinations, or 'investigations', was 32. Each study was assigned to a region to facilitate comparisons of the larval environment.

Four types of feeding-related results from the synthesized investigations were of interest (though not all investigations provided each type of result): (1) daytime feeding incidence (the percentages of examined larvae with food observed in the gut, and restricted to daylight hours since scombroid larvae, similar to other taxa of fish larvae, do not feed at night (Llopiz and Cowen, 2008; Llopiz et al., 2010; Young and Davis, 1990)), (2) quantitative diet composition, (3) the results of prey selectivity analyses for the dominant prey types, and (4) the length at which larvae began an ontogenetic diet shift to piscivory. While the length-frequency distributions of the samples of larvae, as well as possible spatial- and temporal-related factors, could influence these three types of results for a particular investigation (Llopiz, 2013), we take a largely qualitative approach to making comparisons, noting clear instances where feeding differed among regions and scombroid taxa, which can then be viewed in light of environmental differences observed in the regions studied. Other types of analyses often performed in larval fish feeding studies, such as examining trophic niche breadth with growth, were not included in enough studies or regions to make meaningful comparisons.

Though we synthesize feeding results for all scombroid taxa examined in the peer-reviewed literature, the majority of studies focus on the tunas, specifically the genera *Thunnus* (oceanic tunas), *Auxis* (bullet and frigate tunas), and *Euthynnus* (here including little tunny and black skipjack), and the species *Katsuwonus pelamis* (skipjack). As such, comparisons of feeding ecologies are largely limited to the tunas. Moreover, due to the broader spatial extent of tuna studies, larval habitat comparisons (described below) primarily consider regions from which larval tunas were examined (although other species of larval scombroids may be found in those same regions). However, there were several studies that examined *Scomberomorus* mackerels, and, when possible, characteristics of their larval habitats were examined as well (providing an interesting contrast since they are found in nearshore habitats yet have similar morphologies and, possibly, energy requirements when compared to the tunas).

2.2. Environmental analyses

Characterization of larval habitats was undertaken by analyzing hydrographic data for water column and sea surface properties from the general regions where larval scombroid feeding dynamics have been examined (Fig. 1 and Table 2). The few studies on billfish larvae (both swordfish and istiophorids) were either in the same region as a scombrid study (e.g. the Straits of Florida) or over such vast areas (e.g. two entire ocean basins) that characterizing the habitat for these studies would have been uninformative. Thus, habitat comparisons, which are based on the locations of the feeding investigations, are essentially for larval scombrids (tunas and mackerels). We also included one region—the open waters of Gulf of Mexico—where the feeding patterns of Atlantic bluefin tuna larvae have yet to be described (but are currently under investigation). Environmental data were extracted for the seasonal time periods during which larvae occurred, and monthly climatologies were also constructed for sea surface properties to allow insight into the conditions during the spawning and larval period.

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