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FEEDING DYNAMICS OF ATLANTIC BLUEFIN TUNA (*THUNNUS THYNNUS*) LARVAE IN THE GULF OF MEXICO

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SUMMARY

A surprising gap in our knowledge of the early life history of Atlantic bluefin tuna larvae spawned in the Gulf of Mexico has been an understanding of their feeding success and diets. Here we report preliminary results on the feeding habits and feeding success of bluefin larvae collected during two years in the Gulf of Mexico. Daytime feeding incidence (the proportion of larvae with prey in their guts), which can be used to indicate the degree to which larvae are feeding successfully, was 94% overall and 100% for larvae >4 mm in length. Diets shifted from copepod nauplii at the earliest stages to a mixture of prey types that predominantly consisted of calanoid copepods, cladocerans, and appendicularians—the last of these having never been observed in the diets of other bluefin species or those of Mediterranean-spawned Atlantic bluefin larvae. Piscivory (consuming other fish larvae) began at lengths ~6 mm and was observed in 71% of larvae 8–10 mm in length. Such a small size at onset of piscivory, as well as high incidence of piscivory, greatly contrasts with bluefin larvae in the Mediterranean where piscivory has not yet been observed.

RÉSUMÉ

Une lacune étonnante dans nos connaissances du début du cycle vital des larves de thon rouge de l'Atlantique frayées dans le golfe du Mexique portait sur la compréhension de leur capacité à se nourrir et leur régime alimentaire. Le présent rapport contient les résultats préliminaires des habitudes trophiques et de la capacité à se nourrir des larves de thon rouge recueillies pendant deux ans dans le golfe du Mexique. Le taux d'alimentation diurne (la proportion de larves présentant des proies dans leurs entrailles), qui peut être utilisé pour refléter le degré dans lequel les larves sont capables de se nourrir, s'élevait à 94% de manière générale et à 100% pour les larves >4 mm de longueur. Le régime alimentaire passe des nauplius de copépodes, dans les premières phases, à un mélange d'espèces proies constituées principalement de copépodes calanoïdes, cladocères et appendiculaires, ces derniers n'ayant jamais été observés dans les régimes d'autres espèces de thon rouge ou dans ceux des larves de thon rouge de l'Atlantique frayées en Méditerranée. Le comportement piscivore (consommation d'autres larves de poisson) commence chez les larves mesurant environ 6 mm et a été observé dans le cas de 71% des larves de 8 à 10 mm de longueur. Une taille si petite à laquelle le comportement piscivore a commencé, ainsi qu'une incidence élevée de ce comportement, diffère grandement de celui des larves de thon rouge de la Méditerranée où ce comportement piscivore n'a pas encore été observé.

RESUMEN

Una sorprendente laguna en nuestros conocimientos de la primera etapa del ciclo vital de las larvas de atún rojo del Atlántico desovadas en el golfo de México ha sido la comprensión de su capacidad de alimentarse y su dieta. En este documento se presentan los primeros resultados sobre los hábitos alimentarios y la capacidad de alimentarse de las larvas de atún rojo recopiladas durante dos años en el golfo de México. La incidencia de la alimentación diurna (la proporción de larvas con presas en los intestinos), que podría usarse para indicar a qué nivel se están alimentando las larvas con éxito, era del 94% en total y del 100% en larvas de más de 4 mm de talla. Las dietas cambiaban de copépodos nauplii en las primeras etapas a una mezcla de tipos de presas que consistía fundamentalmente en copépodos calanoides, cladóceros y apendicularios, que no se habían observado nunca en las dietas otras especies de

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atún rojo o en las de larvas de atún rojo del Atlántico nacidas en el Mediterráneo. La conducta piscívora (consumo de otras larvas de peces) empieza en tallas de ~6 mm y se observó en el 71% de las larvas de 8-10 mm de talla. Una talla tan pequeña al inicio de la conducta piscívora, al igual que la elevada incidencia de esta conducta piscívora, contrasta enormemente con las larvas de atún rojo en el Mediterráneo, donde no se ha observado aún esta conducta piscívora.

KEYWORDS

Fish larvae, Feeding behavior, Zooplankton, Stomach content, Piscivory, Diet, Fisheries oceanography, Atlantic bluefin tuna, Thunnus thynnus

1. Introduction

Scientists and managers have long recognized the importance in studying the factors governing larval fish survival in order to fully understand why fishery species can exhibit large interannual fluctuations in recruitment (Hjort 1914, Houde 1987, 2008). There are three main sources of larval fish mortality-starvation, predation, and transport to unsuitable juvenile habitat—but there can be substantial interactions among these mechanisms. Poor feeding success, for example, can reduce predator-evasion capabilities, as well as extend the length of the larval stage, prolonging the period of time over which individuals are especially vulnerable to predation (Cushing 1975, Houde 1987, Anderson 1988, Hare & Cowen 1997).

Because of the complexity of the relationship between feeding-related processes and larval survival, an extensive amount of research has been devoted to understanding the diets and feeding success of several species of larval tunas around the world (Llopiz & Hobday 2014). This work includes all three species of bluefin tunas, but, surprisingly, only Atlantic bluefin tuna larvae from the Mediterranean Sea (Catalán *et al.* 2011), and not the Gulf of Mexico (GOM), have been examined for diet composition and feeding success. Here, we present the preliminary results of our efforts to fill this conspicuous gap in our basic understanding of the ecology of Atlantic bluefin tuna larvae in the GOM. We focus on identifying ontogenetic changes in diet composition and prey size, documenting the dynamics of piscivory (the consumption of other fish larvae), and gaining a general understanding of how successful bluefin larvae in the GOM are at finding and consuming prey.

2. Methods

This preliminary report focuses on bluefin tuna larvae collected during two years (2003 and 2011) of sampling in the GOM. Samples were collected as part of the Southeast Area Monitoring and Assessment Program (SEAMAP) spring plankton surveys, which use 60 cm bongo nets (333 µm mesh) and a 2x1 m, surface-towed neuston net (500 µm mesh) at fixed stations throughout the GOM (e.g. Richards *et al.* 1993, Rester *et al.* 2011). From 2010 onwards, a new gear type was introduced, which used a 2x1 m neuston net (505 µm mesh) towed in an undulating fashion from just below the surface to 10 m (Habtes *et al.* 2014). This sampling strategy has been shown to be more effective for catching tuna larvae, and is now deployed as standard on the annual spring cruises. Larvae from 2003 were fixed in 10% buffered formalin and later transferred to 95% ethanol after sorting. 2011 larvae were preserved in 95% ethanol, which was changed after 24 hours.

Larvae were sorted from plankton samples, measured for notochord or standard length, and identified morphologically following Richards (2005) at the Sea Fisheries Institute Plankton Sorting and Identification Center, Gdynia and Szczecin, Poland. A subset of larvae was selected for gut content inspection. Following Llopiz *et al.* (2010), larvae had their entire alimentary canal removed with a microscalpel, and prey items were teased out with minutien pins. Consumed prey were identified to the lowest taxonomic level practical, enumerated, and measured with an ocular micrometer (Leica M205 stereomicroscope). Daytime feeding incidence, or the proportion of daytime-collected larvae with prey present in the gut, is reported since it is a reliable yet simple indicator of feeding success for a given sample of larvae that can be compared to other studies. Similarly, we report the incidence of piscivory by size class, since many species of larval scombrids at some point in their development begin to consume other fish larvae often at species- and region-specific sizes (Llopiz & Hobday 2014). Diets were described as the numerical proportions of prey types by larval bluefin size class, and ontogenetic changes in consumed prey sizes and prey numbers were illustrated by plotting these values against larval length. Due to a limited sample size thus far for 2003, we do not examine the possibility for interannual differences in diets or feeding success. However, this will be investigated in the near future.

3. Results and Discussion

The feeding success of bluefin tuna larvae, as measured by feeding incidence, for individuals collected during daylight hours (n = 89) was 94% (**Table 1**). By size class, larvae 2-4 mm had a feeding incidence of 75%, while all other size classes had a feeding incidence of 100% (i.e. no empty larvae were observed). Such high feeding incidences are consistent with observations of larval tunas in the nearby Straits of Florida (98%; Llopiz *et al.* 2010) and are similar to the high overall value of 94% for Atlantic bluefin larvae from the Mediterranean Sea (Catalán *et al.* 2011). Compared to other bluefin species around the world, Atlantic bluefin tuna larvae appear to feed much more successfully than southern bluefin tuna (53% feeding incidence; Young and Davis 1990) and moderately more successfully than Pacific bluefin (78% feeding incidence; Uotani *et al.* 1990). One factor that could contribute to these differences is the notably reduced levels of chlorophyll and zooplankton biomass off NW Australia and the Nansei Islands (Japan) regions when compared to the GOM and Mediterranean Sea (Llopiz and Hobday 2014). Comparisons of the conditions in the GOM and Mediterranean Sea (Muhling *et al.* 2013, Llopiz & Hobday 2014) suggest a generally similar larval environment is experienced by these two North Atlantic populations, which may be further evidenced by the similar feeding incidences (both 94%) of the larvae from the two regions.

Feeding of nighttime collected larvae differed substantially from that of their daytime counterparts; only 3 out of 19 inspected nighttime collected larvae contained prey. This result is in line with most larval fish feeding studies and supports the likelihood that these visual predators do not feed at night. Frequent, successive sampling of tuna larvae in the Straits of Florida (Llopiz *et al.* 2010) and off NW Australia (Young & Davis 1990) after sunset showed that gut evacuation times of tuna larvae are 3-4 hrs—the time post-sunset at which all sampled larvae were empty.

Results on the diets of bluefin tuna larvae from the GOM illustrate a moderately narrow diet and distinct ontogenetic shifts in prey types (**Figure 1**). Near the first-feeding stage, bluefin larvae fed almost exclusively on copepod nauplii, but rapidly shifted to include three other dominant prey types in their diets: appendicularians, calanoid copepods, and cladocerans. These findings differ markedly from diet studies of other regions and tuna species; notably, this is the first observation of appendicularian consumption by any of the three species of bluefin tunas, including Atlantic bluefin larvae in the Mediterranean Sea. Feeding on appendicularians in the GOM is not overly surprising, however, since appendicularians have been shown to be particularly important to other species of *Thunnus* tunas (blackfin and yellowfin) in the nearby Straits of Florida (Llopiz *et al.* 2010). GOM bluefin diets were also similar to *Thunnus* larvae in the Straits of Florida overall, which are relatively broad (4-5 dominant prey types) when compared to the extremely narrow diets (1-2 prey types) of some other genera of tunas in the region (*Katsuwonus*, *Euthynnus,* and *Auxis*; Llopiz *et al.* 2010) as well as istiophorid billfishes (Llopiz and Cowen 2008).

The most dramatic ontogenetic shift for bluefin larvae in the GOM was the onset of piscivory, which was displayed by 11% of larvae 6–8 mm in length (the smallest being 6.1 mm) and 71% of larvae 8–10 mm in length (**Table 1**). These results run contrary to those for Atlantic bluefin larvae from the Mediterranean, which did not display piscivory at lengths up through 9 mm (the maximum length of larvae examined; Catalán *et al.* 2011). The precocious nature of GOM-spawned Atlantic bluefin larvae is also distinct among other bluefin species. One study on southern bluefin tuna larvae off NW Australia observed piscivory to begin at 8 mm (Young and Davis 1990), while another study in the region did not observe piscivorous feeding behaviors up through lengths of 10 mm (Uotani *et al.* 1981). Pacific bluefin tuna larvae in the Nansei Islands region were not observed to be piscivorous at lengths up to 15 mm, even with a sample size of 1939 inspected larvae (Uotani *et al.* 1990).
Some of the consumed fish larvae extracted from bluefin guts were intact enough to be identified to various taxonomic levels (**Table 2**). In one instance, a bluefin larva had consumed two morphologically identifiable bluefin larvae, thus representing one certain case of cannibalism.

Concurrent with an ontogenetic shift in prey types for bluefin larvae was a shift in prey sizes (**Figure 2**). However, the only distinct shift in size is due to a switch from nauplii to all other zooplankton prey, as appendicularians, copepods, and cladocerans are all of similar sizes. In addition to an increase in prey size, the number of prey per larva also initially increased with bluefin length (**Figure 3**). Yet, this was prior to a decline in the number of prey per larva that began around 8 mm—concurrent with the majority of larvae exhibiting piscivory at these sizes and related to the fact that fish larvae are much larger prey items than the other zooplankton prey consumed. Overall, these results are generally consistent with other studies on larval scombrids.

Our ongoing efforts will expand the number of bluefin larvae examined so that we can relate broad patterns in diets and feeding success to prey availability and environmental conditions, as well as examine the possibility for interannual differences in feeding success that could contribute to observed differences in year-class size. We will also be able to more thoroughly address the degree to which larvae rely upon cannibalism for survival, assisted by the use of molecular identification tools that will help us avoid the difficulties in morphologically identifying bluefin larvae, which, due to digestion, quickly become unidentifiable as prey.

Acknowledgements

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Table 1. Feeding incidence (percentage of larvae inspected containing prey) and incidence of piscivory (feeding larvae containing other fish larvae) by size class for daytime-collected bluefin tuna larvae.

Size class (mm)	**n**	**Feeding incidence**	**Piscivory incidence**
2–4	20	75%	0%
4–6	9	100%	0%
6–8	53	100%	11%
8–10	7	100%	71%

Table 2. Taxonomic information on the intact fish larvae extracted from the guts of bluefin tuna larvae collected in the Gulf of Mexico.

Larvae consumed by piscivorous bluefin larvae	**# individuals**
Unknown	7
Unknown scombrid	3
Thunnus sp.	2
Bluefin tuna	2

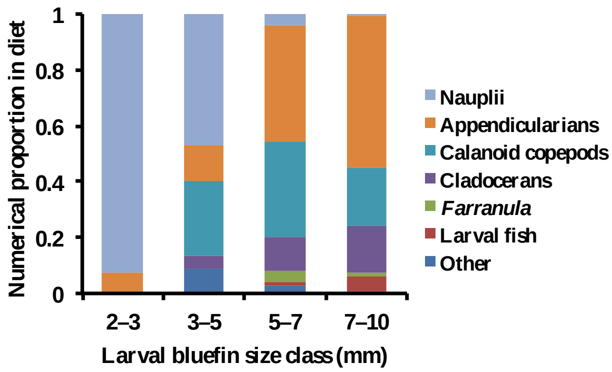

Figure 1. Diet composition of bluefin tuna larvae collected in the Gulf of Mexico. Data are numerical proportions of prey types extracted from bluefin tuna larvae by larval size class.

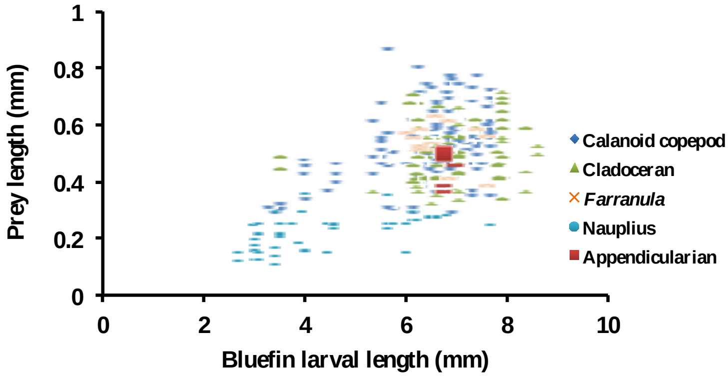

Figure 2. Predator-prey size relationship for larval bluefin tuna and extracted zooplankton prey.

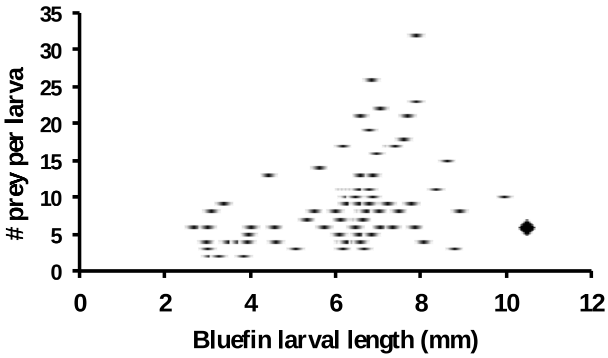

Figure 3. Relationship of larval length versus the number of prey items extracted from bluefin larvae.