Climate sensitivities and uncertainties in food-web pathways supporting larval bluefin tuna in subtropical oligotrophic oceans

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Abstract:

Compared to high-latitude seas, the ecological implications of climate change for top consumers in subtropical regions are poorly understood. One critical area of knowledge deficiency is the nature of food-web connections to larvae during their vulnerable time in the plankton. Bluefin tuna (BFT) are highly migratory temperate species whose early life stages are spent in ultra-oligotrophic subtropical waters. Dietary studies of BFT larvae provide evidence of prey-limited growth coupled with strong selection for specific prey types – cladocerans and poecilostomatoid copepods – whose paradoxical or poorly resolved trophic characteristics do not fit the conventional understanding of open-ocean food web structure and flows. Current knowledge consequently leaves many uncertainties in climate change effects, including the possibility that increased nitrogen fixation by *Trichodesmium* spp. might enhance resiliency of BFT larvae, despite a projected overall decline in system productivity. To advance understanding and future predictions, the complementary perspectives of oceanographers and fisheries researchers need to come together in studies that focus on the trophic pathways most relevant to fish larvae, the factors that drive variability in spawning regions, and their effects on larval feeding, growth and survival.

Introduction

In high latitude systems, rising temperature and density stratification associated with climate change are dramatically altering sea-ice habitats and production cycle phenologies supporting high level consumers (Loeng and Drinkwater, 2007; Wassmann *et al*., 2011; Constable *et al*., 2014). While the ultimate impacts are still to be determined, the directions of change are both measurable and being actively investigated to elucidate cause-and-effect mechanisms and predict future consequences (e.g., Laidre *et al*., 2008; Ducklow *et al*., 2013). In contrast, climate change effects on already warm and nutritionally poor regions of the oceans are less clearly understood and will be more difficult to quantify relative to background variability. For such regions, predicting the consequences of future changes will also strongly challenge our understanding of how these systems and the populations dependent on them actually function in the contemporary ocean. One specific concern is the nature of food webs that underlie successful recruitment of the ocean's top predators. Here, we will use the specific example of bluefin tuna (BFT) to illustrate knowledge and conceptual gaps, arguing that current understanding of the food web structure and dynamics of oligotrophic ocean systems largely ignores the components most relevant and important for understanding the successful development of BFT larvae and their sensitivities to climate change impacts.

The three species of BFT (Atlantic: *Thunnus thynnus*, Pacific: *T. orientalis* and Southern: *T. maccoyii*) are the largest and broadest-migrating tunas. All populations are highly valued economically, subject to heavy fishing pressure, and currently depleted (Fromentin et al., 2014; Pons et al., 2017). Primarily due to their ability to regulate their body temperature through endothermy (Graham & Dickson 2001), juvenile and adult BFT have exceptional environmental tolerances. This allows them to exploit food resources over vast expanses of temperate and subpolar waters. All three species, however, spawn in distinct restricted subtropical areas, which are currently among the most nutritionally deficient habitats in the oceans and expected to get even poorer in the future (Bopp *et al*., 2001; Behrenfeld *et al*., 2006; Chust *et al*., 2014; Doney *et al*., 2014; Fu *et al*., 2016). During their first 2-3 weeks of life, BFT larvae must grow rapidly or die in such waters. They are restricted by daylight feeding and light penetration to the upper 10-20 m of surface waters (Davis *et al*., 1990a; Habtes *et al*., 2014), and will thereby directly experience the major projected consequences of climate forcing – warmer surface temperature, stratification-diminished productivity and increased acidity – which will collectively increase metabolic requirements as food resources presumably decline. This is the climate-vulnerable recruitment bottleneck for BFT that needs to be understood.

Conventional understanding of the food-web structure of warm oligotrophic seas emphasizes the dominance of <1-µm unicellular photosynthetic bacteria, the most efficient competitors when nutrient concentrations are chronically low. In the long-established microbial loop hypothesis (Azam *et al*., 1983), bacteria are consumed by small flagellates, and they, in turn, by ciliated protozoa, leading to inefficient transfer of productivity to small animals of the size (~1-mm) of tuna larvae prey. Increasing oligotrophy would presumably work to lengthen this protistan food chain, decreasing transfer efficiency to higher levels. But is this relevant to BFT larvae? Here, we will highlight that the preferred prey of BFT larvae, namely poecilostomatoid copepods and cladocerans, are organisms associated with alternate and poorly explored trophic pathways in oligotrophic systems. We will outline how the characteristics and variability of different types of zooplankton prey may function in food webs to enhance vulnerability or resiliency of BFT larvae to climate change, the major areas of uncertainty that need to be resolved, and the types of research efforts needed to bridge the knowledge and conceptual gaps between oceanographic and fisheries approaches to elucidating the ecology of open-ocean ecosystems.

Bluefin tuna spawning areas

Bluefin tunas are among the top predators of pelagic ecosystems in all major oceans. They range widely, make large excursions through the water column and can effectively evade or mitigate unfavorable environmental conditions by virtue of their strong swimming abilities and physiological traits such as thermal regulation (Holland *et al.*, 1992; Block *et al.*, 2001). Unlike tropical tunas, which spawn over wide geographical areas throughout much of the year, the large temperate BFTs make long-distance migrations to small geographically restricted areas in oligotrophic subtropical seas (Figure 1) where they spawn over relatively short periods (Schaefer, 2001; Shimose and Farley, 2016). Successful development of their larvae thus depends on the food resources available in narrow portions of the subtropical oceans during limited periods of time.

Southern bluefin tuna (SBFT) forage widely in the Southern Ocean and migrate northward to the waters between Indonesia and northern Australia to spawn during the austral summer (Figure 1; Farley *et al.*, 2015; Hobday *et al.*, 2016). Pacific bluefin tuna (PBFT) range extensively across the northern Pacific Ocean but migrate to the areas between Japan and the Philippine Islands (Nansei area) and in the Sea of Japan to spawn during the boreal spring and summer months (Itoh, 2006; Tanaka and Suzuki, 2016; Fujioka *et al.*, 2016). Atlantic bluefin tuna (ABFT) feed throughout the North Atlantic but migrate to distinct western and eastern spawning areas in the Gulf of Mexico and the Mediterranean Sea, respectively, during boreal spring and early summer (Block *et al.*, 2005; Rooker *et al.*, 2007). ABFT larvae have also recently been recorded in the Slope Sea off the Mid-Atlantic Bight during summer (Richardson et al., 2016), which has similar water temperatures to the Gulf of Mexico during spring and is oligotrophic during warmer months (Xu et al., 2011).

The waters of all known BFT spawning grounds are warm (>24°C), highly stratified and especially nutritionally deficient during the spawning seasons (Matsuura *et al.*, 1997; Alemany *et al.*, 2010; Muhling *et al.*, 2013; Llopiz and Hobday, 2015; Druon *et al.*, 2016). The evolutionary advantages, and ecological consequences, of larvae developing in such waters remain largely unclear. Nonetheless, some hypotheses have been proposed, such as the advantage of reduced predation pressure on eggs and larvae by other pelagic fish species in oligotrophic environments (Bakun and Broad, 2003; Bakun, 2013). Further, though the spawning regions are characterized by mesoscale eddies and fronts, the waters selected for spawning generally have retention characteristics, often with less kinetic energy than at other times of the year (Reglero *et al.*, 2014). With the exception of the Mediterranean, however, these retention areas are also adjacent to strong poleward flowing boundary currents (Gulf Stream, Kuroshio and Leeuwin Currents), which facilitate the transport of surviving post larvae away from the spawning grounds and toward juvenile nursery habitats in more productive temperate ecosystems (Brothers *et al.*, 1983; Kitagawa et al., 2010; Hobday *et al.*, 2016).

Feeding preferences of larval BFT

Bluefin tuna spawn huge numbers of tiny pelagic eggs. Once hatched at ~2 mm body length, the larvae quickly develop eyes, large mouths and a functioning gut (Yúfera *et al.*, 2014), which give them the capability to grow quickly, at rates of 0.3-0.4 mm body length per day, in warm waters with sufficient food (Malca *et al.*, 2017; Muhling *et al.*, 2017). Metamorphosis from the post-flexion larva to juvenile generally occurs at about 22 mm, about four weeks after hatching, after which swimming capabilities increase rapidly, including schooling behavior during daylight hours (Fukuda *et al.*, 2014). Feeding studies of the larvae have focused mainly on individuals <10 mm, after which many switch from zooplankton to a piscivorous, often cannibalistic, diet and eventually become too difficult or too rare to capture in plankton nets towed at moderate speeds.

BFT larvae live in near-surface waters (generally, the upper 20 m) and feed by visual cues during daylight hours (Davis *et al*. 1990; Satoh, 2010). Typical prey are epipelagic zooplankton of 1 mm size or less. While the smallest larvae are known to prey mostly on copepod nauplii, the dietary contributions of different copepod taxa to such prey are unresolved in stomach content analyses. For copepodid and adult stages, however, clear differences emerge among different taxonomic groups (Fig. 2). Among the more numerous and recognizable small copepods in most ocean ecosystems, *Oithona* spp. (Cyclopoida) are rarely reported in significant numbers in larval BFT stomachs. Small calanoid taxa (e.g., *Paracalanus* and *Clausocalanus* spp.) are consumed, but in dietary studies of all BFT species they appear in significantly lower proportions than their contributions to the ambient prey community (Uotani *et al*., 1981; Young and Davis, 1990; Llopiz *et al*., 2015; Kodama *et al*., 2017). In contrast, poecilostomatoid copepods (typically *Corycaeus* or *Farranula* spp.), reported as cyclopoid copepods in earlier studies, appear to be strongly selected. This is clear in studies of SBFT that have expressly compared larval diets to the natural abundances of prey (Uotani *et al*., 1981; Young and Davis 1990), as well as suggested by dietary results for ABFT and PBFT where the natural abundances of prey were not directly assessed (Uotani *et al*., 1990; Tilley *et al*., 2016). Kodama *et al*.'s (2017) atypical dietary results for PBFT in the Sea of Japan were during a time of insignificant natural abundances of *Corycaeus* and *Farranula* spp. as assessed by both microscopical and metagenomics analyses. Tilley *et al*'s. (2016) results for the northern Gulf of Mexico are confounded by unusual feeding on abundant barnacle (*Lepas* sp.) nauplii, which may have arisen from proximity to deep-water oil drilling platforms. We do not present those data in Figure 2 but note that poecilostomatoid copepods (29%) and cladocerans (24%) comprised the majority of the holozooplankton prey consumed by ABFT in that study (Tilley *et al*., 2016).

Figure 2 shows that small marine cladocerans also contribute disproportionately to the diets of BFT larvae with evidence from each of the three species (Uotani *et al*., 1981; Llopiz *et al*., 2015; Kodama *et al*., 2017). In addition, Catalán *et al*. (2011) documented high feeding incidence on cladoceran prey (33.7% of stomach items) and high selectivity relative to either copepod nauplii or copepodids by ABFT larvae in the Mediterranean Sea, which further extends the observations of this feeding preference to both eastern and western ABFT spawning regions. We did not include data from Catalán *et al*. (2011) in Figure 2 because they did not distinguish copepod orders – calanoida, cyclopoida, poecilostomatoid – in their analyses of prey items and natural abundances.

While there is some evidence that appendicularians can be important prey items for BFT larvae (e.g., Llopiz *et al*., 2015; Gulf of Mexico), that is not a common finding from dietary analyses (Fig. 2). Catalán *et al*. (2011) commented about the low incidence of appendicularians in ABFT larvae from the Mediterranean Sea, and Tilley *et al*. (2016) found none in the diets of ABFT in the northern Gulf of Mexico. Kodama *et al*. (2017), however, did report significant feeding on *Oikopleura* spp. from metagenomic analyses of PBFT larval guts compared to no evidence from microscopical analysis, which raises the possibility that soft-bodied appendicularians are systematically underrepresented in gut content enumeration due to their more rapid digestion relative to the recognizable chitinous exoskeletons of crustacean prey. Nonetheless, it is notable that the larvae of other scombrid species, like *Auxis* spp. (bullet tuna), *Euthymmus alletteratus* (little tunny) and *Katsuwonus pelamis* (skipjack), are well documented to specialize on appendicularian prey, with numerical abundances exceeding 50%, and often 90%, of gut contents, often from the same studies, collection regions and analysts that found little or no feeding on appendicularians by

BFT larvae (Uotani *et al*., 1981; Young and Davis, 1990; Llopiz *et al*., 2010; Llopiz and Hobday, 2015). Thus, analytical bias does not easily explain the relatively low incidence of larval BFT feeding on appendicularians. In this regard, BFT larvae share stronger dietary characteristics with other *Thunnus* species (*T. alalunga* – albacore; *T. albacares* – yellowfin; *T. obeseus* – bigeye), as well as the larvae of billfishes (*Makaira nigricans* – blue marlin; *Xiphias gladius* – swordfish; *Tetrapturus angustirostris* – shortbill spearfish; *Istiophorus platypterus* – sailfish), which all show very high feeding incidence, ranging from 33 to >90%, on the combination of *Corycaeus*, *Farranula* and cladoceran species (Uotani *et al*., 1981; Young and Davis, 1990; Uotani and Ueyanagi, 1997; Govoni *et al*., 2003; Llopiz and Cowen, 2008; Llopiz and Hobday, 2015).

The specific characteristics of poecilostomatoid copepods and cladocerans that cause them to be preferred prey of *Thunnus* and billfish larvae are not known. Kodama *et al*. (2017) speculated that apparent prey selection could be driven by the superior escape abilities of copepods, leaving slower-swimming and less-evasive prey like cladocerans and appendicularians to be overrepresented in larval diets. Since poecilostomatoid copepods were largely absent from the water during the Kodama *et al*. (2017) study, however, a broader explanation of the selectivity results would need to consider differential vulnerabilities of the major copepod orders, the fact that appendicularians, with poor escape capabilities, are not typically dominant prey of *Thunnus* and billfish larvae, and inherent differences among species in the prey characteristics that trigger recognition and attack. Considering the characteristics of the preferred BFT prey, both cladocerans and poecilostomatoid copepods lack development of the appendages that generate the smooth swimming currents of calanoid copepods and swim with jerky strokes. Another common denominator is the presence of large and conspicuous eyes, with the paired compound eyes and cuticular lenses of poecilostomatoid copepods (Vaissière, 1961) potentially also enhancing their visibility by reflecting or refracting light. These could be key factors that set cladocerans and poecilostomatoid copepods apart from other zooplankton as prey of *Thunnus* and billfish larvae, whereas other scombrid larvae with similar size, vision and swimming capabilities clearly respond more strongly to the characteristics of appendicularians.

Resource limitation of larval BFT

Regardless of the mechanism(s) underlying prey capture success and dietary selectivity of BFT larvae, certain prey types clearly play disproportionate roles as food resources relative to their abundances in the plankton. Consequently, the quality of the prey environment for larvae cannot be assessed solely in terms of total zooplankton abundance or biomass, but depends on size structure and composition (Robert *et al*., 2013). This would be of little consequence if larvae were always able to achieve optimal or equivalent rates of feeding, growth or survival success despite natural variations in prey. There is ample evidence, however, that food limitation can be a significant factor in the early life history of BFT.

For BFT larvae of a comparable size range (Table 1), the highest estimates of daytime larval feeding indices (>90% with prey and >7 prey per gut; Table 1) are for ABFT populations in the Gulf of Mexico (Llopiz *et al*., 2015) and northwest Mediterranean (Catalán *et al*., 2011). Llopiz *et al*. (2015) further reported an even higher 100% feeding incidence for >4 mm larvae and a 71% incidence of piscivory for larger 8-10 mm larvae, which laboratory and model studies have associated with improved growth and survival (Reglero *et al*., 2011, 2014). Catalán *et al*. (2011) also found that larger (>5 mm) larvae consumed more prey, 11.1 prey/larvae on average (100% feeding incidence), but piscivory was not observed. Compared to these high estimates of larval feeding, the more typical results for SBFT (Uotani *et al*., 1981; Young and Davis, 1990), PBFT (Kodama *et al*., 2017) and even occasionally ABFT

(Tilley *et al*., 2016) show reduced feeding incidence of 53-78% and much lower numbers of prey (1.1-1.3 individuals) in stomach contents (Table 1). The wide range in these values is indicative of suboptimal feeding conditions at least some of the time in BFT spawning grounds, which is consistent with bioenergetic-foraging models that suggest food limitation on a planktivorous diet even when all zooplankton are assumed to be equally available as prey (Reglero *et al*., 2011).

Young and Davis (1990) were the first to address food limitation as an ecological issue for BFT larvae, finding significant positive relationships between feeding indices and zooplankton biomass for SBFT larvae in the eastern Indian Ocean spawning region. For that study, stomach fullness doubled and % larval stomachs with prey increased 3-4 fold, from 20-30% to ~90%, over a 3-fold natural variation in zooplankton biomass. A mean daily ration of 30% of body mass d^{-1} was determined from the prey ingested by 4.5 mm larvae and gut evacuation rates of 3-4 h, suggesting a relatively modest average rate of larval growth, though this is likely to be an underestimate given recent evidence of significantly faster digestion times (2 hours, P. Reglero, pers. com.). For larvae from the same study area, Jenkins *et al*. (1990) found that otolith estimates of growth rate declined by 25% on average in higher density patches of larvae, indicating the possibility for density-dependent depletion of prey resources. Growth rate estimates were positively correlated with feeding indices (feeding incidence, mean stomach fullness and prey number), but not with temperature, which varied narrowly during that study.

For PBFT larvae, Tanaka *et al*. (2008) found 40-90% mortality of hatchery-raised larvae after one day of non-feeding and virtually zero tolerance of 2 days without feeding. Up to 26% of field-collected larvae had low RNA:DNA ratios comparable to larvae starved for 24 h, with the proportion of starving larvae varying by a factor of 6 over a 4-fold range in copepod prey density. The effects of starvation or food-limited growth of larval survival were further tested by analyzing the otoliths of specimens from PBFT larval patches followed by satellite-tracked drifters in the Nansei spawning region (Satoh *et al*., 2013). As hypothesized, the larvae that survived over several days of development were subsets of the original populations with wider otolith radii, higher daily growth rates and larger size at a given age. Such results help to explain the somewhat contradictory conclusions that can be made between demonstrable food-limitation impacts in BFT spawning regions and relatively rapid growth rates of the surviving larvae (Jenkins and Davis, 1990; Shimose and Farley, 2016; Malca *et al*., 2015, 2017). Successful development through the early life stages of BFT thus implies early and continued success in finding and capturing appropriate prey.

Plankton food webs supporting larval BFT

The ecological factors that determine the quality of the food web for successful larval feeding and growth in oligotrophic waters are major unknowns in the early life history of BFT. Based on general understanding of plankton trophic relationships, however, one can envision various pathways that connect the production base of ocean surface waters to potential and selected prey of larval tuna. These are represented in Figure 3 as a starting point for discussing possibilities and specific areas of uncertainty.

The main diagonal arrows in Figure 3 depict a conventional view of the pelagic food web of subtropical oligotrophic waters as might be represented in a simple ocean ecosystem model. Photosynthetic bacteria and picoeukaryotes are the dominant primary producers, and protists are major primary consumers and the main trophic link to mesozooplankton (Azam *et al*., 1983; Sherr and Sherr, 1994; Calbet and Landry, 2004). A more detailed food web would recognize alternate pathways of trophic coupling, including multiple steps of protistan consumers up to mesozooplankton (e.g., Calbet and Landry, 1999) and direct consumption of some primary production by mesozooplankton feeding on larger phytoplankton with strategies (e.g., mixotrophy, nitrogen fixation) adapted to low-nutrient systems. Based on stable isotope analyses of amino acids, however, the three-step food chain from phytoplankton to phagotrophic protists to copepods appears to capture effectively the mean nitrogen enrichment and general trophic structure for such systems (Landry and Décima, 2017), so we use that simple chain here to represent those mean flows.

Figure 3 separately represents large cells associated with nitrogen fixation, an important source of new nitrogen (Mulholland *et al.*, 2006; Raes *et al.*, 2014) and possibly micro-habitat structure in oligotrophic surface waters of BFT spawning grounds. These include the cyanobacterium *Trichodesmium* spp. and large clumping diatoms (*Rhizosolenia, Hemiaulus* and *Mastogloia* spp.) with endo-symbiotic diazotrophs (Kemp and Villareal, 2013) that contribute to nitrogen fixation directly, as well as diatoms that benefit indirectly from the fixed nitrogen released by diazotrophs (Devassy *et al.*, 1979; Bergman *et al.*, 2012; Bonnet *et al.*, 2016).

Enhanced thermal stratification associated with climate warming is predicted to reduce new nutrient delivery to surface waters, reducing general productivity and trophic transfer efficiency, though likely providing relative growth advantages to picophytoplankton and diazotrophs (Ware and Thompson, 2005; Hutchins *et al.*, 2007; Brown et al., 2010; Moore *et al.*, 2013; Litchman *et al.*, 2015; Fu *et al.*, 2016; Follett *et al.*, 2018). If such impacts are passed uniformly by the conventional food web to all components of the zooplankton community, they would exacerbate the already prey-limited resource environment for BFT larvae. If, on the other hand, climate warming disproportionately impacts, positively or negatively, the preferred prey of larvae, the effect on BFT populations could be either positive or negative. We thus consider below some aspects of the trophic ecologies of specific groups of zooplankton prey that set them apart from the community as a whole.

First, we should note that, as is the case for many or most ichthyoplankton (Montagnes *et al.*, 2010), the direct consumption of protistan zooplankton is likely underestimated in dietary analyses of BFT larvae because preservation and measurement techniques are not optimized for soft bodied prey. Since the size range of consumed prey increases rapidly with larval development, this bias should be most relevant for the smallest larvae, and thus potentially important for establishing their success in early feeding. While there is little evidence to evaluate dietary flows through this pathway for natural BFT populations, Nakagawa *et al.* (2007) documented active feeding by PBFT larvae in aquaculture rearing tanks on the large dinoflagellates and ciliates associated with a microbial loop food chain based on bacterial production. Despite comparable or higher standing biomass estimates of heterotrophic microplankton compared to the primary prey (rotifers), however, the microplankton provided a small and declining proportion of the energy flow to larvae (from 13 to 0.6% for 4 to 12 day old larvae, respectively). In addition, the diversion of energy from the primary food chain (algae-rotifers) to heterotrophic protists raised questions as to whether they actually provided a net positive benefit to larval growth and survival (Nakagawa *et al.*, 2007). Such results point to the many unresolved complexities and nuances of energy flows through the microbial food webs of open-ocean systems, which we do not further consider here.

Appendicularians are a specialized component of the zooplankton with the capability of feeding directly on bacterial-sized particles (Scheinberg *et al.*, 2005; Sutherland *et al.* 2010). They can consequently short-circuit the protistan trophic steps in the food web and provide a more efficient transfer to appropriately sized prey for fish larvae than the indirect flow through the conventional food chain. As noted previously, however, appendicularians are generally not preferred prey of BFT larvae. Based on known dietary selectivity, therefore, a shift to greater energy flux through appendicularians would more likely enhance the larval feeding conditions for co-occurring skipjack, little tunny and *Auxis* species over *Thunnus* and billfish species, unless there was some compensatory indirect feedback to the preferred prey of BFT larvae. As will be considered further below, for example, such feedback could occur if large marine snow particles from discarded appendicularian houses were utilized as a food resource or refuge that selectively benefitted a subset of prey.

Compared to the relatively straightforward relationships considered to this point, the trophic strategies of the prey types that BFT larvae select for most strongly -- poecilostomatoid copepods and cladocerans -- are more challenging to understand in an oligotrophic food-web context. For poecilostomatoid copepods, a key issue is trophic position. One important group of poecilostomatoids, the Oncaeidae, is strongly associated with marine snow particles, especially discarded appendicularian houses, to which they adhere and scavenge with modified grasping antennae and maxillipeds (Alldredge 1972, 1974; Steinberg *et al*., 1994; Ohtsuka *et al*., 1996; Green and Dagg, 1997). Recent research in the Sea of Japan has highlighted the possibility that appendicularians enhance transfer to higher trophic levels via the production of *Oncaea* and *Microsetella* spp., whose population abundances are significantly correlated with appendicularians (Kodama *et al*., 2018). Since appendicularian houses typically contain high remnant concentrations of phytoplankton filtered from the water, *Oncaea* spp. could have trophic positions close to the food web base and function relatively efficiently in trophic transfer. However, the rarity of *Oncaea* spp. in BFT larval stomachs suggests that they are largely inaccessible as prey in surface waters, possibly because of the large-particle association, although their population distributions also tend to be deeper in the water column (e.g., McKinnon *et al*., 2013). A similar observation can also be made about the low feeding incidence of BFT larvae on the harpacticoid copepods, *Macrosetella*, *Miracia* and *Microsetella* spp., associated with macroscopic bundles and tufts of *Trichodesmium* (Roman *et al*., 1978; O'Neil and Roman, 1992). Thus, based on the relative absence of such prey in BFT larval diets, one can reasonably conclude that the larvae do not effectively exploit the concentrated prey assemblages associated with large particle aggregates.

While the other abundant poecilostomatoid group, the Corycaeidae, are occasionally found on marine snow particles (e.g., Green and Dagg, 1997), their grasping appendages appear to function mainly for carnivorous feeding. Based on trait similarities, Benedetti et al. (2016) classified all 14 species of *Corycaeus* and *Farranula* in the Mediterranean Sea according to their function as small active-ambush carnivores. In laboratory experiments, *Corycaeus* spp. have been shown to feed effectively on nauplii or copepodid prey of appropriate size (Turner *et al*., 1984; Landry *et al*., 1985), using visual cues with their image-forming binocular eyes, as is evident in much higher feeding rates in the light than dark (Gophen and Harris, 1981). In field studies, however, *Corycaeus* spp. have been linked more strongly to predation on fish larvae and chaetognaths (Brewer et al. 1984; Palomares García and Alejandre, 1995). Assuming similar relationships in the BFT spawning regions, their trophic positions would be TP = 4 if feeding directly on omnivorous copepods, or TP = 5 if feeding on other carnivores. Therefore, relative to comparably sized appendicularians, calanoid and cyclopoid copepods and particle-associated poecilostomatoids or harpacticoids, the trophic pathways to these favored prey of larval tuna and billfish are poorly resolved in plankton trophic studies, but could be unusually long and inefficient.

Of the eight described species of marine cladocerans, most are associated with coastal waters, but at least one -- *Pseudevadne tergestina* (also called *Evadne tergestina* in many studies) -- is broadly distributed in oligotrophic open-ocean BFT spawning regions like the eastern Indian Ocean and Gulf of Mexico (Della Croce and Venugopal, 1972; Della Croce and Angelino, 1987), and thus might be considered a model type for such systems. In a scanning electron microscopy study of the stomach contents of 5 cladoceran species from the Sea of Japan, Kim *et al*. (1989) reported no substantial differences between prey ingested by *P. tergestina* relative to other species. All demonstrated strong preference for centric diatoms over pennates and dinoflagellates, which were also abundant in the ambient plankton, and none showed any indication of feeding on animal prey. Similarly, in a comparative experimental study of 3 cladoceran species by Katechakis and Stibor (2004), each species exhibited a selection maximum on natural food particles between 10 and 100 µm, with little indication of an ability to capture bacterial-sized (<2-µm) prey, as also noted by Paffenhöfer and Orcutt (1986). While *P. tergestina* was not included in the Katechakis and Stibor (2004) study, the morphologically similar *Evadne nordmanni* was suggested to be inefficient in capturing motile prey, notably ciliates and dinoflagellates, in the intermediate size range of 15-70 µm, which points further to the presumptive importance of relatively large and immobile prey like diatoms in the diets of marine cladocerans. Despite seeming to be paradoxically maladaptive for success under the oligotrophic conditions of BFT spawning grounds where small and motile cells are expected to predominate, this feeding relationship is borne out in the observation of *P. tergestina* replacing calanoid copepods (*Paracalanus* spp.) as the zooplankton community dominant at an artificial upwelling installation off Korea that increased phytoplankton abundance (mostly diatoms) by 50 fold (Jeong *et al*., 2013). In contrast, Atienza *et al.* (2006) have suggested that another cladoceran species, *Penilia avirostris*, does better feeding on nanophytoplankton during stratified water periods in the coastal NW Mediterranean because its filter feeding appendages get clogged when diatoms are abundant. Consequently, there is little consensus as to how the cladoceran prey of BFT larvae in oligotrophic open-ocean ecosystems derive nutrition from the alternate pathways depicted in Figure 3.

Given contradictory interpretations of the trophic ecology of cladocerans and their contrasts to the presumptive long food chains to carnivorous poecilostomatoid copepods, current knowledge does not provide coherent answers for how the preferred prey of BFT larvae relate to one another or might respond, separately or together, to climate impacts on open-ocean ecosystems. Sahu *et al*. (2015), however, recently observed that cladocerans (*P. tergestina* in particular, but also *P. avirostris*) became community dominants and carnivorous copepods (poecilostomatoids and cyclopoids) notably more important while calanoids declined during *Trichodesmium* blooms in the coastal Bay of Bengal. Underlying relationships may therefore exist that link these seemingly disparate prey types to each other and to a specific group of phytoplankton (diazotrophic microplankton) with significant ecological advantages in future ocean scenarios (Breitbarth *et al*., 2007; Hutchins *et al.*, 2007; Follett *et al*., 2018).

How this might work mechanistically is a matter of speculation that may or may not include an intermediate step involving diatoms. While most zooplankton cannot feed on *Trichodesmium* directly, diatoms can be stimulated indirectly from the nitrogen released by *Trichodesmium* (Bergman *et al*., 2012) or contribute separately to open-ocean new production as diatom-diazotroph symbiotic associations (Carpenter *et al*., 1999; Dore *et al*., 2008). When either occurs, a rapid cladoceran response might be expected due to their high feeding efficiency on diatoms, prodigious reproductive potential and fast development times (Atienza *et al*., 2008). In an early study of plankton succession in coastal waters of the Arabian Sea, Devassy et al. (1979) showed exactly this scenario, with a declining *Trichodesmium* bloom fueling a *Chaetoceros*-dominated mixed-diatom bloom and a massive population outbreak of *P. tergestina*. This does not match, however, the events described by Sahu *et al.* (2015), who sampled phytoplankton but did not indicate a shadow diatom bloom preceding the cladoceran response. Given the ephemeral boom-bust nature of cladoceran dynamics (Devassy *et al*., 1979; Sahu *et al*., 2015), how their growth response advantages translate to the more steady-state conditions of oligotrophic waters is an important open question, as are details of linkages to diazotrophy or other ecological conditions, that might selectively favor poecilostomatoid copepods. Lastly, recent studies have nicely illustrated how modern analytical methods, like nanoSIMS (nanometer-scale, secondary ion mass spectrometry), can be used to unravel the transfers of diazotroph-derived nitrogen in open-ocean food webs, but they also demonstrate that interpretations can be time or space dependent. Bonnet *et al*. (2016), for example, provided strong support for significant transfer of *Trichodesmium*-fixed nitrogen to diatoms in the ultra-oligotrophic southwest Pacific. With similar methodology and in the same region, however, Caffin *et al.* (2018) reported that picoplankton (*Prochlorococcus*, *Synechococcus* and bacteria) were the main beneficiaries (>90%) of *Trichodesmium* nitrogen, which was then transferred inefficiently to zooplankton. Therefore, to understand the specific circumstances underlying favorable food webs for BFT larvae in spawning regions, there is no substitute for studies conducted in those areas at the appropriate times.

Conclusions and recommendations

Whether BFT populations will be strongly impacted by or resilient to climate change is a complex matter that depends on many factors, including physical and ecological effects on larval, juvenile and adult habitats, the ocean currents that connect them, physiological, behavioral and spawning plasticity, and management strategies (Karnauskas *et al*., 2015; Kimura *et al*., 2010; Llopiz *et al*., 2014; Muhling *et al*., 2011, 2015, 2017). While larval studies alone cannot answer the climate change question, they are nonetheless essential for connecting projections and models of future ocean conditions to a particularly vulnerable phase of BFT life history. In this regard, three major points or conclusions can be drawn from the present review. The first is that BFT have characteristics that can make them excellent model organisms for investigating the linkages between plankton dynamics and economically valuable fisheries in open-ocean ecosystems. Unlike wide-ranging tropical tunas, their use of surface mixed-layer waters in restricted spawning regions during specific times of the year lends itself to defined and tractable research agendas for evaluating the ecological conditions associated with larval success. At the same time, the broad similarities in diet between larval BFT and other *Thunnus* and billfish species suggest that lessons learned from studies in BFT spawning regions may also be broadly applicable to the early life histories of other valuable top consumers throughout warm oligotrophic regions of the oceans.

The second point is that conventional understanding and approaches to studying the food webs of open-ocean ecosystems have not yet led, and likely cannot lead, to the kind of understanding that is needed about habitat qualities that relate most directly to successful larval feeding, growth and survival. Biological oceanographers with the interest and expertise to study the structure and flows of open-ocean food webs have typically had a lower-level, biomass-based (as opposed to taxon-based) focus with little attention to, or apparent awareness of, the unusual trophic pathways to the favored prey of fish larvae. Fisheries researchers have similarly refined techniques for recognizing the physical characteristics of waters where larvae are found and for measuring larval feeding, age and growth, but have not connected to the underlying plankton dynamics of those systems that make them more or less favorable for larvae. Both of these perspectives and areas of expertise must come together in collaborative studies that focus on the trophic pathways most relevant to fish larvae, the factors that drive their variability in spawning regions, and their effects on larval feeding, growth and survival.

Lastly, there are abundant and interesting scientific issues, both basic and applied, to drive research of this kind, as well as modern tools and approaches for doing so. Research that addresses the hypothesized linkage between *Trichodesmium*/diazotrophy and the specific selected prey of tuna larvae would explore end-to-end food-web relationships, from biogeochemistry to fish, in ways that are broadly advocated (Moloney *et al*., 2011; Mitra *et al*., 2014), yet seldom realized. Related questions, such as the roles and implications of habitat variability on food webs and larval growth-survival outcomes, also need to be investigated, as mesoscale ocean features are disproportionately important as spawning sites of adult BFT (Alemany *et al*., 2010; Lindo-Atichati *et al*., 2012; Laiz-Carrion *et al*., 2015; Domingues *et al*., 2016). These are questions that challenge the boundaries of current knowledge about open-ocean food-web structure, highlight the importance of zooplankton differences and diversity (size is not everything) in ocean ecosystem function (Steinberg and Landry, 2017), and have management implications for the possible resiliency of BFT early life history to projected climate impacts. For both larvae and prey, open issues of dietary selectivity and trophic position are amenable for measurement by modern molecular and compound-specific isotopic techniques (Troedsson *et al*., 2009; O'Rorke *et al*., 2012; Décima *et al*., 2017), as are detailed assessments of trophic cycling and transfer by advanced isotope-based technologies (Bonnet *et al*., 2016; Caffin *et al*., 2018). The egg/embryo bearing traits of cladocerans, Corycaeidae and various other potential prey can also be usefully exploited as indices of their relative growth and production (Saunders *et al*., 1999; Nielsen *et al*., 2002), allowing spatial and temporal mapping of the production environments for relevant prey at the same scales as hydrographic, biogeochemical, primary production and larval BFT feeding and growth measurements. These are not research issues that can be resolved by synthesizing existing data into bigger and better models, but require field-focused efforts designed to provide new knowledge that bridges the gap between oceanographic and fisheries perspectives in ocean ecology. We believe that such integrative studies will yield many new insights into the functioning of open-ocean systems that will advance modeling, ecosystem-based fisheries management, and future ocean predictions.

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Figure Legends

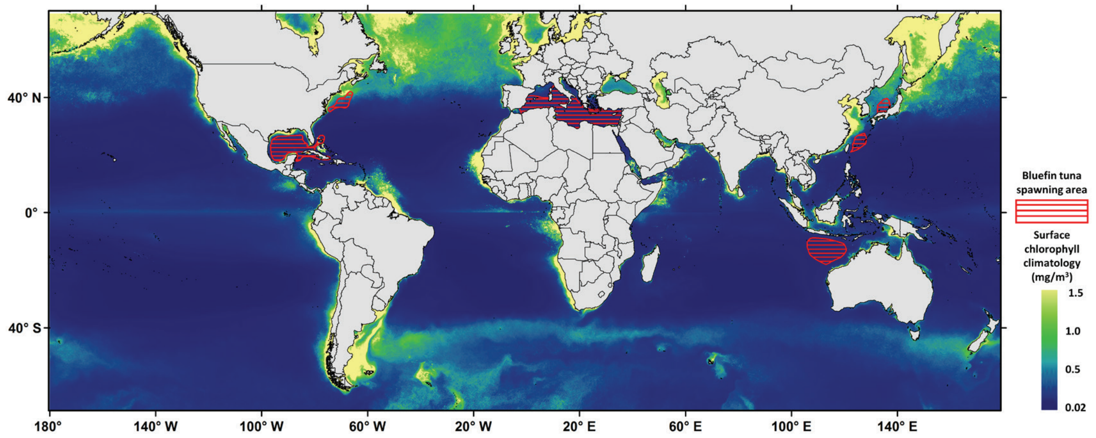
Fig. 1. Global map showing the known spawning areas for Atlantic, Pacific and Southern species of bluefin tuna superimposed on surface chlorophyll climatology from the MODIS Aqua satellite (2003-2016). Southern Hemisphere is the mean chlorophyll for the months of January-March, the peak spawning season of southern bluefin tuna. Northern Hemisphere is the mean surface chlorophyll for May-July, the spawning season of Atlantic and Pacific BFT.

Fig. 2. Summary of dietary studies of bluefin tuna larvae showing percentage composition of diet (% prey abundances) and significant trends in selection (positive = upward arrow; negative = downward arrow; relative to prey abundances in the ambient plankton community). SBT = southern; ABT = Atlantic; PBT = Pacific. Size (mm) is size range of larvae analyzed; n = number of larvae analyzed.

Fig. 3. Schematic diagram of food-web relationships supporting bluefin tuna larvae in open-ocean oligotrophic spawning regions plotted relative to body size and assumed trophic position. Arrows from picophytoplankton depict the conventional microbial food chain via phagotrophic protists to copepod-dominated mesozooplankton and the alternate route of direct picoplankton consumption by appendicularians. Arrows from comparably-sized zooplankton prey highlight the disproportionate importance of less-well-studied cladocerans and carnivorous poecilostomatoid copepods to the diets of BFT larvae compared to appendicularians, cyclopoid, calanoid and particle-associated poecilostomatoid copepods. Double-arrow dotted line represents the consortium of microphytoplankton taxa, *Trichodesmium* and diazotroph-diatom associations, that contribute directly to nitrogen fixation, as well as diatoms that utilize nitrogen released from *Trichodesmium*. Dashed lines with question marks indicate uncertainties in trophic relationships of the major selected prey of BFT larvae.

Table 1. Field estimates of % larvae feeding and number of prey per gut for larvae of southern (SBFT), Atlantic (ABFT) and Pacific (PBFT) bluefin tuna. Med = Mediterranean Sea; GoM = Gulf of Mexico. Size (mm) and *n* are the size range and number of larvae analysed. All data, except for Uotani *et al.* (1981), are for larvae collected during daylight hours only.

Stock	**Size (mm)**	***n***	**% Feeding**	**Prey/gut**	**Reference**
SBFT	2.2-9.6	316	78%	1.3	Uotani et al (1981)
SBFT	2.7-9.8	409	53%	1.2 ± 0.5	Young and Davis (1990)
ABFT-Med	2.6-8.7	107	94%	7.1 ± 5.7	Catalán et al. (2011)
ABFT-GoM	2.0-10	87	94%	7.9 ± 5.8	Llopiz et al. (2015)
ABFT-GoM	3.0-6.7	100	57%	1.1 ± 1.3	Tilley et al. (2016)
PBFT	2.7-7.6	96	64%	1.3 ± 1.7	Kodama et al. (2017)



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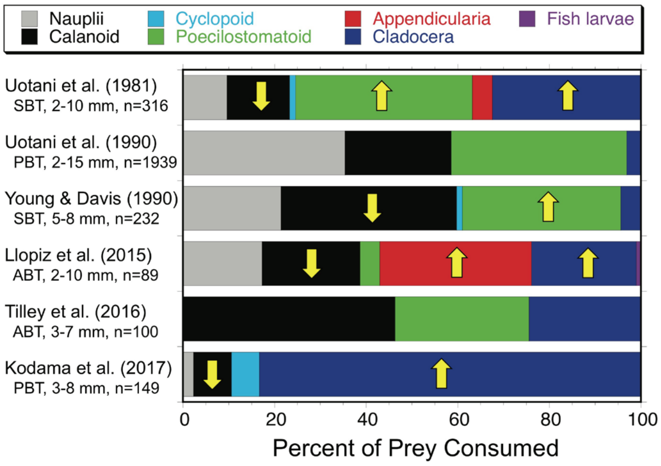

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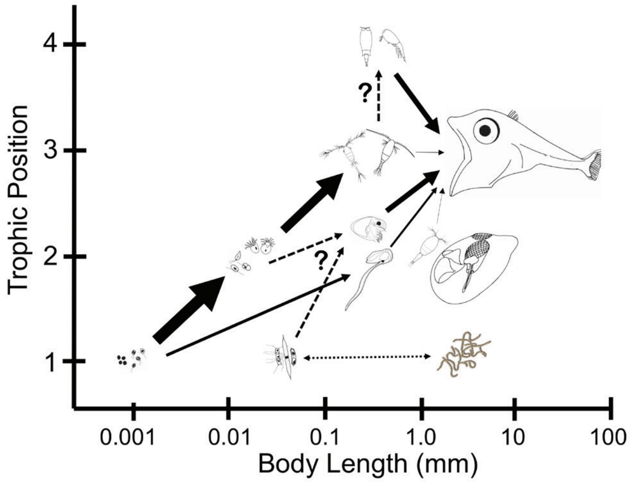

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