Plankton food webs of the Gulf of Mexico spawning grounds of Atlantic Bluefin tuna

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Please note that this pre-print uses extensive unpublished field data that will be included in multiple manuscripts currently in preparation for a special issue of Journal of Plankton Research. Since these manuscripts are not yet available, throughout this pre-print I have cited not only the manuscripts that will eventually contain the data, but also currently available manuscripts that use similar (and often identical) sampling and analytical approaches.

ABSTRACT

We used linear inverse ecosystem modeling techniques to assimilate data from extensive Lagrangian field experiments into a mass-balance constrained food web for the Gulf of Mexico open-ocean ecosystem. This region is highly oligotrophic, yet Atlantic Bluefin Tuna (ABT) travel long distances from feeding grounds in the North Atlantic to spawn there. Our results show that the food web is dominated by the microbial loop (>80% of net primary productivity is respired by heterotrophic bacteria and protists that feed on them). In contrast, herbivorous food web pathways from phytoplankton to metazoan zooplankton process <4% of net primary production in the mixed layer. Nevertheless, ABT larvae feed preferentially on calanoid copepods and other suspension-feeding zooplankton that in turn derive much of their nutrition from diatoms and mixotrophic flagellates. This allows ABT larvae to maintain a comparatively low trophic level (~4.0 for pre-flexion larvae; ~4.2 for post-flexion larvae) that increases trophic transfer from phytoplankton to larval fish.

INTRODUCTION

The open-ocean Gulf of Mexico (GoM) is a nutrient-poor, low plankton biomass region (Biggs & Ressler, 2001, Damien *et al.*, 2018, Muller-Karger *et al.*, 2015, Shropshire *et al.*, 2020). Nevertheless, it is an important region for spawning and larval development of many commercially-important fishes (Cornic *et al.*, 2018, Kitchens & Rooker, 2014, Lindo-Atichati *et al.*, 2012, Rooker *et al.*, 2013, Rooker *et al.*, 2012). The western stock of Atlantic Bluefin Tuna (ABT) travel long distances from feeding grounds throughout the North Atlantic to spawning grounds in the oligotrophic GoM, implying that some characteristics of this region enhance larval success (Rooker *et al.*, 2007, Teo *et al.*, 2007). One strong possibility is that low predator abundances in this food-poor region are a prerequisite for pelagic larvae to survive to maturity (Biggs, 1992). Nevertheless, it remains unclear how ABT and other GoM larval fishes manage to obtain sufficient nutrition during their critical first-feeding period.

Discerning the structure of GoM planktonic food webs is crucial to answering such questions. ABT larvae are selective feeders that rely disproportionately on specific prey taxa including calanoid and poecilostomatoid copepods, cladocerans, and appendicularians (Llopiz *et al.*, 2015, Llopiz *et al.*, 2010, Shiroza *et al.*, in prep., Tilley *et al.*, 2016). These prey items, however, have distinctly different trophic and ecological roles. Appendicularians are filter-feeding pelagic tunicates with fine meshes that give them access to some of the smallest cyanobacteria in the ocean (Alldredge, 1976, Gorsky & Fenaux, 1998). Poecilostomatoid copepods, by contrast, are predators of other metazoan zooplankton, and hence likely feed comparatively high on the food chain (Turner, 1986). Cladocerans and calanoid copepods are often omnivorous filter feeders, although calanoid copepods can fill multiple trophic roles within the planktonic food web (Bode *et al.*, 2015, Katechakis & Stibor, 2004, Mauchline *et al.*, 1998, Uye & Kayano, 1994).

Elucidating the linkages between larval fish, their prey, and the base of the planktonic food web is crucial to predicting climate change impacts on larval survival (Landry *et al.*, 2019). Different phytoplankton functional groups (e.g., *Prochlorococcus*, *Trichodesmium*,

nanoflagellates, unicellular microbial diazotrophs) will have different responses to warming, acidification, and increased stratification in the oligotrophic ocean (Barton *et al.*, 2016, Flombaum *et al.*, 2013, Hong *et al.*, 2017, Rost *et al.*, 2008). These variable responses originate from different physiological responses to stressors, but also to fundamentally different relationships between these groups and limiting nutrient, light, or temperature conditions. For instance: *Trichodesmium* and other diazotrophs are not nitrogen limited, *Prochlorococcus* is well adapted to utilizing recycled nitrogen available at low concentrations in oligotrophic regions, and nanoflagellates may need to rely partially on phagotrophic behavior (mixotrophy) to alleviate nutrient stress (Scanlan & Post, 2008, Stoecker *et al.*, 2017, Zehr, 2011). The pathways that connect different nutrient sources (upwelling, lateral advection, recycled production, and diazotrophy) through phytoplankton and zooplankton to larval fishes will fundamentally determine how these organisms respond to climate change.

In this study, we use linear inverse models (LIM) as a data synthesis tool to constrain pelagic food webs of the oligotrophic GoM. We utilize results from field experiments designed to investigate the open-ocean GoM ecosystem from nutrients to fish (Landry & Lamkin, in prep.). LIM allows us to incorporate diverse ecosystem measurements (e.g., primary productivity, protistan grazing rates, copepod $\delta^{15}\text{N}$, and larval ABT gut contents) into a mass-balance constrained ecosystem model. We use the results to address three distinct questions: What is the trophic level of larval ABT and what is the trophic efficiency of food chains leading to larval ABT? Which phytoplankton groups ultimately support secondary production by larval ABT? Are specific food web pathways to larval ABT less reliant on upwelled nitrate?

METHODS

In situ measurements

Our data are derived from two cruises in ABT spawning grounds in April-May 2017 and 2018 as part of the Bluefin Larvae in Oligotrophic Ocean Foodwebs: Investigating Nutrients to Zooplankton in the Gulf of Mexico (BLOOFINZ-GoM) Project (Table 1). During these cruises, we conducted regional zooplankton sampling surveys, guided in part by the Bluefin Tuna index (Domingues *et al.*, 2016), to identify contrasting open-ocean water parcels with and without high abundances of ABT larvae (Landry & Lamkin, in prep.). We then conducted three- to five-day Lagrangian experiments (hereafter “cycles”), while following satellite-enabled drift arrays with 3×1-m holey-sock drogues centered at 15 m depth (Landry, 2009, Stukel *et al.*, 2015).

During each cycle, we made daily profiles with a CTD-Niskin rosette to measure temperature, salinity, and density and collect samples for: chlorophyll *a* measurements (by the acidification method, Strickland & Parsons, 1972), phytoplankton pigment analyses (by high-pressure liquid chromatography), picophytoplankton and heterotrophic bacteria enumeration (by flow cytometry; Selph *et al.*, 2016, Selph *et al.*, in prep.), nano- and microphytoplankton biomass (Selph *et al.*, in prep., Taylor & Landry, 2018), *Trichodesmium* biomass (Selph *et al.*, in prep.), nutrients (nitrate and ammonium; Knapp *et al.*, in prep.), dissolved organic nitrogen (DON, Knapp *et al.*, in prep.), particulate organic nitrogen (PON, Kelly *et al.*, in prep., Stukel *et al.*,

2016), and $\delta^{15}\text{N}$ of nitrate, DON, and PON (Kelly *et al.*, in prep., Knapp *et al.*, 2005, Knapp *et al.*, in prep., Sigman *et al.*, 2001).

We also conducted a suite of daily *in situ* rate measurements that were incubated in mesh bags affixed at 6 depths (spanning the euphotic zone) on one of the floating arrays (Landry, 2009, Landry & Lamkin, in prep.). These measurements included nitrate uptake (Stukel *et al.*, 2016, Yingling *et al.*, in prep.), net primary production (Yingling *et al.*, in prep.), and group-specific phytoplankton growth and mortality due to protistan grazing (Landry *et al.*, 2016, Landry *et al.*, in prep.). All *in situ* incubations were conducted for 24 h at natural light and temperature conditions. We also conducted shorter (4 – 6 h) deckboard incubations for nitrate and ammonium uptake (Stukel *et al.*, 2016, Yingling *et al.*, in prep.).

Twice per day (mid-day and midnight) we conducted oblique net tows through the euphotic zone to collect mesozooplankton that were analyzed for dry weight, carbon, nitrogen, isotopes and gut pigment content (Décima *et al.*, 2019, Swalethorp *et al.*, in prep.). Gut pigment contents were analyzed as in Décima *et al.* (2016) to estimate grazing rates (Landry *et al.*, in prep.). More frequent net tows were conducted to a depth of 25 m to collect larval ABT for abundance, size, dry weight, gut content, otolith-based age, and isotopic measurements (Laiz-Carrión *et al.*, 2015, Malca *et al.*, 2017, Malca *et al.*, in prep., Shiroza *et al.*, in prep.).

Nitrogen inputs to and outputs from the euphotic zone were constrained using sediment traps, thorium measurements, and Thorpe scale analyses. Surface-tethered drifting sediment traps were used to collect sinking PON, chlorophyll, and phaeopigments at 50 m depth, near the base of the euphotic zone (~120 m), and beneath the euphotic zone (200 m) (Kelly *et al.*, in prep., Stukel *et al.*, 2019). ^{238}U - ^{234}Th disequilibrium was used as an independent estimate of sinking PON (Kelly *et al.*, in prep., Stukel *et al.*, 2019). We used Thorpe-scale analyses to constrain vertical eddy diffusivity and upward nitrate flux (Gargett & Garner, 2008, Kelly *et al.*, in prep.). We combined day-night differences in mesozooplankton biomass with allometric ammonium excretion relationships to quantify active transport by diel vertical migrants (Ikeda, 1985, Kelly *et al.*, in prep.).

<u>Rate Measurements</u>	<u>Units</u>	<u>Cycle 1</u>	<u>Cycle 2</u>	<u>Cycle 3</u>	<u>Cycle 4</u>	<u>Cycle 5</u>	<u>Source</u>
NPP (shallow)	(mmol N m ⁻² d ⁻¹)	2.23 ± 0.13	1.93 ± 0.15	2.46 ± 0.26	2.4 ± 0.11	3.08 ± 0.14	Yingling et al. (this iss
NPP (deep)	(mmol N m ⁻² d ⁻¹)	1.64 ± 0.07	1.75 ± 0.08	1.3 ± 0.08	1.92 ± 0.05	1.34 ± 0.05	Yingling et al. (this iss
f-ratio (shallow)	(mmol N m ⁻² d ⁻¹)	0.06 ± 0.04	0.01 ± 0	0.04 ± 0.04	0.06 ± 0.02	0.14 ± 0.04	Yingling et al. (this iss
f-ratio (deep)	(mmol N m ⁻² d ⁻¹)	0.44 ± 0.3	0.03 ± 0.01	0.07 ± 0.07	0.07 ± 0.02	0.09 ± 0.02	Yingling et al. (this iss
Protistan Grazing Rate (shallow)	(mmol N m ⁻² d ⁻¹)	3.17 ± 1.11	2.22 ± 1.09	2.11 ± 0.57	2.76 ± 0.58	3.51 ± 0.19	Yingling et al. (this iss
Protistan Grazing Rate (deep)	(mmol N m ⁻² d ⁻¹)	3.42 ± 1.15	2.68 ± 1.32	1.64 ± 0.47	2.78 ± 0.5	1.77 ± 0.49	Yingling et al. (this iss
Picophyto NPP (shallow)	(mmol N m ⁻² d ⁻¹)	1.47 ± 0.23	0 ± 0	0 ± 0	0 ± 0	0 ± 0	Landry et al. (this iss
Picophyto NPP (deep)	(mmol N m ⁻² d ⁻¹)	1.26 ± 0.22	0 ± 0	0 ± 0	0 ± 0	0 ± 0	Landry et al. (this iss
Flagellate NPP (shallow)	(mmol N m ⁻² d ⁻¹)	2.79 ± 0.64	2.23 ± 1.75	-	1.41 ± 0.37	0.44 ± 0.17	Landry et al. (this iss
Flagellate NPP (deep)	(mmol N m ⁻² d ⁻¹)	1.52 ± 0.76	0.7 ± 0.55	-	0.48 ± 0.2	0.77 ± 0.53	Landry et al. (this iss
Diatom NPP (shallow)	(mmol N m ⁻² d ⁻¹)	0.16 ± 0.09	0.0028 ± 0.0034	-	0.03 ± 0.01	0.05 ± 0.03	Landry et al. (this iss
Diatom NPP (deep)	(mmol N m ⁻² d ⁻¹)	0.15 ± 0.13	0.002 ± 0.0024	-	0.02 ± 0.01	0.03 ± 0.02	Landry et al. (this iss
Picophyto Mortality (shallow)	(mmol N m ⁻² d ⁻¹)	1.01 ± 0.38	0 ± 0	0 ± 0	0 ± 0	0 ± 0	Landry et al. (this iss
Picophyto Mortality (deep)	(mmol N m ⁻² d ⁻¹)	0.69 ± 0.06	0 ± 0	0 ± 0	0 ± 0	0 ± 0	Landry et al. (this iss
Flagellate Mortality (shallow)	(mmol N m ⁻² d ⁻¹)	2.04 ± 0.35	1.73 ± 1.59	-	0.62 ± 0.14	0.6 ± 0.26	Landry et al. (this iss
Flagellate Mortality (deep)	(mmol N m ⁻² d ⁻¹)	1.34 ± 0.41	0.19 ± 0.17	-	0.17 ± 0.17	0.87 ± 0.6	Landry et al. (this iss
Diatom Mortality (shallow)	(mmol N m ⁻² d ⁻¹)	0.11 ± 0.06	0.001 ± 0.002	-	0.02 ± 0.01	0.04 ± 0.02	Landry et al. (this iss
Diatom Mortality (deep)	(mmol N m ⁻² d ⁻¹)	0.02 ± 0.02	0.001 ± 0.001	-	0.01 ± 0	0.01 ± 0.01	Landry et al. (this iss
NVM Mesozoo Grazing	(mmol N m ⁻² d ⁻¹)	0.39 ± 0.1	0.15 ± 0.02	0.46 ± 0.05	0.21 ± 0.04	0.52 ± 0.1	Landry et al. (this iss
VM Mesozoo Grazing	(mmol N m ⁻² d ⁻¹)	0.03 ± 0.06	0.13 ± 0.06	0.09 ± 0.05	0.02 ± 0.02	0.15 ± 0.08	Landry et al. (this iss
SedTrap Flux (shallow)	(mmol N m ⁻² d ⁻¹)	1.53 ± 0.55	0.82 ± 0.05	0.98 ± 0.26	0.59 ± 0.04	1.08 ± 0.07	Kelly et al. (this iss
SedTrap Flux (deep)	(mmol N m ⁻² d ⁻¹)	0.46 ± 0.02	0.52 ± 0.18	1.14 ± 0.18	0.47 ± 0.1	0.87 ± 0.18	Kelly et al. (this iss
Thorium Flux (shallow)	(mmol N m ⁻² d ⁻¹)	-	-	-	-	-	Kelly et al. (this iss
Thorium Flux (deep)	(mmol N m ⁻² d ⁻¹)	-	-	-	-	-	Kelly et al. (this iss
Chl Sinking (shallow)	(mmol N m ⁻² d ⁻¹)	0.02 ± 0.02	0.02 ± 0.01	-	0.01 ± 0	0.03 ± 0.02	Kelly et al. (this iss
Chl Sinking (deep)	(mmol N m ⁻² d ⁻¹)	0.02 ± 0.01	0.06 ± 0.02	-	0.02 ± 0.02	0.05 ± 0.04	Kelly et al. (this iss
Fecal Pellet Sinking (shallow)	(mmol N m ⁻² d ⁻¹)	0.03 ± 0.03	0.01 ± 0.01	-	0 ± 0	0.02 ± 0.02	Kelly et al. (this iss
Fecal Pellet Sinking (deep)	(mmol N m ⁻² d ⁻¹)	0.13 ± 0.06	0.09 ± 0.06	-	0.14 ± 0.14	0.25 ± 0.2	Kelly et al. (this iss
Microzoo to Preflex	(mmol N m ⁻² d ⁻¹)	0.16 ± 0.08	-	-	-	-	Shiroza et al. (this iss
Microzoo to Postflex	(mmol N m ⁻² d ⁻¹)	2.06 ± 0.33	-	-	-	-	Shiroza et al. (this iss
Appendicularian to Preflex	(mmol N m ⁻² d ⁻¹)	0.45 ± 0.18	-	-	-	-	Shiroza et al. (this iss
Appendicularian to Postflex	(mmol N m ⁻² d ⁻¹)	3.27 ± 0.23	-	-	-	-	Shiroza et al. (this iss
Cladoceran to Preflex	(mmol N m ⁻² d ⁻¹)	0.28 ± 0.28	-	-	-	-	Shiroza et al. (this iss
Cladoceran to Postflex	(mmol N m ⁻² d ⁻¹)	22.03 ± 2.12	-	-	-	-	Shiroza et al. (this iss
Calanoids to Preflex	(mmol N m ⁻² d ⁻¹)	5.46 ± 2.27	-	-	-	-	Shiroza et al. (this iss
Calanoids to Postflex	(mmol N m ⁻² d ⁻¹)	37.72 ± 0.57	-	-	-	-	Shiroza et al. (this iss
Poecilastomatoids to Preflex	(mmol N m ⁻² d ⁻¹)	0 ± 0.01	-	-	-	-	Shiroza et al. (this iss
Poecilastomatoids to Postflex	(mmol N m ⁻² d ⁻¹)	8.47 ± 0.63	-	-	-	-	Shiroza et al. (this iss
<u>Biomass and other measurements</u>							
Temperature (0-50)	deg C	24.31	25.16	26.18	25.22	24.44	CTD

Temperature (50-120)	deg C	22.14	23.87	23.96	24.4	21.68	CTD
Temperature (120-300)	deg C	16.41	19.28	18.99	18.91	16.46	CTD
HerbNVM biomass (shallow)	($\mu\text{mol N m}^{-2}$)	8.94	-	-	-	45.44	Shiroza et al. (this issue)
App Biomass (shallow)	($\mu\text{mol N m}^{-2}$)	0.22	-	-	-	0.32	Shiroza et al. (this issue)
Clad Biomass (shallow)	($\mu\text{mol N m}^{-2}$)	14.91	-	-	-	18.13	Shiroza et al. (this issue)
NVM Cal Biomass (shallow)	($\mu\text{mol N m}^{-2}$)	2.74	-	-	-	1.92	Shiroza et al. (this issue)
Chaeto Biomass (shallow)	($\mu\text{mol N m}^{-2}$)	107.04	-	-	-	130.13	Shiroza et al. (this issue)
Poecil Biomass (shallow)	($\mu\text{mol N m}^{-2}$)	10.82	-	-	-	11.07	Shiroza et al. (this issue)
Gel Pred Biomass (shallow)	($\mu\text{mol N m}^{-2}$)	-	-	-	-	-	
Preflex Biomass (shallow)	($\mu\text{mol N m}^{-2}$)	0.1	-	-	-	-	Shiroza et al. (this issue)
Postflex Biomass (shallow)	($\mu\text{mol N m}^{-2}$)	1.12	-	-	-	-	Shiroza et al. (this issue)
HerbVM Biomass	($\mu\text{mol N m}^{-2}$)	34.3	-	-	-	-	Shiroza et al. (this issue)
vmCal Biomass	($\mu\text{mol N m}^{-2}$)	26.4	-	-	-	-	Shiroza et al. (this issue)
HerbNVM biomass (deep)	(mmol N m^{-2})	-	-	-	-	-	
App Biomass (deep)	(mmol N m^{-2})	-	-	-	-	-	
Clad Biomass (deep)	(mmol N m^{-2})	-	-	-	-	-	
NVM Cal Biomass (deep)	(mmol N m^{-2})	-	-	-	-	-	
Chaeto Biomass (deep)	(mmol N m^{-2})	-	-	-	-	-	
Poecil Biomass (deep)	(mmol N m^{-2})	-	-	-	-	-	
Gel Pred Biomass (deep)	(mmol N m^{-2})	-	-	-	-	-	
Cyano Biomass (shallow)	(mmol N m^{-2})	9.39	7.45	7.71	12.86	18.39	Selph et al. (this issue)
Tricho Biomass (shallow)	($\mu\text{mol N m}^{-2}$)	27.23	5.15	17.05	3.5	0.97	Selph et al. (this issue)
Diatom Biomass (shallow)	(mmol N m^{-2})	0.13	0.003	1.12	0.03	0.08	Selph et al. (this issue)
Flag Biomass (shallow)	(mmol N m^{-2})	4.84	2.82	6.74	1.61	2.74	Selph et al. (this issue)
HNF Biomass (shallow)	(mmol N m^{-2})	-	-	-	-	-	
MIC Biomass (shallow)	(mmol N m^{-2})	-	-	-	-	-	
Cyano Biomass (deep)	(mmol N m^{-2})	8.22	8.93	9	15.41	6.77	Selph et al. (this issue)
Tricho Biomass (deep)	($\mu\text{mol N m}^{-2}$)	0.77	0.3	1.62	0.08	0.11	Selph et al. (this issue)
Diatom Biomass (deep)	(mmol N m^{-2})	0.12	-0.003	-1.12	0.03	0.04	Selph et al. (this issue)
Flag Biomass (deep)	(mmol N m^{-2})	6.97	8.97	5.43	1.63	3.63	Selph et al. (this issue)
HNF Biomass (deep)	(mmol N m^{-2})	-	-	-	-	-	
MIC Biomass (deep)	(mmol N m^{-2})	-	-	-	-	-	
HerbNVM Size	($\mu\text{g C ind}^{-1}$)	1.35	1.35	1.35	1.35	1.35	Shiroza et al. (this issue)
App Size	($\mu\text{g C ind}^{-1}$)	0.07	0.07	0.07	0.07	0.07	Shiroza et al. (this issue)
Clad Size	($\mu\text{g C ind}^{-1}$)	2.63	2.63	2.63	2.63	2.63	Shiroza et al. (this issue)
NVM Cal Size	($\mu\text{g C ind}^{-1}$)	4.44	4.44	4.44	4.44	4.44	Shiroza et al. (this issue)
Chaeto Size	($\mu\text{g C ind}^{-1}$)	20.83	20.83	20.83	20.83	20.83	Shiroza et al. (this issue)
Poecil Size	($\mu\text{g C ind}^{-1}$)	2.33	2.33	2.33	2.33	2.33	Shiroza et al. (this issue)
Gel Pred Size	($\mu\text{g C ind}^{-1}$)	-	-	-	-	-	
Preflex Size	($\mu\text{g C ind}^{-1}$)	83.71	83.71	83.71	83.71	83.71	Laiz-Carrion et al. (this issue)
Postflex Size	($\mu\text{g C ind}^{-1}$)	179.75	179.75	179.75	179.75	179.75	Laiz-Carrion et al. (this issue)
HerbVM Size	($\mu\text{g C ind}^{-1}$)	4.44	4.44	4.44	4.44	4.44	Laiz-Carrion et al. (this issue)

vmCal Size	($\mu\text{g C ind}^{-1}$)	4.44	4.44	4.44	4.44	4.44	Laiz-Carrión et al. (this issue)
Maximum upwelling rate (shallow)	($\mu\text{mol N m}^{-2} \text{d}^{-1}$)	0.09	0.09	0.09	0.09	0.09	Kelly et al. (this issue)
Maximum upwelling rate (deep)	($\mu\text{mol N m}^{-2} \text{d}^{-1}$)	366.79	1142.9	1200.44	1020.28	1543.33	Kelly et al. (this issue)
$\delta^{15}\text{N}$ Values							
Upwelled Nitrate	$\delta^{15}\text{N}_{\text{AIR}} (\text{‰})$	3.20	3.10	2.80	2.00	2.90	Knapp et al. (this issue)
Preflex ABT	$\delta^{15}\text{N}_{\text{AIR}} (\text{‰})$	4.63	-	-	-	7.50	Swalethorp et al. (this issue)
Postflex ABT	$\delta^{15}\text{N}_{\text{AIR}} (\text{‰})$	4.21	-	-	-	6.16	Swalethorp et al. (this issue)
Shallow SedTrap	$\delta^{15}\text{N}_{\text{AIR}} (\text{‰})$	2.90	2.51	1.68	2.50	3.80	Kelly et al. (this issue)
Deep SedTrap	$\delta^{15}\text{N}_{\text{AIR}} (\text{‰})$	4.89	2.86	3.71	3.73	4.55	Kelly et al. (this issue)
Shallow DON	$\delta^{15}\text{N}_{\text{AIR}} (\text{‰})$	3.37	3.37	3.37	3.45	3.27	Knapp et al. (this issue)
Deep DON	$\delta^{15}\text{N}_{\text{AIR}} (\text{‰})$	3.31	3.31	3.31	3.33	3.39	Knapp et al. (this issue)
Shallow PON	$\delta^{15}\text{N}_{\text{AIR}} (\text{‰})$	1.44	1.20	1.11	2.13	2.66	Kelly et al. (this issue)
Deep PON	$\delta^{15}\text{N}_{\text{AIR}} (\text{‰})$	1.80	1.57	2.45	1.78	1.63	Kelly et al. (this issue)

Table 1. Rate, biomass, and $\delta^{15}\text{N}$ measurements used as inputs to the inverse model.

Food web structure

Our food web structure was specifically designed to address the variability in GoM food chains that channel energy towards the prey of ABT larvae (either efficiently or inefficiently) or to the multiple plankton taxa that are not suitable prey for ABT larvae (Fig. 1). The model includes three nutrient classes (NO_3^- , NH_4^+ , and N_2) and three non-living organic matter pools (DOM, small detritus, and large detritus). It includes four phytoplankton: *Trichodesmium* and unicellular cyanobacteria (which are assumed to be potentially diazotrophic), diatoms, and mixotrophic flagellates. It also includes heterotrophic bacteria, heterotrophic nanoflagellates, and microzooplankton. Six suspension-feeding mesozooplankton are included: appendicularians (which are the only suspension feeders capable of feeding on cyanobacteria and heterotrophic bacteria), vertically-migrating calanoid copepods, non-vertically migrating calanoid copepods, cladocerans, other non-vertically migrating herbivorous suspension feeders, and other vertically-migrating herbivorous suspension feeders. It includes two small predatory mesozooplankton: chaetognaths and poecilostomatoid copepods. It also includes 4 “higher trophic levels” that serve as closure terms in the model: preflexion ABT larvae, postflexion ABT larvae, other planktivorous fish, and predatory gelatinous zooplankton (e.g., ctenophores and cnidarians). Trophic pathways are determined based on known predator-prey relationships. Because ABT larvae feed only in the mixed layer, we include two layers in the model: mixed layer, and deep euphotic zone. All model compartments are identical, except that ABT larvae only exist in the mixed layer. The two layers are connected through upward flux of nitrate, downward flux of sinking particles and the motions of vertical-migratory taxa, which are assumed to be able to freely migrate between the two layers during the night, but reside beneath the euphotic zone (i.e., outside the model) during the day. Inputs to the model include upwelled nitrate, diazotrophy, and lateral advection of POM and DOM. Closure terms include secondary production of higher

trophic levels, sinking of large detritus, sinking of diatoms, and sinking of mixotrophic flagellates, and excretion of vertical migratory taxa beneath the euphotic zone. We assume Redfield stoichiometry for all model flows, which allows us to relate respiration to ammonium excretion. We thus use the term “respiration” when relating respiratory or excretory fluxes to primary production and use the term “excretion” when discussing nutrient recycling. Supp. Table. 1 shows all model flows.

Fig. 1 – Food web structure. All major food web flows are shown (i.e., all flows between living organism groups). However, for visual simplicity, we omit production of NH_4^+ , DOM, and detritus by all living groups as well as consumption of detritus by protistan zooplankton and suspension-feeding metazoans. Stars indicate the highest trophic levels in the model. The secondary production of these groups is a closure term in the model. The model utilizes a two-layer structure (~mixed layer and deep euphotic zone). All trophic food web components exist in both layers except for larval ABT. For all model flows, see Supp. Table 1.

Inverse model solution

To constrain the flux of nitrogen through unmeasured ecosystem pathways, we used linear inverse modeling (LIM) techniques (Van Oevelen *et al.*, 2010, Vézina & Platt, 1988). LIM allows investigators to specify mass balance constraints that must be exactly fit by food web solutions ($A\vec{x} = \vec{b}$), approximate equations that quantify measured rates with associated measurement uncertainty ($E\vec{x} \approx \vec{f}$), and inequality constraints ($G\vec{x} \geq \vec{h}$) that represent *a priori* acceptable ranges for different ecosystem properties (e.g., gross growth efficiency of zooplankton is between 10% and 40%). We used a total of 44 mass-balance constraints (exact equalities), 82 *in situ* measurements (approximate equalities), and 248 inequality constraints.

However, with 302 total unknown food web flows ($\vec{x}$), the system remains under-constrained. To objectively determine a representative solution (and confidence limits) we used the Markov Chain Monte Carlo (MCMC) with ^{15}N approach (Stukel *et al.*, 2018a, Stukel *et al.*, 2018b). The MCMC approach initially uses the exact mass balance constraints to remove degrees of freedom from the solution and then creates bounds on the solution as formed by the hyperplanes prescribed by the inequality constraints (Kones *et al.*, 2009, Soetaert *et al.*, 2009, Van Den Meersche *et al.*, 2009). Then, starting with an initial guess of the solution that satisfies the equality and inequality constraints, the MCMC approach then conducts a random walk through the solution space bounded by $A\vec{x} = \vec{b}$ and $G\vec{x} \geq \vec{h}$. New solutions are accepted based on the relative misfits of the new and previous solution with respect to the approximate equality measurements ($E\vec{x} \approx \vec{f}$). This generates a set of solutions satisfying the equality and inequality constraints, and with the probability of inclusion of a specific solution related to how well it satisfies the combined field measurement constraints. The mean solution of the MCMC approach has been shown to more accurately recover withheld measurement constraints than the previously used L_2 minimum norm approach (Saint-Béat *et al.*, 2013, Stukel *et al.*, 2012). The MCMC+ ^{15}N approach builds on this previous work, but allows for the incorporation of non-linear constraints associated with unknown $\delta^{15}\text{N}$ values for some organisms or non-living nitrogen pools in the ecosystem. It uses a second varying solution vector ($\vec{\delta}$) quantifying the ^{15}N isotope fraction for each unknown nitrogen pool. A new solution set for $\vec{\delta}$ is determined at the same time as the new solution set for $\vec{x}$. $\vec{\delta}$ modifies approximate equality constraints associated with ^{15}N mass balance. For additional details, see Stukel *et al.* (2018a).

Food web analyses

Trophic levels (TL) for all zooplankton were computed as one plus the ingestion-weighted mean TL of prey. All phytoplankton were assumed TL=1, except mixotrophic flagellates, which had $TL = (1 - p_{phag}) + p_{phag}(1 + TL_{prey})$, where p_{phag} is the proportion of their nitrogen derived from phagotrophy (rather than dissolved nutrient uptake). Heterotrophic bacteria were assumed to have a TL equal to one plus the TL of the organism producing the organic matter they utilized.

To quantify indirect nitrogen flows through the food web, we used indirect food web flow analysis (Hannon, 1973). The normalized amount of nitrogen (direct and indirect) that any organism derives from any other organism (or non-living nitrogen pool) can be computed as $(I - G)^{-1}$, where I is the identity matrix and G is the normalized production matrix (i.e., a matrix giving the percentage of an organism's nitrogen requirement derived from any other organism).

Following Stukel *et al.* (2012) we defined three major food web pathways that describe energy and nutrient fluxes from the base of the food web: the herbivorous food chain, the multivorous food chain, and the microbial loop. The herbivorous food chain was defined as the sum of nitrogen flux from phytoplankton to metazoan zooplankton. The multivorous food chain was defined as the sum of nitrogen flux that reaches metazoan zooplankton after passing through

protistan grazers. The microbial loop was defined as the sum of bacterial respiration and the fraction of protistan respiration that was supported by bacterial production.

RESULTS

Model performance

The LIEM model did a decent job of matching field measurements. The square root mean squared error, which can be thought of as the average number of standard errors that model estimates were from the measurements, was 1.33 if we consider only the field rate measurements. It was 0.81 for all approximate equality equations (including the $\delta^{15}\text{N}$ mass balance equations). The largest mismatches between model and measurements were with respect to growth and grazing estimates for specific phytoplankton taxa (particularly mixotrophic flagellates). These model-data misfits are driven in large part by inconsistency in the field measurements; the sum of phytoplankton production for all taxa as determined by the microzooplankton dilution approach was higher than primary production estimated using $\text{H}^{13}\text{CO}_3^-$ uptake (Fig. 2). In comparison to rate measurements associated with lower trophic levels, the model very accurately recovered ingestion rates of larval ABT on different mesozooplankton groups (Fig. 2b). Model solutions were also strongly constrained by the comparatively low $\delta^{15}\text{N}$ of larval ABT (Fig. 3). The model struggled to determine solution vectors that matched the comparatively low $\delta^{15}\text{N}$ of larval ABT with the fairly similar measured $\delta^{15}\text{N}$ of upwelled nitrate, sinking detritus, and bulk suspended organic matter, thus leading to model misfits in the $\delta^{15}\text{N}$ mass balance equations.

Fig. 2 – Comparison between field measurements and model estimates for planktonic ecosystem rate measurements (a) and ABT feeding measurements (b).

Fig. 3 – Boxplots (median, inter-quartile ranges, and 95% C.I.) for $\delta^{15}\text{N}$ of mixed layer model compartments (light blue), deep euphotic zone compartments (dark blue), and vertically-migrating groups (red). Stars indicate field measurements.

Food web dynamics

Food web dynamics broadly reflected those expected for an oligotrophic, recycling-dominant ecosystem. NH_4^+ was the dominant source of nitrogen to phytoplankton (mean = 82%; 95% C.I. = 70 – 92%). NO_3^- uptake (15%; 6 – 27%) and N_2 fixation (2.9%; 0.12 – 7.5%) were comparatively less important. Nutrient utilization patterns were broadly similar in the vicinity of the deep chlorophyll max (>50 m depth), although NH_4^+ uptake was slightly less important (59%; 27 – 88%) and NO_3^- uptake was comparatively more important (40%; 11 – 72%), with a negligible role for N_2 fixation (1%; 0.023 – 3.6%). Total productivity was slightly higher in the shallow euphotic zone ($2.4 \text{ mmol N m}^{-2} \text{ d}^{-1}$; $2.2 - 2.6 \text{ mmol N m}^{-2} \text{ d}^{-1}$) than in the deep euphotic zone ($1.9 \text{ mmol N m}^{-2} \text{ d}^{-1}$; $1.7 - 2.0 \text{ mmol N m}^{-2} \text{ d}^{-1}$).

Picophytoplankton (54%; 38% - 68%) and flagellates (39%; 25 – 53%) were responsible for most of the primary production in the shallow euphotic zone. These contributions were notably flipped relative to the field data, which suggested greater production by flagellates. The model-data discrepancy related to the overall over-estimation of taxon-specific NPP by the dilution method, relative to $\text{H}^{14}\text{CO}_3^-$ uptake measurements, and also due to the fact that the solution vectors originating from cyanobacteria were more likely than those originating from flagellates, given other constraints on the ecosystem. Diatoms were comparatively less important (6.9%; 3.7 – 9.5%), while *Trichodesmium* production was negligible. The relative proportions of each group were similar at the deep chlorophyll max.

Phytoplankton mortality was dominated by protistan grazing. These zooplankton (including mixotrophic flagellates) consumed 67% (48 – 81%) of phytoplankton production. Metazoan

zooplankton consumed a much lower portion of phytoplankton production (13%; 8 – 19%), although they consumed more of the production of diatoms than protists did. Suspension-feeding metazoans also relied heavily on protistan zooplankton as dietary sources. This was reflected in trophic positions that averaged greater than 3.0 for all metazoans except appendicularians (Fig. 4). Predatory zooplankton (poecilostomatoid copepods, chaetognaths, and gelatinous predators) had particularly high trophic positions of 4.3, 4.3, and 4.6, respectively, in the upper euphotic zone. Their mean trophic positions in the deep euphotic zone were slightly lower (4.0, 3.9, and 4.3, for poecilostomatoid copepods, chaetognaths, and gelatinous predators, respectively).

Fig. 4 – Violin plots of trophic level of zooplankton and fish in the mixed layer (a) and deep chl max (b). Blue plots are ABT prey. Red plots are ABT.

Quantification of major food web pathways showed that the GoM euphotic zone is dominated by the microbial loop (Fig. 5). The microbial loop (defined as the respiration of heterotrophic bacteria and the proportion of protistan respiration supported by bacterial production) processed 76% (52 – 106%) of net primary production in the shallow euphotic zone and 81% (68 – 92%) of net primary production in the deep euphotic zone. Note that microbial loop respiration can exceed net primary production, because net primary production does not include phytoplankton

Fig. 5 – Flux through the herbivorous food chain, multivorous food chain, and microbial loop normalized to net primary production.

exudation of organic matter. For comparison, the herbivorous and multivorous food chains were responsible for 3.3% and 15% of NPP, respectively, in the shallow euphotic zone and 26% and 36%, respectively in the deep euphotic zone. The dominance of microbial loop pathways aligns with the importance of recycled NH_4^+ for phytoplankton production and conforms with an expectation of tight recycling in oligotrophic ecosystems with limited new nutrient supply. In the shallow euphotic zone, where recycling and the microbial loop were most important, phytoplankton and protistan zooplankton had approximately equal roles in DON production (32% and 33%, respectively), with much of the remainder coming from dissolution of detritus. Mesozooplankton excretion was responsible for only 3.3% of DOM production. Bacterial excretion was in turn responsible for 57% of NH_4^+ regeneration in the shallow euphotic zone, with protist excretion generating an additional 37% of the NH_4^+ used by phytoplankton.

Larval Atlantic Bluefin Tuna in the GoM Ecosystem

As suggested by the gut content data, our model results show that larval ABT feed predominantly on calanoid copepods, with a lesser role for microzooplankton, appendicularians, cladocerans, and poecilostomatoid copepods in their diets (Fig. 6). Calanoid copepods comprised 88.1% of the diet of preflexion ABT (95% C.I. = 77.4 – 94.9%). Microzooplankton (2.0%; C.I. = 0.4% - 4.2%), appendicularians (5.4%; 1.4 – 10.7%), and cladocerans (4.4%; 0.3 – 11.3%) were all small contributors to the diets of preflexion ABT, while poecilostomatoid copepods were negligible contributors to preflexion ABT diets (<0.3%). Although calanoid copepods were also the dominant dietary source for postflexion ABT (51.2%; 48.1 – 54.5%), these larger larvae had more varied diets with important contributions from cladocerans (30%; 25.9 – 33.9%) and poecilostomatoid copepods (11.5%; 9.9% -

Fig. 6 – Violin plots of larval ABT diets

Fig. 7 – The ratio of the trophic level of different modeled zooplankton and fish to the trophic level they would have in the longest possible model food chain.

13.1%).

The prevalence of suspension-feeding zooplankton in the diets of both pre-flexion and post-flexion diets led to relatively low trophic levels for ABT larvae (Fig. 4). Given the ecosystem structure used in the model (Fig. 1), larval ABT could potentially have a trophic level between 3 and 7. However, both preflexion and postflexion larvae had trophic levels on the low end of this range. Preflexion ABT had a trophic level of 4 (95% C.I. = 3.6 – 4.5), while postflexion ABT had a trophic level of 4.2 (3.9 – 4.5). Both groups of ABT larvae thus had a trophic level that averaged approximately 0.6 of their maximum possible trophic level (Fig. 7) and only one trophic level higher than the lowest theoretically possible trophic level they could take on within the food web. The trophic positions of larval ABT were thus notably low relative to the trophic positions they would take on if feeding on the longest possible food chains that the model allowed. Based on this metric, they were also notably lower in trophic position than many of the zooplankton and other fish in the model.

The food chains supporting larval ABT were diverse and relied on significant production of picophytoplankton, flagellates, and diatoms (while the production of *Trichodesmium* was insignificant for ABT food chains). Preflexion ABT excreted $1.6 \text{ nmol N m}^{-2} \text{ d}^{-1}$ ($0.58 - 3.4 \text{ nmol N m}^{-1} \text{ d}^{-1}$) derived from the production of flagellates, $0.97 (0.34 - 2.1) \text{ nmol N m}^{-1} \text{ d}^{-1}$ from picophytoplankton, and $0.75 (0.17 - 1.7) \text{ nmol N m}^{-1} \text{ d}^{-1}$ from diatoms (Fig. 8a). Post-flexion larvae excreted $12 (6.4 - 23) \text{ nmol N m}^{-1} \text{ d}^{-1}$ from flagellates, $7.6 (3.5 - 15) \text{ nmol N m}^{-1} \text{ d}^{-1}$ from picophytoplankton, and $4.3 (1.5 - 8.6) \text{ nmol N m}^{-1} \text{ d}^{-1}$. These values were influenced in large part by the different production rates of each phytoplankton taxa (flagellate, picophytoplankton, and diatom NPP in the shallow euphotic zone were $2.0, 1.5,$ and $0.1 \text{ mmol N m}^{-2} \text{ d}^{-1}$). When normalized to phytoplankton NPP it becomes clear that larval tuna rely disproportionately on the production of large phytoplankton (Fig. 8b). Pre-flexion ABT respired $3.6 \times 10^{-4} \%$ of diatom

Fig. 8 – Indirect foodweb flows to larval tuna (a, b), protists (c), and mesozooplankton (d). Panel a shows the amount of organic matter derived from each phytoplankton taxon that was respired by larval tuna. Panels b, c, and d show the proportion of the production of each phytoplankton taxon that was respired by either larval tuna (b), protists (c), or mesozooplankton (d). Only ABT prey are shown in d.

NPP and 1.1×10^{-4} % of flagellate NPP, compared to only 5.7×10^{-5} % of picophytoplankton NPP. Post-flexion larvae respired 2.1×10^{-3} % of diatom NPP, 8.4×10^{-4} % of flagellate NPP, and 4.4×10^{-4} % of picophytoplankton NPP. The proportion of *Trichodesmium* NPP respired by larvae was poorly constrained by the model, although *Trichodesmium* production was consistently low in all model solution vectors. The disproportionately large role of diatoms in larval ABT diets was reflected in the roles of diatoms in supporting their mesozooplankton prey (Fig. 8d). All four mesozooplankton prey taxa respired a higher proportion of diatom taxa than any other phytoplankton and three of the four had flagellates as the second most important phytoplankton taxa. Only appendicularians excreted a higher proportion of picophytoplankton production than flagellate production. These results for mesozooplankton were in stark contrast to similar proportional roles for phytoplankton in protists (Fig. 8c). Heterotrophic nanoflagellates relied disproportionately on picophytoplankton, respiring 26% of picophytoplankton NPP, while microzooplankton relied disproportionately on the NPP of flagellates (respiring 29% of flagellate NPP).

DISCUSSION

The open-ocean Gulf of Mexico is an incredibly oligotrophic ecosystem with low productivity and a deep nitracline (Biggs, 1992, Gomez *et al.*, 2018, Knapp *et al.*, in prep., Yingling *et al.*, in prep.). Nevertheless, it is an important spawning ground for many migratory fish species, including multiple species of tuna, dolphinfish, sailfish, and marlin (Cornic *et al.*, 2018, Kitchens & Rooker, 2014, Rooker *et al.*, 2012). Models suggest that vertical mixing is an important structuring process for productivity in the open-ocean Gulf (Gomez *et al.*, 2018). If vertical mixing is indeed crucial for supporting these oligotrophic systems, predicted future warming and increased stratification could have deleterious impacts on taxa living in the mixed layer (Liu *et al.*, 2015, Muhling *et al.*, 2011, Muhling *et al.*, 2015). Understanding how pelagic ecosystems, and the larval fish they support, will respond to climate change requires knowledge of the food web pathways that convert phytoplankton production into the preferred prey of different species (Landry *et al.*, 2019).

We can hypothesize two potential ways in which an organism's diet could make it well adapted to life in an oligotrophic region. First, it could feed preferentially on taxa that have either direct or indirect linkages to some of the most abundant primary producers in the ecosystem (e.g., cyanobacteria). For instance, a reliance on appendicularians would give larval fish access to a suspension-feeder that can feed directly on picophytoplankton (Gorsky & Fenaux, 1998, Llopiz *et al.*, 2010). Conversely, preference for calanoid copepods would make a larval fish more dependent on the production of diatoms and other large phytoplankton. A second, but not mutually-exclusive, hypothesis states that larval fish are more likely to thrive in oligotrophic ecosystems if they feed at a low trophic position, thus maximizing trophic transfer efficiency from phytoplankton to larvae, regardless of the source of the production.

Our results show no evidence for the former hypothesis. Although diatom production only contributed to ~20% of ABT larval diets, this was a disproportionately high fraction of the ABT

diet relative to the proportional role of diatoms to total primary production (<10%). Indeed, relative to a phytoplankton taxon's productivity, the proportional contribution of each phytoplankton taxon to foodweb pathways that support ABT larvae increased with increasing phytoplankton size from picophytoplankton to flagellates to diatoms (Fig. 8). The disproportionately large role of diatom-driven pathways was largely the result of non-vertically migrating calanoid copepods (and to a lesser extent cladocerans), which formed a large portion of the diet of ABT larvae and fed substantially on diatoms. In contrast, while an efficient pathway from cyanobacteria to ABT larvae existed (through appendicularians), appendicularians were not abundant in either ABT guts or in the water column. Instead, the majority of cyanobacteria were consumed by heterotrophic nanoflagellates. These heterotrophic nanoflagellates had a relatively low gross growth efficiency in the model (~20%) and their primary predators were other protists (microzooplankton). Cyanobacteria and heterotrophic nanoflagellates thus contributed substantially to the recycling pathways of the microbial loop, forming a largely distinct food web from the multivorous and herbivorous pathways, which mostly began with mixotrophic flagellates and diatoms and supported the production of larval ABT and other planktivorous fish.

Our results offer more support for the hypothesis that ABT larvae feed at a relatively low trophic level to maximize the proportion of primary productivity available to them (Fig. 7). The trophic position of ABT larvae (~4) is much closer to the minimum trophic level that our model allows (3: phytoplankton → prey → larvae) than to the maximum allowed trophic level (7: phytoplankton → bacteria → nanoflagellates → microzooplankton → suspension-feeders → carnivorous zooplankton → larvae). The low trophic position of ABT larvae is particularly striking considering how weak the herbivorous food chain is. Generally, planktivorous fish are more likely to be at a low trophic level if they are feeding on an ecosystem dominated by large phytoplankton and herbivorous mesozooplankton. However, the herbivorous food chain was responsible for only 3.3% of net primary production in the shallow euphotic zone where ABT larvae feed; the multivorous food chain processed 15% of NPP, while the microbial loop processed 76% (Fig. 5). The low trophic position of ABT larvae was primarily due to two factors: 1) although total protistan secondary production was higher than total mesozooplankton secondary production, a comparatively small proportion of this secondary production proceeded to food chains ending in larval tuna. Instead, much of it was dissipated as respiration within the microbial loop. Food chains supporting larval ABT were largely distinct from food chains involving the smallest class of heterotrophic protists. 2) Both size classes of ABT larvae fed primarily on non-vertically migrating calanoid copepods and these calanoid copepods tended to feed lower on the food chain than other similar suspension-feeding taxa.

While this trophic level of ~4 is low for a species known to preferentially feed on carnivorous copepods (poecilostomatoids) in a cyanobacteria and microbial loop-driven ecosystem, it is important to note that this is not actually a low trophic level relative to some other mass-balance constrained marine food web models. Many models based on ECOPATH software include only one (or zero) protistan trophic steps and many include a single mesozooplankton group (Arreguin-Sanchez *et al.*, 2004, Geers *et al.*, 2016, Walters *et al.*, 2008). Thus many of these models constrain zooplankton to a trophic level of 2 or 3 and hence the

maximum allowed trophic level for planktivores becomes only 3 or 4. The additional complexity associated with planktonic ecosystems in our model is a far more realistic depiction of the complexity of these food webs (Fig. 1). Nevertheless, our model only allows a maximum of two trophic steps within the protistan zooplankton (heterotrophic nanoflagellates and microzooplankton). This is in many ways an artificial distinction. Protistan food webs are fluid. Some protists (e.g., pallium-feeding dinoflagellates) routinely feed at a 1:1 predator:prey size ratio, while others (e.g., ciliates) often feed at closer to a 10:1 predator:prey size ratio (Fuchs & Franks, 2010, Kiorboe, 2008). Some protists are thus likely to take on a higher trophic position than the maximum value allowed by our model. Indeed, the high energy dissipation rates that our model finds for protists (model average for heterotrophic nanoflagellate gross growth efficiency is only ~20%) suggest that other model constraints (e.g., $\delta^{15}\text{N}$ of consumers and sinking detritus) are pushing the model towards lower trophic efficiency amongst the protistan food web, possibly indicating that there are in fact more trophic links amongst this group than we allow.

Although our cruise plan was not designed to focus on spatial variability and mesoscale features, it is important to note that mesoscale eddies may play an important role in structuring GoM ecosystems. The GoM is a region with very high mesoscale energy, with the Loop Current (and the eddies that it sheds) forming some of the most prominent (but certainly not only) features in the open-ocean GoM (Forristall *et al.*, 1992, Oey *et al.*, 2005, Schmitz *et al.*, 2005). These features have the potential to fundamentally restructure open-ocean ecosystems, with warm-core eddies (including Loop Current Eddies) depressing the nutricline and hence primary production and cold-core eddies leading to increased open-ocean upwelling and productivity (Biggs & Müller-Karger, 1994). These altered nutrient supply and phytoplankton regimes lead to substantially higher zooplankton biomass within cold-core eddies (Wells *et al.*, 2017). However, the relative importance of each eddy type, as well as the distinct gradient regions that form on their edges, on larval ABT remains a topic of active debate (Domingues *et al.*, 2016, Muhling *et al.*, 2010, Shropshire *et al.*, in prep.). Determining the response of pelagic food webs and ABT larval tuna to climate change will thus require characterizing not only how GoM circulation will respond to a future climate, but also food web variability across these features (Liu *et al.*, 2015, Muhling *et al.*, 2011). Our study offers substantial insight into the processes allowing larval ABT to survive in a food-scare environment. However, substantial future research is necessary to quantify the impact of spatial and interannual variability, as well as secular change, on these ecosystems and potentially threatened species.

CONCLUSIONS

The larvae of ABT feed in oligotrophic ecosystems, dominated by cyanobacteria and other small phytoplankton. These ecosystems are dominated by the microbial loop, within which both bacteria and protists play important roles in regenerating nutrients. However, larval ABT feed preferentially on less dominant food web pathways associated with herbivorous and multivorous food chains. Consequently, they are reliant on the production of diatoms and mixotrophic flagellates that support herbivorous zooplankton taxa, particularly calanoid copepods and

cladocerans. Preferential utilization of these more direct trophic pathways allows larval ABT to feed at relatively low trophic levels despite the fact that the taxa responsible for the majority of secondary production in the food web (bacteria and heterotrophic nanoflagellates) are not accessible as prey to them. Further research is needed to understand how these ecological interactions shift under different disturbance regimes.

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Supplementary Table 1 – Model Solutions

	<u>Model Flux</u>	<u>Mean solution</u>	<u>Standard deviation</u>
1	Upwellings	4.56E-05	2.49E-05
2	LateralInputDONs	6.94E-02	5.60E-02
3	LateralInputPONs	8.36E-02	6.04E-02
4	NH4toNO3s	4.88E-01	1.78E-01
5	NfixCyanos	9.04E-02	6.46E-02
6	NO3toCyanos	1.73E-01	1.44E-01
7	NH4toCyanos	1.44E+00	3.69E-01
8	CyanoTOhnfs	7.90E-01	2.51E-01
9	CyanoTOMics	8.88E-02	5.62E-02
10	CyanoTOflags	2.39E-04	1.81E-04
11	CyanoTOapps	2.15E-04	1.54E-04
12	CyanoTODoms	4.07E-01	2.24E-01
13	CyanoTOSdets	4.15E-01	2.62E-01
14	NfixTrichos	3.62E-04	2.15E-04
15	NO3toTrichos	2.92E-03	1.50E-03
16	NH4toTrichos	1.23E-03	7.94E-04
17	TrichoTODoms	2.60E-03	1.69E-03
18	TrichoTOLDets	1.91E-03	1.75E-03
19	NO3toDTMs	1.01E-01	6.01E-02
20	NH4toDTMs	1.07E-01	6.68E-02
21	dtmTOMics	2.73E-02	2.35E-02
22	dtmTOherbnvms	4.38E-04	2.79E-04
23	dtmTOherbvms	1.51E-02	1.34E-02
24	dtmTOapps	1.55E-04	1.20E-04
25	dtmTOclads	1.14E-02	1.08E-02
26	dtmTONvmCals	2.75E-03	1.76E-03
27	dtmTOvmCals	5.96E-03	5.14E-03
28	dtmTODoms	4.25E-02	2.12E-02
29	dtmTOLDets	8.20E-02	4.17E-02
30	NO3TOflags	2.12E-01	1.62E-01
31	NH4TOflags	1.03E+00	3.05E-01
32	flagTOMics	1.09E+00	2.14E-01
33	flagTOherbnvms	1.05E-02	9.08E-03
34	flagTOherbvms	1.19E-02	1.06E-02
35	flagTOapps	1.74E-04	1.49E-04
36	flagTOclads	1.42E-02	1.33E-02
37	flagTONvmCals	4.32E-03	3.34E-03
38	flagTOvmCals	1.81E-02	1.76E-02
39	flagTODoms	3.20E-01	1.26E-01
40	flagTOSdets	1.20E-01	5.94E-02

41	hnfTOMics	2.87E-01	1.45E-01
42	hnfTOapps	1.76E-04	1.45E-04
43	hnfTOherbnvms	1.32E-02	1.06E-02
44	hnfTOherbvms	1.90E-02	1.68E-02
45	hnfTOclads	2.18E-02	1.74E-02
46	hnfTONvmCals	3.76E-03	3.23E-03
47	hnfTOvmCals	2.09E-02	1.95E-02
48	hnfTONh4s	5.62E-01	2.11E-01
49	hnfTOdoms	3.24E-01	1.42E-01
50	hnfTOsdets	5.51E-01	3.24E-01
51	micTOherbnvms	2.29E-02	1.30E-02
52	micTOherbvms	1.23E-01	3.19E-02
53	micTOclads	4.25E-02	2.26E-02
54	micTONvmCals	4.44E-03	3.37E-03
55	micTOvmCals	8.00E-02	2.81E-02
56	micTOPreflexs	1.66E-07	7.22E-08
57	micTOpostflexs	2.07E-06	3.35E-07
58	micTONh4s	5.67E-01	1.66E-01
59	micTOdoms	3.01E-01	1.00E-01
60	micTOsdets	5.56E-01	2.22E-01
61	herbnvmTOchaetos	4.63E-03	3.75E-03
62	herbnvmTOpoecils	4.88E-03	3.88E-03
63	herbnvmTOgels	4.04E-03	3.31E-03
64	herbnvmTOplankfishs	3.92E-03	3.42E-03
65	herbnvmTONh4s	1.73E-02	4.15E-03
66	herbnvmTOdoms	9.51E-03	2.81E-03
67	herbnvmTOldets	1.27E-02	4.80E-03
68	appTOchaetos	8.15E-05	7.11E-05
69	appTOpoecils	8.32E-05	7.39E-05
70	appTOgels	8.09E-05	7.15E-05
71	appTOplankfishs	8.21E-05	7.16E-05
72	appTOPreflexs	4.59E-07	1.79E-07
73	appTOpostflexs	3.27E-06	2.24E-07
74	appTONh4s	3.39E-04	1.03E-04
75	appTOdoms	1.71E-04	6.03E-05
76	appTOldets	2.66E-04	1.09E-04
77	cladTOchaetos	1.00E-02	7.44E-03
78	cladTOpoecils	1.21E-02	9.16E-03
79	cladTOgels	4.37E-03	3.50E-03
80	cladTOplankfishs	8.75E-03	8.07E-03
81	cladTOPreflexs	3.78E-07	2.31E-07
82	cladTOpostflexs	2.22E-05	2.13E-06
83	cladTONh4s	2.74E-02	4.89E-03

84	cladTOdoms	1.66E-02	4.63E-03
85	cladTOldets	2.22E-02	5.96E-03
86	nvmCalTOchaetos	1.50E-03	1.19E-03
87	nvmCalTOpoecils	1.81E-03	1.53E-03
88	nvmCalTOgels	1.57E-03	1.30E-03
89	nvmCalTOplankfishs	1.45E-03	1.23E-03
90	nvmCalTOpreflexs	7.89E-06	1.96E-06
91	nvmCalTOpostflexs	3.78E-05	5.71E-07
92	nvmCalTOnh4s	5.39E-03	1.25E-03
93	nvmCalTOdoms	3.01E-03	8.47E-04
94	nvmCalTOldets	4.35E-03	1.51E-03
95	chaetoTOgels	8.18E-03	6.49E-03
96	chaetoTOplankfishs	8.56E-03	4.76E-03
97	chaetoTOnh4s	2.57E-02	8.61E-03
98	chaetoTOdoms	7.40E-03	4.74E-03
99	chaetoTOldets	1.69E-02	6.91E-03
100	poecilTOgels	2.12E-03	1.51E-03
101	poecilTOplankfishs	1.30E-02	6.17E-03
102	poecilTOpreflexs	1.10E-08	6.75E-09
103	poecilTOpostflexs	8.49E-06	6.15E-07
104	poecilTOnh4s	2.39E-02	7.44E-03
105	poecilTOdoms	8.93E-03	5.05E-03
106	poecilTOldets	1.13E-02	4.21E-03
107	gelTOhtls	1.10E-02	4.37E-03
108	gelTOnh4s	1.43E-02	6.64E-03
109	gelTOdoms	3.86E-03	9.89E-04
110	gelTOldets	1.22E-02	4.70E-03
111	plankfishTOhtls	1.74E-02	6.46E-03
112	plankfishTOnh4s	2.53E-02	6.99E-03
113	plankfishTOdoms	1.07E-02	4.51E-03
114	plankfishTOpoops	2.08E-02	1.21E-02
115	preflexTOgrowths	9.60E-07	6.79E-07
116	preflexTOMorts	9.43E-07	6.83E-07
117	preflexTOnh4s	3.09E-06	1.09E-06
118	preflexTOdoms	1.61E-06	6.33E-07
119	preflexTOpoops	2.31E-06	1.02E-06
120	postflexTOgrowths	8.34E-06	5.45E-06
121	postflexTOMorts	8.22E-06	5.39E-06
122	postflexTOnh4s	2.24E-05	6.64E-06
123	postflexTOdoms	1.23E-05	3.78E-06
124	postflexTOpoops	2.26E-05	7.68E-06
125	bacTOflags	3.65E-01	1.43E-01
126	bacTOhnfs	1.53E-01	1.24E-01

127	bacTOMics	7.41E-02	6.54E-02
128	bacTOapps	1.99E-04	1.65E-04
129	bacTOnh4s	1.74E+00	3.49E-01
130	domTObacs	2.33E+00	4.77E-01
131	sdefTOhnfs	8.59E-01	6.22E-01
132	sdefTOMics	1.28E-01	1.16E-01
133	sdefTOapps	1.89E-04	1.68E-04
134	sdefTODoms	7.39E-01	4.14E-01
135	ldetTOherbnvms	9.92E-03	8.26E-03
136	ldetTOclads	1.16E-02	7.88E-03
137	ldetTONvmCals	3.85E-03	3.17E-03
138	ldetTOherbvms	1.60E-02	8.76E-03
139	ldetTOvmCals	1.00E-02	7.83E-03
140	ldetTODoms	3.99E-02	3.40E-02
141	herbvmTOSchaetom	2.52E-02	1.31E-02
142	herbvmTOSpoecilm	1.93E-02	1.10E-02
143	herbvmTOSgelm	1.94E-02	8.61E-03
144	herbvmTOSplankfishm	2.52E-02	1.52E-02
145	herbvmTOSnh4m	3.73E-02	1.25E-02
146	herbvmTOSdomm	1.57E-02	7.67E-03
147	herbvmTOSldetm	2.56E-02	1.58E-02
148	herbvmTODchaetom	1.16E-02	8.73E-03
149	herbvmTODpoecilm	2.18E-03	1.18E-03
150	herbvmTODgelm	1.64E-03	1.26E-03
151	herbvmTODplankfishm	1.08E-02	9.73E-03
152	herbvmTODnh4m	1.51E-02	2.13E-03
153	herbvmTODdomm	1.32E-02	8.42E-03
154	herbvmTODldetm	1.29E-02	8.28E-03
155	herbvmTOexportNH4m	8.91E-03	6.06E-03
156	herbvmTOexportDOMm	4.98E-03	3.80E-03
157	herbvmTOexportdetm	1.08E-03	7.77E-04
158	herbvmTOexportmortm	2.25E-03	1.29E-03
159	vmCalTOSchaetom	2.53E-02	1.31E-02
160	vmCalTOSpoecilm	2.12E-02	1.62E-02
161	vmCalTOSgelm	1.54E-03	1.35E-03
162	vmCalTOSplankfishm	1.31E-02	7.80E-03
163	vmCalTOSnh4m	1.92E-02	1.03E-02
164	vmCalTOSdomm	1.38E-02	8.61E-03
165	vmCalTOSldetm	1.24E-02	8.06E-03
166	vmCalTODchaetom	1.36E-03	9.52E-04
167	vmCalTODpoecilm	3.98E-03	1.08E-03
168	vmCalTODgelm	5.01E-03	2.24E-03
169	vmCalTODplankfishm	7.67E-03	2.69E-03

170	vmCalTOdnh4m	2.20E-02	1.10E-02
171	vmCalTOddomm	1.06E-02	8.40E-03
172	vmCalTOlddetm	1.69E-03	1.13E-03
173	vmCalTOexportNH4m	8.17E-03	5.30E-03
174	vmCalTOexportDOMm	4.62E-03	3.23E-03
175	vmCalTOexportdetm	1.65E-02	1.12E-02
176	vmCalTOexportmortm	4.72E-03	2.19E-03
177	diatomSinkm	2.06E-02	1.40E-02
178	FlagSinkm	1.78E-02	1.30E-02
179	dldetSinkm	1.11E-01	5.42E-02
180	Upwellingd	3.61E-02	3.68E-02
181	LateralInputDONd	5.04E-02	4.27E-02
182	LateralInputDONs	4.10E-01	1.11E-01
183	NH4toNO3d	1.19E+00	4.82E-01
184	NfixCyanod	2.92E-02	2.88E-02
185	NO3toCyanod	1.00E+00	4.89E-01
186	NH4toCyanod	1.20E+00	5.28E-01
187	CyanoTOhnfd	4.66E-01	1.20E-01
188	CyanoTOMICd	9.67E-02	8.73E-02
189	CyanoTOflagd	1.13E-01	8.74E-02
190	CyanoTOappd	1.62E-01	1.10E-01
191	CyanoTODOCd	8.96E-01	1.10E-01
192	CyanoTOSdetd	5.00E-01	2.31E-02
193	NfixTrichod	9.57E-06	6.77E-06
194	NO3toTrichod	5.93E-05	4.16E-05
195	NH4toTrichod	5.91E-05	4.19E-05
196	TrichoTODomd	1.04E-04	4.17E-05
197	TrichoTOLDetd	2.43E-05	1.10E-05
198	NO3toDTMd	9.03E-02	6.84E-02
199	NH4toDTMd	1.19E-01	7.31E-02
200	dtmTOMICd	2.27E-02	1.56E-02
201	dtmTOherbnvmd	2.76E-02	2.52E-02
202	dtmTOherbvmd	1.04E-02	9.99E-03
203	dtmTOappd	2.77E-02	2.49E-02
204	dtmTOcladd	3.27E-02	2.74E-02
205	dtmTONvmCald	2.99E-02	2.43E-02
206	dtmTOvmCald	1.45E-02	1.11E-02
207	dtmTODomd	4.52E-02	2.07E-02
208	dtmTOLDetd	8.07E-03	2.59E-03
209	NO3TOflagd	1.30E-01	1.09E-01
210	NH4TOflagd	3.82E-01	2.06E-01
211	flagTOMICd	2.96E-01	1.80E-01
212	flagTOherbnvmd	6.65E-02	5.86E-02

213	flagTOherbvmd	1.49E-02	1.22E-02
214	flagTOappd	5.27E-02	4.80E-02
215	flagTOcladd	9.57E-02	7.10E-02
216	flagTONvmCald	8.18E-02	6.37E-02
217	flagTOvmCald	1.23E-02	1.15E-02
218	flagTOdomd	1.48E-01	6.59E-02
219	flagTOsdetd	9.88E-02	5.58E-02
220	hnfTOMICd	4.44E-02	4.04E-02
221	hnfTOappd	4.80E-02	3.89E-02
222	hnfTOherbnvmd	9.73E-02	9.13E-02
223	hnfTOherbvmd	7.31E-03	6.83E-03
224	hnfTOcladd	6.73E-02	5.81E-02
225	hnfTONvmCald	6.44E-02	5.52E-02
226	hnfTOvmCald	1.02E-02	9.40E-03
227	hnfTONh4d	2.29E-01	7.63E-02
228	hnfTOdomd	1.34E-01	5.00E-02
229	hnfTOsdetd	2.87E-01	1.40E-01
230	micTOherbnvmd	8.89E-02	7.49E-02
231	micTOherbvmd	1.69E-02	1.57E-02
232	micTOcladd	1.06E-01	8.59E-02
233	micTONvmCald	9.85E-02	8.17E-02
234	micTOvmCald	1.11E-02	6.57E-03
235	micTONh4d	2.26E-01	6.35E-02
236	micTOdomd	1.35E-01	4.45E-02
237	micTOsdetd	2.94E-01	1.24E-01
238	herbnvmTOchaetod	1.70E-02	1.41E-02
239	herbnvmTOpoecild	5.65E-02	4.45E-02
240	herbnvmTOgeld	3.75E-02	3.38E-02
241	herbnvmTOplankfishd	3.77E-02	3.01E-02
242	herbnvmTONh4d	1.24E-01	3.79E-02
243	herbnvmTOldetd	1.55E-01	7.70E-02
244	herbnvmTOdomd	7.28E-02	2.61E-02
245	appTOchaetod	1.18E-01	8.02E-02
246	appTOpoecild	1.19E-01	7.77E-02
247	appTOgeld	6.85E-02	5.88E-02
248	appTOplankfishd	5.16E-02	4.64E-02
249	appTONh4d	2.45E-01	6.85E-02
250	appTOdomd	1.31E-01	4.45E-02
251	appTOldetd	4.06E-01	1.27E-01
252	cladTOchaetod	4.31E-02	3.87E-02
253	cladTOpoecild	4.15E-02	3.47E-02
254	cladTOgeld	3.40E-02	3.09E-02
255	cladTOplankfishd	8.81E-02	4.63E-02

256	cladTOnh4d	1.49E-01	3.94E-02
257	cladTOdomd	7.63E-02	2.79E-02
258	cladTOldetd	1.91E-01	8.16E-02
259	nvmCalTOchaetod	5.02E-02	4.35E-02
260	nvmCalTOpoecild	4.72E-02	3.94E-02
261	nvmCalTOgeld	3.77E-02	3.21E-02
262	nvmCalTOplankfishd	3.11E-02	2.89E-02
263	nvmCalTOnh4d	1.30E-01	3.95E-02
264	nvmCalTOdomd	6.74E-02	2.70E-02
265	nvmCalTOldetd	1.66E-01	7.71E-02
266	chaetoTOgeld	3.64E-02	2.67E-02
267	chaetoTOplankfishd	2.91E-02	2.37E-02
268	chaetoTOnh4d	6.47E-02	2.51E-02
269	chaetoTOdomd	3.68E-02	1.59E-02
270	chaetoTOldetd	7.46E-02	3.88E-02
271	poecilTOgeld	4.25E-02	3.00E-02
272	poecilTOplankfishd	3.29E-02	2.51E-02
273	poecilTOnh4d	7.20E-02	2.56E-02
274	poecilTOdomd	4.14E-02	1.66E-02
275	poecilTOldetd	8.15E-02	4.12E-02
276	gelTOhtld	6.65E-02	2.66E-02
277	gelTOnh4d	7.25E-02	2.57E-02
278	gelTOdomd	3.74E-02	1.63E-02
279	gelTOldetd	8.69E-02	4.05E-02
280	plankfishTOhtld	4.33E-02	1.80E-02
281	plankfishTOnh4d	9.47E-02	2.96E-02
282	plankfishTOdomd	4.88E-02	1.89E-02
283	plankfishTOpoopd	1.02E-01	4.40E-02
284	bacTOflagd	2.37E-01	1.26E-01
285	bacTOhnfd	1.57E-01	1.29E-01
286	bacTOMICd	8.72E-02	7.50E-02
287	bacTOappd	1.02E-01	9.62E-02
288	bacTOnh4d	1.45E+00	1.03E-01
289	domTObacd	2.03E+00	1.45E-01
290	sdefTOhnfd	3.65E-01	2.42E-01
291	sdefTOMICd	4.29E-01	2.93E-01
292	sdefTOappd	7.46E-01	2.91E-01
293	sdefTOdomd	4.94E-02	4.68E-02
294	ldetTOherbnvmd	2.20E-01	1.61E-01
295	ldetTOcladd	3.22E-01	1.73E-01
296	ldetTONvmCald	2.55E-01	1.59E-01
297	ldetTOherbvmd	1.79E-02	1.14E-02
298	ldetTOvmCald	9.87E-03	7.57E-03

299	IdetTOdomd	3.74E-02	3.61E-02
300	DiatomSinkd	1.13E-02	8.54E-03
301	FlagSinkd	1.33E-02	9.15E-03
302	DIDetSinkd	4.32E-01	2.62E-02

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