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Trophodynamics and mercury bioaccumulation in reef and open-ocean fishes from The Bahamas with a focus on two teleost predators

Oliver N. Shipley[1,*], Cheng-Shiuan Lee[1], Nicholas S. Fisher[1], Georgiana Burruss[2], Michael G. Frisk[1], Edward J. Brooks[3], Zachary C. Zuckerman[4], Achim D. Herrmann[5], Daniel J. Madigan[1,6]

[1]School of Marine and Atmospheric Sciences, 100 Nicholls Road, Stony Brook University, Stony Brook, NY 11794, USA
[2]Department of Fisheries and Wildlife, Michigan State University, East Lansing, MI 48824, USA
[3]The Cape Eleuthera Institute, PO Box EL-26029 Cape Eleuthera, The Bahamas
[4]Louisiana Department of Wildlife and Fisheries, Grand Isle, LA 70358, USA
[5]Department of Geology and Geophysics, Louisiana State University, Baton Rouge, LA 70803, USA
[6]Gulf of California International Research Center, Santa Rosalía, BCS 23920, Mexico

ABSTRACT: Identifying prey resource pools supporting fish biomass can elucidate trophic pathways of pollutant bioaccumulation. We used multiple chemical tracers (carbon [$\delta^{13}C$] and nitrogen [$\delta^{15}N$] stable isotopes and total mercury [THg]) to identify trophic pathways and measure contaminant loading in upper trophic level fishes residing at a reef and open-ocean interface near Eleuthera in the Exuma Sound, The Bahamas. We focused predominantly on the trophic pathways of mercury bioaccumulation in dolphinfish *Coryphaena hippurus* and wahoo *Acanthocybium solandri*, 2 commonly consumed pelagic sportfish in the region. Despite residing within close proximity to productive and extensive coral reefs, both dolphinfish and wahoo relied almost exclusively on open-ocean prey over both short and long temporal durations. A larger isotopic niche of dolphinfish suggested a broader diet and some potential prey differentiation between the 2 species. THg concentrations in dolphinfish (0.2 ± 0.1 ppm) and wahoo (0.3 ± 0.3 ppm) were mostly below recommended guidelines for humans (US Environmental Protection Agency (EPA) = 0.3 ppm, US Food and Drug Administration (FDA)= 1.0 ppm) and were within ranges previously reported for these species. However, high THg concentrations were observed in muscle and liver tissue of commonly consumed reef-associated fishes, identifying a previously unrecognized route of potentially toxic Hg exposure for human consumers on Eleuthera and neighboring islands.

KEY WORDS: Stable isotope analysis · Contaminant loading · Dolphinfish · Wahoo · The Bahamas

1. INTRODUCTION

The amount of inorganic mercury (Hg) entering aquatic systems has increased considerably, largely due to high levels of fossil fuel combustion and artisanal gold mining (Porcella et al. 1997, Gibb & O'Leary 2014). In higher trophic level aquatic organisms, such as large fish, Hg is predominately in the toxic form monomethylmercury (MeHg), which forms via the methylation of inorganic Hg by bacteria in the sediment or water column (Fleming et al. 2006, Blum et al. 2013) and subsequently enters food webs primarily via phytoplankton. The rate and magnitude of bioaccumulation can vary between specific algal taxa, but all species biomagnify MeHg out of ambient water by 10^4 to 10^5-fold (Lee & Fisher 2016). Further, most animals excrete MeHg from their tissues at low rates, resulting in MeHg bioaccumulation with

Corrresponding author: oliver.shipley@stonybrook.edu

each successive trophic level (Bloom 1992, Mathews & Fisher 2008, Karimi et al. 2010) such that the tissues of higher predators can reach MeHg concentrations which can be harmful to human consumers (Dietz et al. 2013). Human ingestion of MeHg can influence neurological processes such as synapse transmission, cellular oxidization, and cellular migration (Hong et al. 2012). While debate exists over understanding the toxicity of Hg to humans from fish consumption (Egeland & Middaugh 1997), both region-specific and global cycling of Hg and its bioaccumulation remains a global environmental priority (Driscoll et al. 2013). Examining trophic pathways and associated magnitude of MeHg loading in marine fishes is therefore of importance to environmental managers, as the ability to identify routes of MeHg accumulation can pinpoint habitats that may require mitigation and/or avoidance of fish consumption (e.g. Castilhos et al. 2006).

Large-bodied, highly mobile marine teleosts, such as tunas, billfish, and dolphinfishes are prized target species in both recreational and commercial fisheries and are a significant proportion of human seafood demand (Sunderland 2007, Rudershausen et al. 2010). As many of these taxa perform extensive movements across broad geographical ranges (Block et al. 2001, Merten et al. 2014a), significant interest lies in understanding region-specific prey pools supporting fish biomass. Many of these species are highly exploited and contribute substantial Hg to human diet (Sunderland 2007), adding to the importance of tracing trophic pathways that lead to Hg bioaccumulation. In The Bahamas, high levels of biological productivity and subsequent predator diversity (Brooks et al. 2011) provide an important economical resource, supporting artisanal and recreational fisheries and ecotourism operations year-round (Chiappone et al. 2000, Haas et al. 2017). The mosaic of interconnected ecosystems across The Bahamas archipelago provides a unique opportunity to study energy flow and Hg accumulation in species residing close to multiple resource pools. One unique aspect of the region is the narrow interface between fringing reef and open-ocean ecosystems, in contrast to many other oceanic regions with long coastal shelves separating coastal and open-ocean habitats. Despite the proximity and potential ecological porosity of these habitats and the presence of predator species that utilize the interface, there is limited understanding of whether these predators obtain energy from multiple resource pools. Understanding resource use dynamics of these species, and how this relates to the loading of Hg, can inform holistic management efforts and provide basic information on Hg concentrations and thus potential Hg-related toxicity of commonly consumed fishes.

Quantifying trophic pathways of contaminant loading requires tools that identify habitat use and feeding habits of target species. Stable isotope analysis (SIA) is an increasingly used tool to determine the trophic structure(s) and energy flow within ecological systems (Rundel et al. 2012). Analyses of carbon stable isotopes ($\delta^{13}C$) typically allow for the assignment of consumers to specific primary production sources, as differential assimilation of light carbon during C_3 or C_4 photosynthesis drives isotopically distinct $\delta^{13}C$ values, which typically do not fractionate substantially during trophic transfer (DeNiro & Epstein 1978). Although nitrogen baselines can vary regionally between marine primary producers, the isotopic composition of nitrogen ($\delta^{15}N$) is commonly used to estimate relative trophic position, as various metabolic processes (e.g. protein synthesis and urea excretion) result in a relatively large ^{15}N enrichment (2 to 4‰) between subsequent trophic levels (DeNiro & Epstein 1981, Post 2002). In more recent years, development of isotope-specific modelling approaches has allowed users to elucidate major prey resources (and their associated habitats), which support predator diets (Parnell et al. 2013) as well as demonstrate the size and relative overlap of ecological niches (Jackson et al. 2011, Swanson et al. 2015). Further, through captive experiments and subsequent SIA measurements in tissues with variable isotopic turnover rates (e.g. in fish, liver ≤4 mo, muscle ≥1 yr; Madigan et al. 2012a), temporal variability in resource use dynamics can also be explored using SIA of multiple tissue types. To track Hg sources in fish tissues, combining SIA and Hg measurements can therefore identify the trophic pathways responsible for Hg bioaccumulation (Cabana & Rasmussen 1994) and help explain how habitat and diet influence relative magnitudes of Hg loading.

In this study, we examined trophic pathways of total mercury (THg) bioaccumulation in 2 large, commonly captured and consumed predators (dolphinfish *Coryphaena hippurus* and wahoo *Acanthocybium solandri*) that, relative to other large pelagic predators, show common residency at the reef–open-ocean interface of the Exuma Sound, The Bahamas. We assessed the relative prey contributions of these 2 systems (reef and open-ocean) to dolphinfish and wahoo to elucidate trophic pathways for contaminant loading using $\delta^{13}C$ and $\delta^{15}N$ signatures combined with measurements of THg as a proxy for MeHg (since MeHg is usually >95% of THg in high trophic level fish; Bloom 1992). We also report stable isotope

signatures and THg concentrations in liver and muscle tissues for a broader range of species that are known to be entirely reef- or open-ocean-associated. Our results identify the habitats supporting the biomass of these local predators and provide information on relative Hg levels in local fish resources.

2. MATERIALS AND METHODS

2.1. Sample collection

Tissue samples for all open-ocean and reef-associated fishes were collected between October 2015 and May 2016 under permits MAF/FIS/17 and MAF/FIS/13, issued by the Bahamian Department of Marine Resources. White muscle and liver tissues were opportunistically sampled from artisanal and recreational fishers located at 2 marinas (Davis Harbour and Cape Eleuthera Marina in South Eleuthera, The Bahamas; Fig. 1). Morphometrics (fork length [FL] and total length [TL]) were recorded, and approximately 3 g of dorsal white muscle tissue was excised from ~2 cm below the skin. Liver tissue was also collected for SIA to examine resource use over shorter timeframes (Madigan et al. 2012a). For some fish, only muscle or liver samples could be collected from the same individual. Samples were frozen at −20°C, then freeze-dried for >72 h and homogenized to a fine powder using a mortar and pestle for elemental analyses.

Approximate capture locations were recorded and were within common recreational fishing grounds along the reef open-ocean interface of the Exuma Sound (Fig. 1). The Exuma Sound and surrounding neritic waters are geologically unique; the region is categorized by narrow limestone shelves of the Great Bahama Banks, which rapidly slope to depths exceeding 1600 m in the center of the Exuma Sound (Buchan 2000).

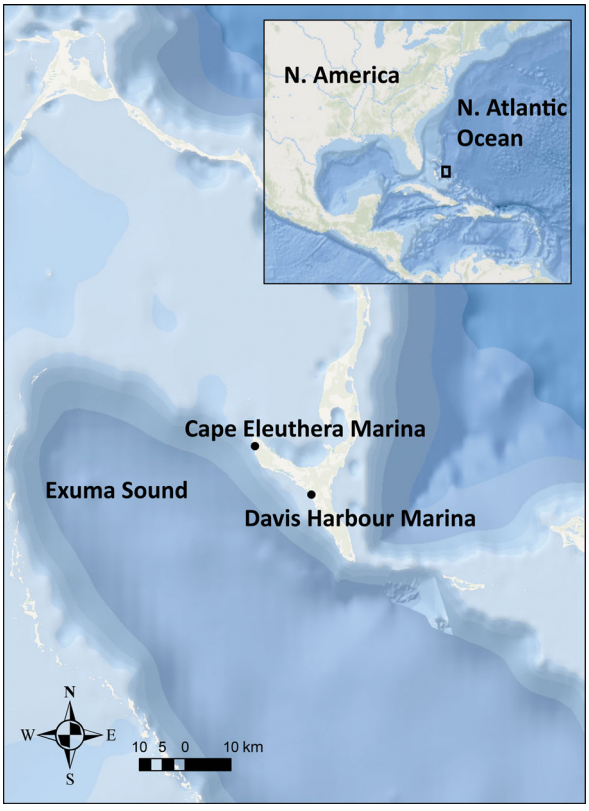

Fig. 1. Site map of South Eleuthera highlighting the 2 sampling locations: Davis Harbour (24° 44′ 18″ N, 76° 13′ 59″ W) and Cape Eleuthera marinas (24° 50′ 10″ N, 76° 20′ 34″ W). It is assumed that all fish had been captured in the Exuma Sound or surrounding waters. Inset shows location of South Eleuthera relative to North America. Sources: ESRI, GEBCO, NOAA, National Geographic, DeLorme, HERE, Geonames.org, and other

2.2. SIA

SIA of dried fish tissue was performed at Louisiana State University. Samples were flash-combusted in a 950°C furnace using elemental analyzer (Micro Vario Cube, Isoprime). The resulting CO_2 and N_2 gases were analyzed by continuous flow using an Isoprime100 gas source mass spectrometer. Organic carbon (C_{org}) and nitrogen isotope ratios are reported in the conventional delta notation ($\delta^{nn}X$) as permil variations relative to Vienna PeeDee Belemnite (VPDB) (for $\delta^{13}C$) and air (for $\delta^{15}N$). Samples were weighed out in ~1 mg aliquots into combustible tin capsules for nitrogen isotope analysis, targeting ~100 µg of N. Nitrogen isotopic composition was calibrated using glycine standards (high with $\delta^{15}N_{air}$ = +40.83 ‰ and low with $\delta^{15}N_{air}$ = +1.35‰). Analytical precision (SD) was < 0.1‰. Glycine standards were used for isotopic value calibration (high with $\delta^{13}C_{VPDB}$ = −0.67 ‰ and low with $\delta^{13}C_{VPDB}$ = −40.81 ‰). Analytical precision (SD) was <0.1‰. Sample $\delta^{13}C_{org}$ values were replicable to an error of ±0.1‰. As lipids can confound $\delta^{13}C$ values of fish tissues, $\delta^{13}C$ values of liver and muscle tissue were mathematically normalized based on Hoffman & Sutton (2010), for all individuals exhibiting a tissue C:N >3.4 (commonly accepted threshold above which lipids commonly cause lower $\delta^{13}C$ values), using the equation:

$$\delta^{13}C_{Corrected} = \delta^{13}C_{Bulk} + [-6.39 \times (3.76 - C{:}N_{Bulk})] / C{:}N_{Bulk} \quad (1)$$

2.3. THg analysis

Since the concentration of Hg in fish tissues is most frequently reported on a wet weight basis, but variable water content in tissues can confound the actual concentration of Hg present in muscle tissue, samples were analyzed for THg both dry (THg_{Dry}) and wet (THg_{Wet}). Dried samples were freeze-dried for approximately 72 h and homogenized using a mortar and pestle as above for SIA. THg was analyzed using a DMA-80 direct Hg analyzer (Milestone) calibrated with Hg standard liquid solution (VHG Labs). All THg values are reported in ppm. To validate machine precision, a standard reference material (DORM-4, NRCC), and a random duplicate sample were measured at the end of every run. THg concentrations of reference material fell within certified ranges (certified = 0.41 ± 0.06 ppm; observed = 0.38 ± 0.03 ppm, n = 23), and error between duplicate samples (ppm SD) was <0.06. In cases where duplicate wet and dry samples could not be run for a single fish, we used wet:dry conversion ratios calculated from the sample set for which wet and dry samples were run (n = 121). Calculated conversion factors from THg_{Dry} to THg_{Wet} were 0.40 (±0.12) and 0.25 (±0.08) for liver and muscle tissue, respectively.

2.4. Statistical analyses

All data analyses were performed in R (version 3.4.3, R Core team 2017) with significance level α set at 0.05 for pairwise comparisons. We estimated the contribution of reef vs. open-ocean prey resources to the diet of dolphinfish and wahoo using Bayesian isotope mixing models (R package 'simmr'; Parnell 2016). To examine resource use over different timeframes, we used $\delta^{13}C$ and $\delta^{15}N$ values of tissues with different isotopic turnover rates: muscle, representing months to >1 yr in pelagic tunas, and liver, representing weeks to months in pelagic tunas (Madigan et al. 2012a). We used an isotopic end-member approach, where 'source' inputs were comprised of mean (±SD) isotopic compositions of predatory fish known to be strictly associated with either reef or open-ocean ecosystems (see McCauley et al. 2012). Reef end-members were SIA values of amberjack *Seriola* sp. (n = 1), mutton snapper *Lutjanus analis* (n = 3), queen triggerfish *Balistes vetula* (n = 2), yellowtail snapper *Ocyurus chrysurus* (n = 3), Nassau grouper *Epinephelus striatus* (n = 1), red hind *Epinephelus guttatus* (n = 1), and vermilion snapper *Rhomboplites aurorubens* (n = 1). Pelagic end-members were Atlantic flying fish *Cheilopogon melanurus* (n = 1), blackfin tuna *Thunnus atlanticus* (n = 8), and yellowfin tuna *Thunnus albacares* (n = 1). King mackerel *Scomberomorus cavalla* and Spanish mackerel *S. maculatus* are categorized as reef-associated species herein. However, we acknowledge that these 2 species associate largely with sandy habitats and thus were not included as mixing model end-member species. Isotopic mixing models use Markov Chain Monte Carlo (MCMC) simulations to derive probable estimates of consumer diet contribution, which were calculated from 10 000 posterior draws. Models employed an initial burn-in period of 1000, which were thinned by the first 10 to remove poor model solutions often occurring within the initial burn-in (Parnell 2016). Model convergence was validated by visually inspecting Gelman diagnostics from each run, whereby point estimates and upper credibility intervals should be approximately 1 (Gelman & Rubin 1992). Our model used tissue-specific diet-tissue discrimination factors (DTDFs) observed in white muscle ($\Delta^{13}C$ = 1.8 ± 0.3, $\Delta^{15}N$ = 1.9 ± 0.4) and liver ($\Delta^{13}C$ = 1.2 ± 0.3, $\Delta^{15}N$ = 1.1 ± 0.6) tissues of Pacific bluefin tuna *Thunnus orientalis* (Madigan et al. 2012a), as have been applied to other pelagic fish in the absence of species-specific DTDFs (e.g. Madigan et al. 2012b, Papastamatiou et al. 2015). As mixing model solutions can be sensitive to variable DTDF estimates (Bond & Diamond 2011, Parnell et al. 2013), we ran a second model with different DTDF values for dolphinfish and wahoo to test whether DTDF selection influenced mixing model results. This second model used DTDFs generated from a broad, multi-taxa literature review that provided a general DTDF for fish tissues ($\Delta^{13}C$ = 0.5 ± 1.2, $\Delta^{15}N$ = 2.9 ± 1.8; Zanden & Rasmussen 2001).

Data were assessed for normality using Shapiro-Wilk tests, and heteroscedasticity were inferred through *F*-tests. We tested for differences in THg_{Dry}, $\delta^{13}C$, and $\delta^{15}N$ between muscle and liver tissue of dolphinfish and wahoo using pairwise comparisons; Wilcoxon signed-ranks tests or *t*-tests were used based on normality and heteroscedasticity. We examined core isotopic niche width, a conservative metric used to define diversity of resource use, for dolphinfish and wahoo using standard ellipse area (SEA) (Jackson et al. 2011). Independent estimates were calculated for both liver and muscle tissue for both species. SEA is calculated through a maximum likelihood approach and is insensitive to small sample sizes (where n = ≥10, SEA_C). Bayesian-estimated SEA (SEA_B) was also calculated to validate maximum likelihood estimates. To provide a conservative esti-

mate of niche overlap, we calculated overlap of the total trophic niche (an ellipse including 95% of the available data; see Shipley et al. 2018) using Bayesian implemented methods in the R package nicheROVER (Swanson et al. 2015). Overlap estimates were calculated from a run of 10 000 iterations.

Relationships between THg_{dry} and fish size and tissue isotopic composition (FL, $\delta^{13}C$, $\delta^{15}N$) in dolphinfish was examined using generalized linear models (GLMs) fit with a Gaussian distribution. In the full model, $\delta^{13}C$, $\delta^{15}N$, and FL were included as fixed effects, and due to potential covariance between independent variables, we included interactions of $\delta^{13}C \times \delta^{15}N$, FL × $\delta^{13}C$, and FL × $\delta^{15}N$. We used a stepwise, forward and backward elimination of non-significant effects (R package 'MASS'; Venables & Ripley 2002) and determined model parsimony using Akaike's information criterion (AIC) and small sample size-corrected AIC (AIC_c). For wahoo, relationships between THg_{Dry} and size were examined using simple linear regressions, and covariates were not explored due to low sample sizes for SIA measurements.

3. RESULTS

Stable isotope and THg data were generated from a total of 234 individuals representing 17 species, collected from reef and open-ocean ecosystems (Table 1). Across the sampled community, for liver tissue, $\delta^{13}C$ and $\delta^{15}N$ ranged from −18.9 to −8.6‰ and 4.5 to 9.7‰, respectively. For muscle tissue, $\delta^{13}C$ and $\delta^{15}N$ ranged from −18.6 to −9.5‰ and 6.1 to 15.1‰, respectively. This relatively wide range of $\delta^{13}C$ and $\delta^{15}N$ values was primarily driven by differences between reef and open-ocean species, with high $\delta^{13}C$ and low $\delta^{15}N$ in reef-associated species and low $\delta^{13}C$ and high $\delta^{15}N$ in open-ocean species (Table 1). Pooled reef and open-ocean end-member species displayed significantly different $\delta^{13}C$ signatures (t = 5.79, df = 11.63, p < 0.001, open-ocean = −17.3‰ ± 0.4, reef = −13.4‰ ± 2.3), making them robust choices for end-members in mixing models in other species. However, no statistically significant differences were observed between end-member $\delta^{15}N$ values (open-ocean = 8.3 ± 1.2, reef = 8.3 ± 0.7; t = 0.15, df = 16.93, p = 0.89). Bayesian mixing models indicated that open-ocean food items were consistently the dominant energy resource supporting the biomass of dolphinfish and wahoo. Models run for liver (median diet input estimates: reef ~3%, open-ocean ~98%; reef ~7%, open-ocean ~93%, respectively) and muscle (reef ~2%, open-ocean ~98%; reef ~ 7%, open-ocean ~93%, respectively) yielded consistent results (Fig. 2). Models appeared insensitive to the 2 different DTDFs applied, with both combinations of DTDFs providing nearly identical solutions (Table 2). The isotopic niche width of dolphinfish was approximately twice as large as wahoo, and this pattern was consistent across estimates derived from muscle and liver tissue

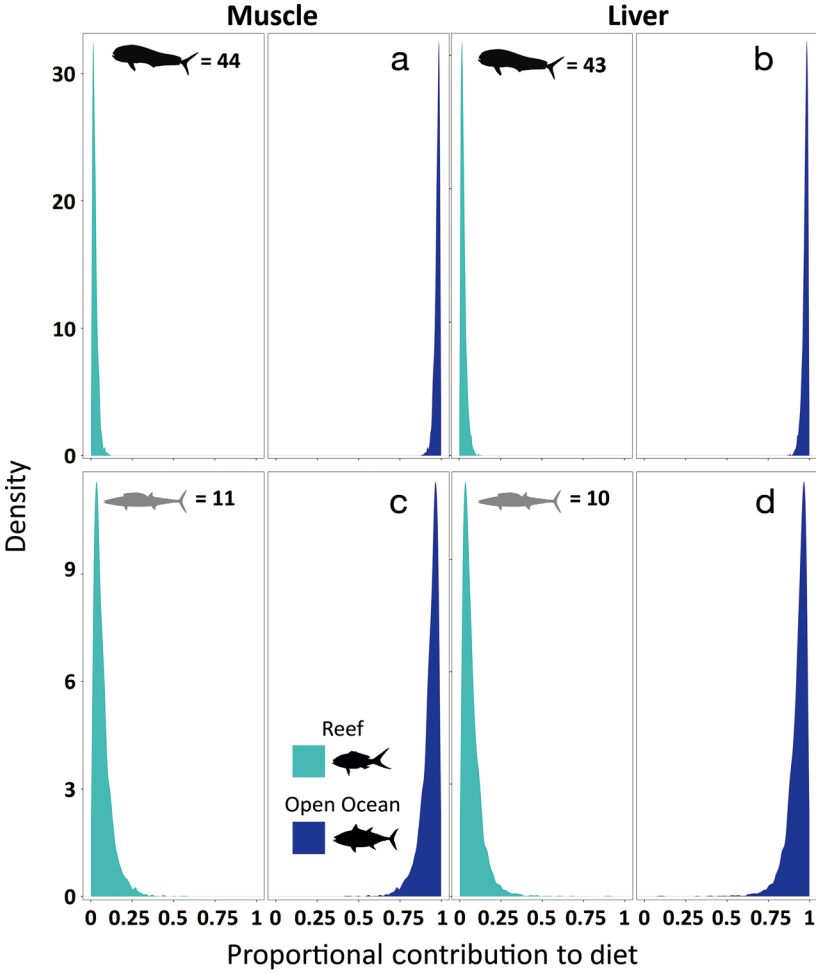

Fig. 2. Posterior density distributions estimated from Bayesian isotope mixing models illustrating contribution of reef vs. open-ocean prey items to the diet of (a,b) dolphinfish *Coryphaena hippurus* and (c,d) wahoo *Acanthocybium solandri*. Models were run across multiple tissues with variable isotopic turnover rates: muscle tissue (slow, panels a,c) and liver (fast, panels b,d). Models used reef and open-ocean predators as end-members and tissue-specific diet-tissue discrimination factors from Madigan et al. (2012)

Table 1. Mean (±SD) measurements of $\delta^{13}C$, $\delta^{15}N$, and total mercury (THg) and associated information (estimated trophic level, primary habitat) of fish in South Eleuthera, The Bahamas. Summary information for trophic position (TP) is based on Fishbase.org (Froese & Pauly 2018). THg (dry and wet values, ppm) and stable isotope ratios (‰) were directly measured from liver and muscle tissue of teleost fishes sampled in South Eleuthera

Species	Scientific name		Muscle					Liver				
		TP (Fishbase)	n	THg_{Dry}	THg_{Wet}	n	$\delta^{13}C$	$\delta^{15}N$	n	THg_{Dry}	THg_{Wet}	n	$\delta^{13}C$	$\delta^{15}N$
Open-ocean-associated														
Atlantic flying fish	*Cheilopogon melanurus*	3.6 (0.5)	3	0.2 (0.1)	0.1	1	−17.1	7.1	3	0.2 (0.1)	0.1 (0.1)	1	−14.9	7.6
Wahoo	*Acanthocybium solandri*	4.3 (0.2)	23	1.2 (1.0)	0.3 (0.3)	11	−16.8 (0.4)	9.3 (0.8)	21	1.2 (1.5)	0.4 (0.2)	10	−17.3 (0.4)	7.9 (0.9)
Dolphinfish	*Coryphaena hippurus*	4.4 (0.0)	91	1.0 (0.4)	0.2 (0.1)	44, 48	−17.1 (0.8)	9.73 (1.3)	85	0.6 (0.5)	0.2 (0.2)	43, 44	−17.2 (1.0)	7.6 (0.9)
Blackfin tuna	*Thunnus atlanticus*	4.4 (0.3)	10	0.6 (0.3)	0.1 (0.1)	8	−17.4 (0.4)	8.33 (0.5)	11	0.4 (0.2)	0.2 (0.1)	5, 6	−17.4 (0.5)	6.6 (0.5)
Yellowfin tuna	*Thunnus albacares*	4.4 (0.4)	1	0.9	0.2	1	−17.3	9.1	2	0.6 (0.2)	0.2 (0.1)	1	−17.5	6.1
Reef-associated														
French grunt	*Haemulon flavolineatum*	3.5 (0.1)	–	–	–	–	–	–	1	1.6	0.7	–	–	–
Queen triggerfish	*Balistes vetula*	3.8 (0.1)	3	0.8 (0.2)	0.2 (0.1)	2	−14.0 (0.4)	6.7 (0.9)	3	0.8 (0.4)	0.3 (0.2)	–	–	–
Red hind	*Epinephelus guttatus*	3.8 (0.3)	1	0.8	0.3	1	−13.1	8.6	1	9.3	3.9	1	−11.7	8.5
Mutton snapper	*Lutjanus analis*	3.9 (0.2)	4	1.0 (0.5)	0.3 (0.2)	3	−11.5 (2.9)	8.4 (0.7)	3	2.2 (1.5)	0.9 (0.6)	1	−8.6	7.6
Yellowtail snapper	*Ocyurus chrysurus*	4.0 (0.3)	8	0.8 (0.6)	0.2 (0.1)	3	−13.8 (3.3)	8.52 (0.6)	8	1.0 (0.9)	0.5 (0.4)	5	−14.4 (1.8)	6.4 (1.4)
Nassau grouper	*Epinephelus striatus*	4.1 (0.0)	1	1.1	0.2	1	−13.2	7.7	1	1.7	0.7	1	−12.8	7.5
Black snapper	*Apsilus dentatus*	4.1 (0.5)	3	0.2 (0.1)	0.1 (0.0)	–	–	–	3	0.7 (0.4)	0.3 (0.1)	1	−16.9	5
King mackerel	*Scomberomorus cavalla*	4.4 (0.3)	4	3.2 (1.9)	0.8 (0.5)	1	−15.4	7.9	3	4.1 (3.7)	1.7 (1.5)	3	−15.8 (0.5)	7.4 (0.5)
Vermilion snapper	*Rhomboplites aurorubens*	4.4 (0.2)	6	1.6 (0.8)	0.4 (0.2)	1	−15.8	8.47	5	3.8 (2.9)	1.4 (1.2)	4	−15.9 (1.0)	6.5 (1.1)
Spanish mackerel	*Scomberomorus maculatus*	4.5 (0.5)	2	1.2 (0.3)	0.2 (0.1)	1	−16.9	9.5	3	4.2 (5.8)	1.6 (1.2)	1	−16.9	6.7
Great barracuda	*Sphyraena barracuda*	4.5 (0.6)	10	2.8 (1.7)	0.8 (0.6)	4	−12.4 (2.6)	10.6 (3.1)	13	4.1 (4.3)	1.4 (1.3)	1	−13.8	8.7
Amberjack	*Seriola* sp.	4.5 (0.0)[a]	1	2.3	0.7	1	-15.1	11.2	1	1	0.3	–	–	–

[a]Based on *Seriola dumerili*

(Table 3, Fig. 3). Both species exhibited relatively high total niche overlap (>42%), as inferred from SIA of both muscle and liver tissue (Table 3, Fig. 3). For dolphinfish, there was no statistically significant difference between mean muscle and liver $\delta^{13}C$ (Wilcoxon-test, W = 832, p = 0.34). However, a significant difference was observed for $\delta^{15}N$ (W = 152, p < 0.001). For wahoo, statistically significant differences were observed between muscle and liver $\delta^{13}C$ (t = −2.70, df = 18.86, p = 0.01) and $\delta^{15}N$ (t = −3.73, df = 17.81, p = 0.002) values.

For all fishes analyzed, in both muscle and liver tissues, THg_{Dry} and THg_{Wet} levels between species differed by as much as 3 orders of magnitude. THg_{Dry} and THg_{Wet} of liver tissue ranged from 0.07 to 15.61 ppm, and 0.06 to 5.34 ppm, respectively. THg_{Dry} and THg_{Wet} of muscle tissue ranged from 0.09 to 6.35 ppm, and 0.02 to 2.31 ppm, respectively. The highest THg values were observed in the liver tissues of Spanish mackerel, great barracuda, and king mackerel (Table 1). For dolphinfish, statistically significant differences were observed between liver and muscle THg_{Dry} (W = 1374, p < 0.001), which was higher in liver than muscle (Fig. 4). For wahoo, there was no statistically significant difference in THg_{Dry} between liver and muscle tissue (W = 233, p = 0.85, Fig. 4).

Several significant relationships were found between size and THg_{Dry} for muscle and liver tissue of dolphinfish and wahoo (Table 4, Fig. 5). For dolphinfish muscle tissue, GLMs revealed a strong effect of FL on THg_{Dry}, but effects of other variables were not significant. For liver tissue THg_{Dry}, the most parsimonious model included the effects of FL, $\delta^{13}C$, and FL × $\delta^{13}C$. However, none of these variables alone were statistically significant (Table 4). For wahoo, we observed no relationship between size and THg_{Dry} in muscle tissue (F = 1.94, df = 1, 19, r^2 = 0.09, p > 0.05, Fig. 5). However, a significant negative relationship between size and THg_{Dry} was observed for liver (F = 12.89, df = 1, 17, r^2 = 0.43, p = 0.002; Fig. 5).

Table 2. Outputs of Bayesian stable isotope mixing models, highlighting mean (±SD) contribution of reef and open-ocean-based prey items to the diets of dolphinfish *Coryphaena hippurus* and wahoo *Acanthocybium solandri*. Models were run using 2 different diet-tissue discrimination factors (DTDFs): tissue-specific DTDFs generated from Pacific bluefin tuna *Thunnus orientalis* (Madigan et al. 2012a), and a multi-taxon-derived DTDF (Zanden & Rasmussen 2001)

Species	Tissue	n	DTDF	Reference	Proportion of diet	
					Reef	Open-ocean
Dolphinfish	Muscle	44	$\Delta^{13}C = 1.8 (\pm 0.3)$ $\Delta^{15}N = 1.9 (\pm 0.4)$	Madigan et al. (2012a)	0.02 (0.02)	0.98 (0.02)
			$\Delta^{13}C = 0.47 (\pm 1.23)$ $\Delta^{15}N = 2.92 (\pm 1.78)$	Zanden & Rasmussen (2001)	0.05 (0.02)	0.95 (0.02)
	Liver	43	$\Delta^{13}C = 1.2 (\pm 0.3)$ $\Delta^{15}N = 1.1 (\pm 0.6)$	Madigan et al. (2012a)	0.03 (0.02)	0.98 (0.02)
			$\Delta^{13}C = 0.47 (\pm 1.23)$ $\Delta^{15}N = 2.92 (\pm 1.78)$	Zanden & Rasmussen (2001)	0.04 (0.02)	0.96 (0.02)
Wahoo	Muscle	11	$\Delta^{13}C = 1.8 (\pm 0.3)$ $\Delta^{15}N = 1.9 (\pm 0.4)$	Madigan et al. (2012a)	0.07 (0.06)	0.93 (0.06)
			$\Delta^{13}C = 0.47 (\pm 1.23)$ $\Delta^{15}N = 2.92 (\pm 1.78)$	Zanden & Rasmussen (2001)	0.11 (0.06)	0.89 (0.06)
	Liver	10	$\Delta^{13}C = 1.2 (\pm 0.3)$ $\Delta^{15}N = 1.1 (\pm 0.6)$	Madigan et al. (2012a)	0.07 (0.06)	0.93 (0.06)
			$\Delta^{13}C = 0.47 (\pm 1.23)$ $\Delta^{15}N = 2.92 (\pm 1.78)$	Zanden & Rasmussen (2001)	0.09 (0.05)	0.91 (0.05)

4. DISCUSSION

Results from this study largely suggest that open-ocean ecosystems are the major route of contaminant bioaccumulation for dolphinfish and wahoo, despite the fact that both species reside close to coastal production systems. Bayesian mixing models were not sensitive to DTDFs, suggesting that solutions showing minimal reef prey subsidies are highly plausible for both species, though discrimination between resource pools was driven mostly by strong differences in $\delta^{13}C$ between reef and open-ocean fish. Despite a lack of observation from Eleuthera waters, both focal predators did not typically display THg concentrations above FDA and EPA guidelines, and values fell within expected ranges from other regions in The Bahamas and Florida, USA. Elevated THg concentrations were, however, observed in reef-

Table 3. Estimates of niche width and total niche overlap for dolphinfish *Coryphaena hippurus* and wahoo *Acanthocybium solandri* in South Eleuthera, The Bahamas. Niche width estimates are based on small sample size-corrected maximum likelihood and Bayesian standard ellipse area (SEA_C and SEA_B in ‰^{2}, respectively). Niche overlap estimates represent Bayesian estimated isotopic overlap (%) where $\alpha = 0.05$

	White muscle				Liver			
	n	SEA_C	SEA_B	Niche overlap (%)	n	SEA_C	SEA_B	Niche overlap (%)
Dolphinfish	44	2.18	2.25	42.83	43	2.81	2.81	50.61
Wahoo	11	0.92	0.93	89.09	10	1.21	1.20	94.29

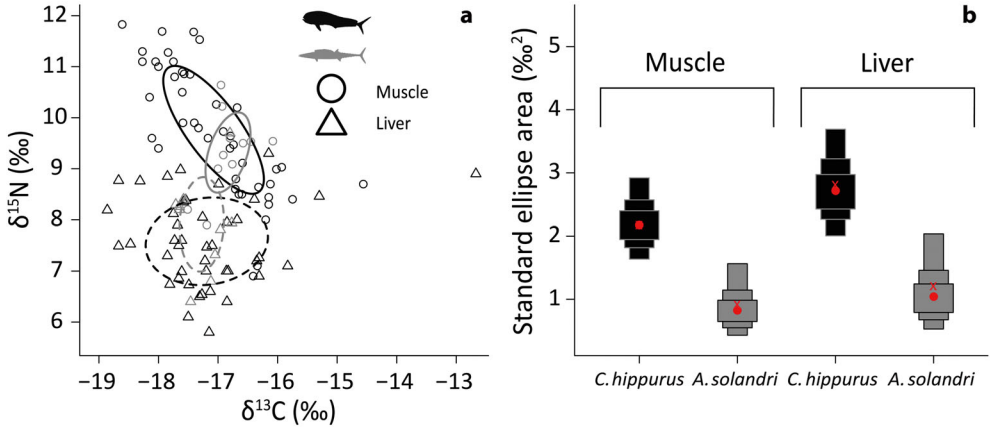

Fig. 3. (a) Standard ellipse area (SEA) for muscle (solid lines) and liver (hashed lines) tissue of dolphinfish *Coryphaena hippurus* (black) and wahoo *Acanthocybium solandri* (grey). (b) Bayesian estimated SEA (SEA_B). Red circle: mean SEA_B; red ×: maximum likelihood estimated SEA. Both shown with 50, 75, and 95% credible intervals

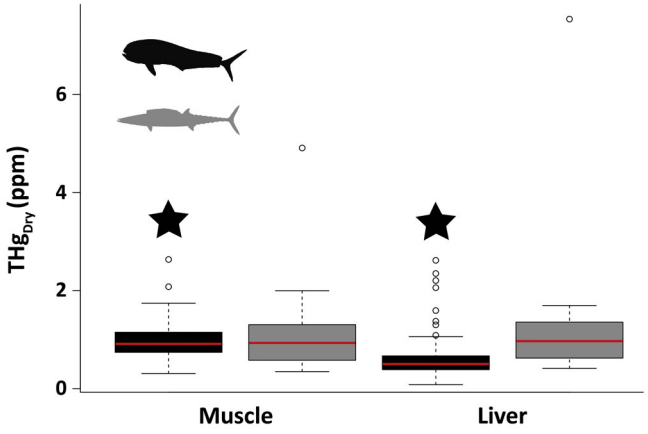

Fig. 4. Boxplots highlighting dry total mercury (THg_{Dry}) generated from dried muscle and liver tissues of dolphinfish *Coryphaena hippurus* (black) and wahoo *Acanthocybium solandri* (grey). Red line indicates median values. Lower and upper bounds are 25 and 75% confidence intervals surrounding median. Whiskers represent data falling within 1.5 of the interquartile range (IQR); points represent outliers, and large stars indicate statistically significance differences for pairwise comparisons between tissue types

associated fishes, which may provide a potential route of toxic Hg exposure for human consumers.

4.1. Resource-use dynamics

Predominant utilization of the open-ocean resource pool was coupled with relatively high isotopic niche overlap between the 2 predators, which was consistent across both tissue types. However, dolphinfish displayed a broader isotopic niche, especially in $\delta^{15}N$ space. This result is supported by prior studies in multiple ocean basins using traditional diet analysis, which have illustrated high opportunism and a generalist diet (Oxenford & Hunte 1999, Tsai FY et al. 2016). Specifically, comparisons in western North Atlantic waters off North Carolina, USA, suggested that dolphinfish typically display a broader diet than wahoo (Rudershausen et al. 2010), which may feed more exclusively on larger teleost prey (Oxenford et al. 2003). Similarly, large migratory pelagic predators often perform extensive vertical movements throughout the water column, which can also impact predator fitness and contaminant loading (e.g. Dewar et al. 2011, Madigan et al. 2018), and different vertical habitat use could further explain the larger isotopic niche of dolphinfish relative to wahoo. This is plausible, as although dolphinfish are predominantly epipelagic, existing satellite tracking data suggests that they can perform oscillatory movements to depths exceeding 200 m (Merten et al. 2014b) to feed on both pelagic and mesopelagic prey items. Wahoo, on the other hand, typically prefer strictly epipelagic waters above the thermocline (Sepulvida et al. 2011). One caveat is that isotopic niches were derived from a smaller sample size for wahoo, though we corrected for small sample size when generating SEA, which appears relatively insensitive to sample sizes ≥10 (Jackson et al. 2011). While this suggests that a lower sample size would not adversely affect ecological interpretation of isotopic niche dynamics, a lower sample size inherently represents fewer individuals and thus may not fully account for intra-specific feeding variability.

Isotopic niche width estimates for dolphinfish and wahoo did not vary by tissue type for either species, but liver tissue (representing more recent feeding) exhibited a ^{15}N enrichment of approximately 2‰ compared to muscle. Since both predators are oppor-

Table 4. Full and reduced generalized linear model outputs (t. value [p.value]) exploring size and isotopic drivers of dry total mercury (THg_{Dry}) for dried dolphinfish muscle (n = 42) and liver (n = 38) tissue. FL: fork length. AIC: Akaike's information criterion; AIC_c: small sample size-corrected AIC. *Statistical significance at α = 0.05

Model	Intercept	FL	$\delta^{13}C$	$\delta^{15}N$	$\delta^{13}C \times \delta^{15}N$	$FL \times \delta^{13}C$	$FL \times \delta^{15}N$	AIC	AIC_c
Muscle									
$THg_{Dry} \sim FL + \delta^{13}C + \delta^{15}N + \delta^{13}C \times \delta^{15}N + FL \times \delta^{13}C + FL \times \delta^{15}N$	−0.49 (0.63)	0.79 (0.44)	−0.23 (0.82)	0.16 (0.87)	−0.08 (0.94)	0.40 (0.69)	−0.53 (0.60)	47.09	51.45
$THg_{Dry} \sim FL$	−0.67 (0.50)	3.19 (0.003*)	–	–	–	–	–	40.86	41.49
Liver									
$THg_{Dry} \sim FL + \delta^{13}C + \delta^{15}N + \delta^{13}C \times \delta^{15}N + FL \times \delta^{13}C + FL \times \delta^{15}N$	−0.27 (0.79)	0.80 (0.43)	−0.41 (0.68)	−0.45 (0.66)	−0.17 (0.87)	1.19 (0.24)	0.71 (0.49)	48.02	52.98
$THg_{Dry} \sim FL + \delta^{13}C + FL \times \delta^{13}C$	−1.35 (0.19)	1.55 (0.13)	−1.24 (0.22)	–	–	1.38 (0.18)	–	43.32	45.19

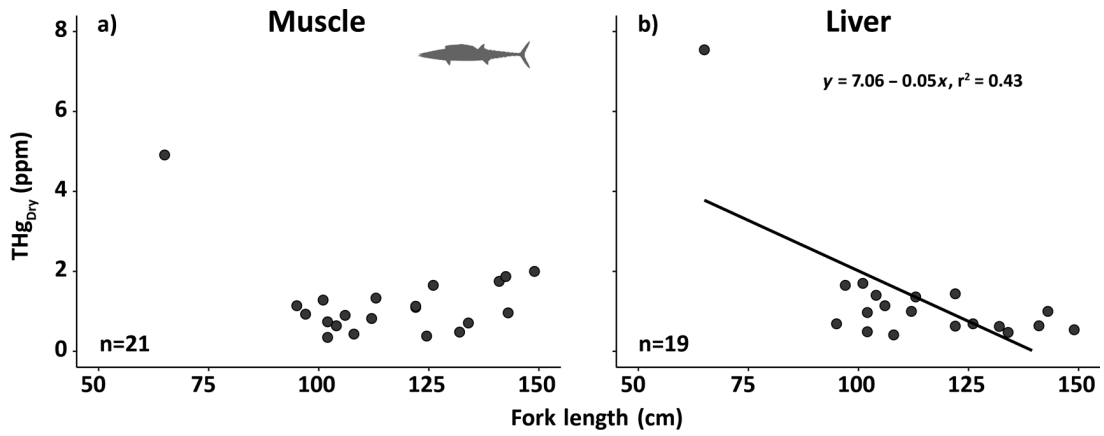

Fig. 5. Size-based linear regressions for wahoo *Acanthocybium solandri* for dried (a) muscle and (b) liver tissues. THg_{Dry}: dry total mercury

tunistic, seasonal prey availability is the most likely driver of diet variability and is demonstrated in existing stomach content studies for both dolphinfish (Oxenford & Hunte 1999) and wahoo (Oyafuso et al. 2016). Interestingly, in this study similar isotopic differences were also observed for other pelagic species sampled, such as blackfin tuna and yellowfin tuna (Table 1). Whether diet switching is due to changes in prey abundance within the Exuma Sound or is an isotopic reflection of seasonal migrations remains unconfirmed. For dolphinfish and wahoo, seasonal movements between the Caribbean and US east coast have been documented, with northern migrations occurring in the spring/summer before individuals return south in the fall/winter (Oxenford et al. 2003, Merten et al. 2014b). If the individuals sampled from The Bahamas did indeed perform extensive north–south migrations, it is possible that more enriched $\delta^{15}N$ values of liver tissue may reflect recent migration from northern waters with elevated $\delta^{15}N$ baselines (values at the base of the pelagic food web; e.g. McMahon et al. 2013). Further work utilizing compound-specific amino acid $\delta^{15}N$ signatures (Popp et al. 2007, Ohkouchi et al. 2017) would provide definitive resolution on whether these shifts are in fact driven by local (i.e. within the Exuma Sound) changes in dominant prey items or feeding across different $\delta^{15}N$ baselines during seasonal migrations. Additional sources of ^{15}N variability could result from differential isotopic routing and associated fractionation between tissue types of variable turnover rate and metabolic function, especially as $\delta^{15}N$ signatures have been shown to vary based on nutrient recycling processes and amino acid composition (Schmidt et al. 2004, MacNeil et al. 2006). Due to the difficulty of measuring patterns of isotopic fractionation *in situ*, a substantial amount of work may be required to elucidate whether specific metabolic reactions are responsible for driving variable patterns of ^{15}N fractionation across tissues.

We cannot fully discount the importance of fringing reef systems as an indirect energy source for pelagic fishes. Many fringing reef fish species have a juvenile pelagic phase, and juvenile coastal fishes (e.g. *Sebastes* spp.) have been observed in stomachs of pelagic fishes in the California Current Ecosystem (Madigan et al. 2015), in dolphinfish off Taiwan (Tsai FY et al. 2016), in dolphinfish in the eastern Caribbean (Oxenford & Hunte 1999), and observationally during a companion study in this area (D.J.M. pers. obs.). Reef fish larvae would predominantly exhibit a pelagic isotopic signature (due to planktivorous feeding during the pelagic larval phase (Jones et al. 2005), and they could still provide an important energy source for pelagic predators, particularly for smaller-bodied individuals who are unable to forage on larger prey such as flying fish. Since many reef fish larvae have been shown to settle close to residential regions of adults, reef health could thus indirectly affect foraging opportunities for dolphinfish and wahoo, certainly in this region of The Bahamas. This could be further assessed with traditional diet studies, which could identify the relative contribution of pelagic juvenile reef fishes, both by mass and by energy, to pelagic predators in this region. Finally, although we did not detect prey contribution from reef-associated prey, the unique physical structure of the reef–open-ocean interface may aggregate important prey pools, which attract dolphinfish and wahoo to the shelf break, acting similarly to seamounts, fish aggregation devices (FADS), and floating *Sargassum* mats (Girard et al. 2007, Monteiro et al. 2008, Farrell et al. 2014).

4.2. Factors affecting THg bioaccumulation

Dolphinfish and wahoo did not exhibit THg_{Wet} concentrations above current guidelines set by various government bodies (US Environmental Protection Agency [EPA] = 0.3 ppm, US Food and Drug Administration [FDA] = 1.0 ppm) and fell within expected ranges reported in previous studies (e.g. Adams 2009, 2010). However, reported concentrations are not negligible, and prolonged, consistent exposure may still allow for accumulation of relatively high Hg levels in human consumers (e.g. Zahir et al. 2005). For both species, patterns of Hg variability were observed, and significant relationships were found in comparisons of size with THg_{Dry}. In general, liver THg_{Dry} was more variable than muscle THg_{Dry} with increasing fish size, resulting in weaker relationships and/or those that were not statistically significant. This variability may be due to the functional complexity and cyclical metabolic processes occurring in the liver (Madigan et al. 2012a). When coupled with a faster metabolic turnover rate (which reflects recent feeding), this may mask longer term, more stable trends represented by muscle. For example, Hg biotransformation occurs mostly in the liver of animals, where Hg can be partially removed via chelation, and/or mobilized in eggs prior to spawning (Boening 2000). More sex-specific information, as well as measurement of THg across egg tissue, may help explain the variability observed in THg accumulation in liver tissue of the fishes sampled. The generally low THg values of dolphinfish, despite their large size, may be due in part to the high intrinsic rate of growth (r_{in} = 0.77), and low maximum age (T_{max} ~5 yr, Froese & Pauly 2018), as both of these factors result in lower Hg levels in fish (Mason et al. 2000). The size range of individuals studied may be biased by fisher's selectivity for larger individuals. Thus, observed relationships may be stronger if THg was measured over the complete size range of dolphinfish (especially smaller individuals). The lack of significant relationships between size and $\delta^{13}C$ for either tissue suggests that dolphinfish sampled in this study forage, and thus bioaccumulate Hg, strictly in open-ocean food webs. For wahoo, sample size limited statistical analysis to relationships between size and THg_{Dry}, and we observed a significant, negative linear trend between size and THg_{dry} in liver. It is possible that this could be driven in part by growth dilution (Karimi et al. 2010), such that THg biomagnification factors decline with a reduction of growth rate and/or growth efficiency, which may occur throughout ontogeny (see Trudel & Rasmussen 2006). Alternatively, individuals may undergo shifts in dietary preference throughout ontogeny, such that common prey items of larger individuals exhibit lower THg concentrations (Colman et al. 2015). Further work is needed to fully support/refute both hypotheses, given the relatively small number of wahoo available and the non-significant trend between size and THg_{Dry} of muscle tissue.

A number of commonly consumed fishes from Eleuthera did show relatively high (i.e. above US EPA guidelines of 0.3 ppm) concentrations of THg in muscle and liver tissue. Notably high concentrations were observed in reef-associated fishes such as barracuda, amberjack, vermilion snapper, king mackerel and Spanish mackerel. Despite relatively low sample sizes, these observations suggest that reef-associated target species may present a potential, previously undocumented route of toxic Hg exposure for consumers of fish from artisanal fisheries. Whether this observation is a result of a local point source(s) of Hg contaminating nearshore systems or a result of certain reef fish life history characteristics (e.g. growth rates, age, trophic level, internal lipid content) is unclear. For example, elevated THg concentrations of king mackerel and Spanish mackerel may be associated with the high lipid content of tissues, which results in high binding affinity of lipophilic MeHg. Observations could also be an artefact of food-chain length; oligotrophic open-ocean systems of sub-tropical and tropical latitudes commonly exhibit fewer trophic links, which may reduce the capacity for significant THg bioaccumulation compared to more productive and complex coastal food webs (Ward & McCann 2017). It is difficult to infer *a priori* any specific anthropogenic inputs of mercury from Eleuthera Island, which is relatively undeveloped compared to neighboring islands such as New Providence and Grand Bahama. Based on THg levels observed in Eleuthera reef fishes and the high tourist-driven seafood demand of these larger islands, quantifying local contaminant concentrations of commonly consumed fishes may be considered a pertinent priority. Further work may show temporal trends or atypically high regional Hg loading in local reef fish, especially in countries or regions where efflux of Hg into marine environments is not well regulated or monitored.

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