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2 TROPHIC ECOLOGY OF BARRELFISH (*HYPEROGLYPHE PERCIFORMIS*) IN OCEANIC
3 WATERS OFF SOUTHEAST FLORIDA
4

5 Barrellfish Trophic Ecology
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33 ABSTRACT

34 Deep-water demersal fishes represent an understudied but ecologically important group
35 of organisms. Select species of demersal fishes rely on pelagic prey items, representing a direct
36 transport of surface carbon to greater depths. Barrelfish *Hyperoglyphe perciformis* (Mitchell,
37 1818), which inhabit deep slope waters, are a species that has been suggested to fill this role, as
38 congeners consume primarily pelagic gelatinous zooplankton; however, there is a dearth of
39 information on the trophic ecology of barrelfish. Stomach content and stable isotope analyses
40 were conducted on barrelfish caught by recreational fishers off Miami, Florida to improve our
41 understanding of the feeding of this species. *Pyrosoma atlanticum* (Péron, 1804), a pelagic,
42 vertically migrating tunicate, represented 89% of the barrelfish diet by weight. Mesopelagic fish
43 and shrimp contributed much smaller proportions. Standard ellipse areas corrected for sample
44 size (SEA_c) showed a substantially smaller isotopic niche width for barrelfish (0.606 ‰²) than
45 dolphinfish (2.16 ‰²), king mackerel (3.04 ‰²), or wahoo (1.97 ‰²). Coupled with dependence
46 on a singular prey item, the low SEA_c of barrelfish suggests they occupy a limited trophic niche
47 space. Overlap of barrelfish SEA_c with dolphinfish (99.5% overlap) and king mackerel (100%
48 overlap) indicate that the carbon sources as well as the number of trophic steps for barrelfish are
49 similar to king mackerel and dolphinfish and are linked to surface waters. This trophic linkage
50 suggests that barrelfish may play a role in carbon export and further study into their behavior and
51 daily consumption rates is warranted for quantifying this role.

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57 TEXT

58 Pathways of carbon export have become an increasingly important area of research with
59 the increased input of inorganic carbon into the ocean from anthropogenic activities (Sabine et
60 al. 2004, Riebesell et al. 2007, Siegel et al. 2014). A primary interest in these pathways is the
61 vertical transfer of carbon fixed by primary producers in the euphotic zone to deeper regions in
62 the ocean basin (Ducklow et al. 2001). Key steps in understanding this process involve knowing
63 the community structure of both primary producers and primary consumers (Steinberg et al.
64 2000, Richardson and Jackson 2007, Laurenceau-Cornec et al. 2015, Siegel et al. 2016). While
65 most research focuses on lower trophic levels, higher trophic levels such as fishes can play a
66 significant role in the export and sequestration of carbon to deeper waters (Smith et al. 2009,
67 Davison et al. 2013, Trueman et al. 2014).

68 Deep-water fishes are critical components of oceanic ecosystems as they are the most
69 abundant group of fishes on earth, with recent estimates of biomass representing 10,000 million
70 tonnes (Irigoien et al. 2014). These fishes are predominantly zooplanktivorous and often display
71 diel vertical migrations that follow their prey items (Merrett and Roe 1974, Sutton and Hopkins
72 1996, Pusch et al. 2004, Catul et al. 2011). However, significant consumption of vertically
73 migrating species can occur by demersal fishes that do not migrate but live near the bottom and
74 feed in the midwater (making them more benthopelagic), thus providing a means to export
75 carbon through consumption of vertically migrating organisms (Mauchline and Gordon 1991,
76 Trueman et al. 2014).

77 An example of such benthopelagic fishes are members of the *Hyperoglyphe* genus, which
78 are known to consume vertically migrating gelatinous zooplankton. These fishes are poorly
79 understood with most studies focused on *Hyperoglyphe antarctica* (Carmichael, 1919), the blue-

80 eye trevalla, in the Indian and Pacific Oceans (Winstanley 1978, Bolch et al. 1993, Robinson et
81 al. 2008, Fay et al. 2011). Barrelfish *Hyperoglyphe perciformis* (Mitchell, 1818) are an
82 understudied congener present throughout the slope waters of the western central Atlantic Ocean
83 (Filer and Sedberry 2008, Goldman and Sedberry 2011). Barrelfish, much like the blue-eye
84 trevalla, are a demersal/benthopelagic fish that are caught at depths ranging from 200 to 400 m,
85 grow slowly, reach maturity at six years of age, and may live as long as 85 years (Filer and
86 Sedberry 2008). The diet of barrelfish has been examined along the Charleston Bump region (off
87 South Carolina) where they primarily consume the tunicate *Pyrosoma atlanticum* (Péron, 1804;
88 Goldman and Sedberry 2011). These pyrosome tunicates are an example of a gelatinous
89 zooplankter that has substantial potential as a vector for carbon export. With filtering rates of 35
90 $l\ hr^{-1}$, pyrosomes can graze a considerable amount of primary productivity and return it to depth
91 (~ 400 m) during daylight hours (Andersen and Sardou 1994, Perissinotto et al. 2007).
92 Furthermore, pyrosome tunicates have one of the highest carbon contents of gelatinous
93 organisms, enhancing its potential as a mechanism for carbon transport (Lebrato and Jones
94 2009). Large concentrations of pyrosomes can occur but are very patchy in time and space
95 (Cowper 1960, Lebrato et al. 2013). These pyrosome “falls” can contribute substantially to
96 carbon export, as the sinking of moribund pyrosomes are often consumed by benthic organisms
97 (Lebrato and Jones 2009). Consumption of live tunicates by barrelfish may provide a means to
98 export carbon outside of these falls but our understanding of this mechanisms is still limited.

99 This study employs diet and stable isotope analysis to better understand the trophic
100 ecology of barrelfish. The analysis of stomach content here provides improved geographic
101 resolution to diet studies of this species, accounting for the second diet study ever completed on
102 this species, while our analysis of the stable isotope signatures of barrelfish is the first for the

103 species. Stable isotope analysis was employed to compare carbon source and trophic level of
104 barrelfish to that of epipelagic species in the same region, specifically the ubiquitous dolphinfish
105 *Coryphaena hippurus* (Linnaeus, 1758), the oceanic wahoo *Acanthocybium solandri* (Cuvier,
106 1832), and the more coastal king mackerel *Scomberomorus cavalla* (Cuvier, 1829).

107 A total of 29 barrelfish, 46 dolphinfish, 18 king mackerel, and 14 wahoo were collected
108 from fishers at Crandon Park Marina on Key Biscayne, Florida from November 2014 to
109 November 2015. Each specimen was kept on ice after capture, and upon returning to shore, fork
110 length, standard length, and sex were recorded. The gut cavity of each fish was opened and an
111 incision was made at the base of the throat to remove the stomach and intestine from the fish.
112 From this, the stomach was separated from the intestine through incisions made at the pyloric
113 sphincter.

114 Upon returning to the lab, the stomach contents were immediately placed in 95%
115 ethanol. Later, the stomach contents were identified to the lowest possible taxonomic unit and
116 the mass of each item was recorded (tunicates were treated as one prey item despite being a
117 colonial organism and often being broken into multiple pieces). These data were then used to
118 calculate an index of relative importance (IRI) for each prey item using the formula

$$IRI = (%N + \%W) * \%F$$

119 where %N represents the numerical percentage of individuals of a particular prey type in relation
120 to the total number of prey items. %W represents the percentage by weight of a particular prey
121 type in relation to the total weight of all prey. %F represents the percent frequency that a prey
122 type occurred in the total number of stomachs analyzed. The percentage of total IRI for each
123 species was then calculated:

$$124 \%IRI_i = \frac{100 * IRI_i}{\sum_{i=1}^n IRI_i}$$

125 Where i represents a particular prey type and n represents the total number of unique prey types
126 for a predator species.

127 Dorsal muscle samples were also collected from fish specimens, and were stored on ice
128 for approximately 30 minutes until they could be placed in a -20°C freezer. Samples were dried
129 at 50°C in a drying oven for 48 hours, or until adequately dry for processing. Subsamples (1.2-
130 1.5 mg) were then analyzed with an Isoprime isotope ratio mass spectrometer (IRMS; GV
131 Instruments, Manchester, UK), which yielded carbon to nitrogen ratios (C:N) and the isotopic
132 ratios for both carbon ($^{13}\text{C}:^{12}\text{C}$) and nitrogen ($^{15}\text{N}:^{14}\text{N}$) in each sample. Values reported use the δ
133 notation (e.g. Fry 2006) and are relative to the standards PeeDee belemnite (carbon) and
134 atmospheric nitrogen. Using the C:N values from the mass spectrometry results, a lipid
135 correction curve was applied to each sample following Logan et al. (2008):

$$136 \quad \delta^{13}\text{C corrected} = \delta^{13}\text{C} + (7.489 - (7.489 * 3.097) / (\text{C:N}))$$

137 Muscle isotope ratios were successfully attained from 26 barrelfish, 36 dolphinfish, 17
138 king mackerel, and 12 wahoo. Isotopic niche widths for each species were compared using
139 standard ellipse areas with a sample size correction. The standard ellipse is the bivariate
140 equivalent of standard deviation and the standard ellipse area is calculated using the variance and
141 covariance of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values, encompassing 40% of the data for each species (Batschelet
142 1981, Ricklefs and Nealen 1998). The area of this ellipse is then corrected through the following
143 equation:

$$144 \quad \text{SEA}_c = \text{SEA} * (n-1) / (n-2)$$

145 Where SEA is the standard ellipse area, SEA_c is the sample size corrected ellipse area, and n is
146 the number of samples for a species (Jackson et al. 2011, Jackson et al. 2012) while SEA_c
147 values allow a comparison of isotopic niche breadth, comparisons in the overlap of these ellipses

148 quantifies the overlap in isotopic niche space between two species (Jackson et al. 2012). Further,
149 Bayesian inference was used to create credible intervals around the Bayesian standard ellipse
150 areas (SEA_B). Details of this method are described in Jackson et al. (2011), but, briefly, vague
151 normal priors are assigned to the means and an Inverse-Wishart prior is used as the covariance
152 matrix of isotope values for each species. The isotope data are then used to form likelihood
153 values, which are then combined with the priors to form posterior distributions (in this case the
154 posterior estimate of the covariance matrix is simulated using the Markov Chain Monte Carlo
155 method). From these posterior distributions, a set of 4000 estimates of the standard ellipse area
156 are calculated to provide the mode of the Bayesian standard ellipse areas and credible intervals.

157 Over 90% of the barrelfish's diet IRI was attributed to a single species, *P. atlanticum*
158 constituting 89% of the biomass of the barrelfish's diet and 47% of the diet by number (Table 1).
159 Other organisms consumed consisted of ruby red shrimp (Solenoceridae, IRI: 1.6%) and
160 mesopelagic fishes (Stomiidae, IRI: 2.5%; Sternoptychidae, IRI: 0.4%; Tetragonuridae, IRI:
161 0.1%). It is likely that some or all of the items identified as squid (IRI: 4.1%) were bait used by
162 fishers.

163 Analysis of standard ellipses for each species revealed substantial differences in the SEA_c
164 values and substantial isotopic niche overlap of barrelfish with the three epipelagic fishes
165 studied. The SEA_c values were much lower for barrelfish (0.606 ‰^2) than dolphinfish, king
166 mackerel, and wahoo (2.16 ‰^2 , 3.04 ‰^2 , 1.97 ‰^2 , respectively), with the isotopic niche of
167 barrelfish occupying an area less than a third the size of each of the other species. This was
168 bolstered by substantial differences in the SEA_B values between barrelfish and the three
169 epipelagic species, with little difference in SEA_B among the epipelagic species (Figure 1).
170 Further, the SEA_c for barrelfish overlapped with the epipelagic fishes, most prominently with

171 king mackerel, showing 100% of barrelfish's isotopic niche overlapping with that of king
172 mackerel (Figure 2). This was closely followed by overlap with dolphinfish (99.5%) but much
173 less overlap with wahoo (26%).

174 The stomach contents of barrelfish analyzed in this study suggest an obligate connection
175 with *P. atlanticum*. The IRI value (91.2%) is also deflated by the percent number metric, which
176 was a conservative estimate because it was not possible to determine individual pelagic tunicates
177 in barrelfish stomachs due to the breakdown from stomach action and the pharyngeal bones of
178 barrelfish. Goldman and Sedberry (2011) found *P. atlanticum* to have an IRI of 87% for
179 barrelfish using similar methods of enumeration, suggesting that dependence upon *P. atlanticum*
180 by barrelfish is not unique to the waters off southeast Florida. A congener, the blue-eye trevalla
181 *Hyperoglyphe antarctica*, has also been shown to primarily consume pyrosomids, leading to the
182 possibility that an obligate connection with pyrosomids may extend to other members of the
183 *Hyperoglyphe* genus (Winstanley 1978).

184 The small isotopic niche of barrelfish substantiates that they are specialist consumers
185 with a narrow range in their carbon source and trophic level. Their isotopic niche is also nearly
186 entirely contained within the isotopic niche space of two of the epipelagic fishes, indicating that
187 pyrosomes represent a vector of surface carbon to depth. ^{13}C is often more labile, thus $\delta^{13}\text{C}$ of
188 particulate organic matter is often depleted during remineralization near the pycnocline and
189 fluctuates with depth within 400 m of the surface, suggesting the $\delta^{13}\text{C}$ signature of barrelfish is a
190 result of consuming carbon transported to depth from the euphotic zone by pyrosomids (Jeffrey
191 et al. 1983, Drits et al. 1992, Druffel et al. 1992, Andersen and Sardou 1994, Perissinoto et al.
192 2007). This is further supported by the consumption of epipelagic organisms by king mackerel
193 and dolphinfish in this study (and others) and their rather limited vertical range, rarely exceeding

194 200 m in the case of dolphinfish (Table 1; Finucance et al. 1990, Oxenford 1999; Oxenford and
195 Hunte 1999, Rudershausen et al. 2010, Tripp-Valdez et al. 2010, Merten et al. 2014a, Moore
196 2014, Teffer et al. 2015). However, dolphinfish exhibit highly migratory behavior and king
197 mackerel exhibit seasonal migrations in southeast Florida which may lead to the substantially
198 broader range in $\delta^{13}\text{C}$ in these epipelagic species when compared to barrelfish (Sutter III et al.
199 1991, Schaefer and Fable Jr. 1994, Merten et al. 2014b, Merten et al. 2016).

200 Owing to the strong trophic coupling between barrelfish and *P. atlanticum*, fluctuations
201 of *P. atlanticum* or barrelfish may affect the population of the other species. However,
202 quantification of this coupling strength through incorporating barrelfish abundance, growth rates,
203 rates of *P. atlanticum* consumption by barrelfish, and potential bottom up effects on barrelfish
204 survival (manifested through changes in *P. atlanticum* growth) is necessary to determine if this
205 interaction is excitable (oscillatory) or unstable, a result predicted by strong coupling strengths
206 (Wootton 1997, McCann et al. 2011). Further, being a consumer of gelatinous zooplankton may
207 have implications for carbon export, particularly with the consumption of a zooplankter known
208 to have massive “falls” representing significant carbon export (Lebrato and Jones, 2009, Lebrato
209 et al. 2013). While it is uncertain if there is enough top down pressure from barrelfish on *P.*
210 *atlanticum* to affect *P. atlanticum* populations, this potential link warrants further study. More
211 studies into diet seasonality and daily rations for barrelfish are also needed to estimate the
212 biomass of *P. atlanticum* that barrelfish consume. Given the site fidelity of barrelfish to deep
213 water structure and their presence below fast moving Gulf Stream waters, it seems unlikely that
214 barrelfish partake in vertical migrations to the surface, resulting in the possibility that barrelfish
215 can serve as a mode of carbon export through consumption of pyrosomes in the aphotic zone

216 (Goldman and Sedberry 2011). However, there is a dearth of data on the movement of barrelfish
217 and further studies into their vertical movements are warranted.

218 Observations from this study that barrelfish rely largely on a single prey item bolsters the
219 connection between the *Hyperoglyphe* genus and pyrosome tunicates, representing a form of
220 benthic-pelagic coupling near the shelf edge. Specifically, this insight into the strong connection
221 between a demersal fish and a vertically migrating filter feeder—and thus potential implications
222 for carbon export—provides a basis for learning more about such interactions and their role in
223 carbon export in shelf break waters.

224

225 ACKNOWLEDGMENTS

226 Supplies for this study were provided by the Rosenstiel School of Marine and
227 Atmospheric Science (RSMAS) Undergraduate program through L Merly and G Hitchcock.
228 Stable isotope analysis was done through the L7 laboratory at the University of Miami Biology
229 Department with assistance from L Sternberg. Funding was provided to JJS from a Small
230 Undergraduate Research Grant Experience (SURGE). JKL was supported as a Cooperative
231 Institute for the North Atlantic Region fellow with funds from NOAA. Special thanks to D Olson
232 of RSMAS and L Rasmuson of the National Marine Fisheries Service for scientific guidance and
233 S Mahanes for sample processing assistance. Thank you to C Hernandez for writing style
234 suggestions and A Solow for discussions on statistical methods. Additional thanks to the fishers
235 at Crandon Park Marina, particularly Capt. N Martinez of Top Gun Charters, Capt. J David of
236 L&H Sportfishing, and Jesús of Sonny Boy Charters.

237 LITERATURE CITED:

- 238 Andersen V, Sardou J. 1994. *Pyrosoma atlanticum* (Tunicata, Thaliacea): diel migration
239 and vertical distribution as a function of colony size. J Plankton Res. 16(4): 337-349.
- 240 Batschelet, E. 1981. Circular statistics in biology. London: Academic press.
- 241 Bolch CJ, Elliott NG, Ward RD. 1993. Enzyme variation in south-eastern
242 Australian samples of the blue-eye or deepsea trevalla, *Hyperoglyphe antarctica*
243 Carmichael 1818 (Teleostei: Stromateoidei). Mar Freshw Res. 44(5):
244 687-697.
- 245 Catul V, Gauns M, Karuppasamy PK. 2011. A review on mesopelagic fishes belonging
246 to family Myctophidae. Rev Fish Biol Fisher. 21(3): 339-354.
- 247 Cowper TR. 1960. Occurrence of *Pyrosoma* on the continental Slope. Nature 187(4740): 878-
248 879.
- 249 Davison PC, Checkley DM, Koslow JA, Barlow J. 2013. Carbon export mediated by
250 mesopelagic fishes in the northeast Pacific Ocean. Prog Oceanogr. 116:14-
251 30.
- 252 Drits AV, Arashkevich EG, Semenova TN. 1992. *Pyrosoma atlanticum* (Tunicata,
253 Thaliacea): grazing impact on phytoplankton standing stock and role in organic carbon
254 flux. J Plankton Res. 14(6): 799-809.
- 255 Druffel ER, Williams PM, Bauer JE, Ertel JR. 1992. Cycling of dissolved and particulate organic
256 matter in the open ocean. J Geophys Res-Oceans. 97(10): 15639-15659.
- 257 Ducklow HW, Steinberg DK, Buesseler KO. 2001. Upper ocean carbon export and the biological
258 pump. Oceanography 14(4): 50-58.
- 259 Fay G, Punt AE, Smith AD. 2011. Impacts of spatial uncertainty on performance of
260 age structure-based harvest strategies for blue eye trevalla (*Hyperoglyphe*
261 *antarctica*). Fish Res. 110(3): 391-407.
- 262 Fry B. 2006. Stable isotope ecology. New York: Springer Science & Business Media.
- 263 Filer KR, Sedberry GR. 2008. Age, growth and reproduction of the barrelfish
264 *Hyperoglyphe perciformis* (Mitchill) in the western North Atlantic. J Fish Biol. 72(4):
265 861-882.
- 266 Finucance JH, Grimes CB, Naughton SP. 1990. Diets of young king and Spanish mackerel off
267 the southeast United States. Northeast Gulf Sci. 2.
- 268 Goldman SF, Sedberry GR. 2011. Feeding habits of some demersal fish on the
269 Charleston Bump off the southeastern United States. ICES J Mar Sci. 68 (2): 390-398.
- 270 Irigoien X, Klevjer TA, Røstad A, Martinez U, Boyra G, Acuña JL, Bode A, Echevarria F,
271 Gonzalez-Gordillo JI, Hernandez-Leon S, et al. 2014. Large mesopelagic fishes biomass
272 and trophic efficiency in the open ocean. Nat. Commun. 5.
- 273 Jackson AL, Inger R, Parnell AC, Bearhop S. 2011. Comparing isotopic niche widths among and
274 within communities: SIBER—Stable Isotope Bayesian Ellipses in R. J Anim Ecol. 3:595
275 602
- 276 Jackson MC, Donohue I, Jackson AL, Britton JR, Harper DM, Grey J. 2012. Population-level
277 metrics of trophic structure based on stable isotopes and their application to invasion
278 ecology. PloS One, 7(2):e31757.
- 279 Jeffrey AW, Pflaum RC, Brooks JM, Sackett WM. 1983. Vertical trends in particulate organic
280 carbon ¹³C: ¹²C ratios in the upper water column. Deep-Sea Res Part A: Oceanogr Res
281 Pap. 30(9): 971-983.

282 Lebrato M, Jones DOB. 2009. Mass deposition event of *Pyrosoma atlanticum* carcasses
283 off Ivory Coast (West Africa). *Limnol Oceanogr.* 54(4): 1197-1209.

284 Lebrato M, Mendes PDJ, Steinberg DK, Cartes JE, Jones BM, Birsa LM, Benavides R,
285 Oschlies A. 2013. Jelly biomass sinking speed reveals a fast carbon export
286 mechanism. *Limnol Oceanogr.* 58(3): 1113-1122.

287 Laurenceau-Cornec EC, Trull TW, Davies DM, Bray SG, Doran J, Planchon F, Carlotti F,
288 Jounadet MP, Cavagna AJ, Waite AM, Blain S. 2015. The relative importance of
289 phytoplankton aggregates and zooplankton fecal pellets to carbon export: insights from
290 free-drifting sediment trap deployments in naturally iron-fertilised waters near the
291 Kerguelen Plateau. *Biogeosciences* 12: 1007-1027.

292 Logan JM, Jardine TD, Miller TJ, Bunn SE, Cunjak RA, Lutcavage ME. 2008. Lipid corrections
293 in carbon and nitrogen stable isotope analyses: comparison of chemical extraction and
294 modelling methods. *J Anim Ecol.* 77(4): 838-846.

295 Mauchline J, Gordon, JD. 1991. Oceanic pelagic prey of benthopelagic fish in the benthic
296 boundary layer of a marginal oceanic region. *Mar Ecol Prog Ser.* 74(2): 109-115.

297 McCann KS. 2011. Food webs (MPB-50). New Jersey: Princeton University Press.

298 Merten W, Appeldoorn R, Rivera R, Hammond D. 2014a. Diel vertical movements of
299 adult male dolphinfish (*Coryphaena hippurus*) in the western central Atlantic as
300 determined by use of pop-up satellite archival transmitters. *Mar Biol.* 161(8): 1823-
301 1834.

302 Merten W, Appeldoorn R, Hammond D. 2014b. Movements of dolphinfish (*Coryphaena*
303 *hippurus*) along the US east coast as determined through mark and recapture data. *Fish*
304 *Res.* 151: 114-121.

305 Merten W, Appeldoorn R, Hammond D. 2016. Movement dynamics of dolphinfish (*Coryphaena*
306 *hippurus*) in the northeastern Caribbean Sea: Evidence of seasonal re-entry into domestic
307 and international fisheries throughout the western central Atlantic. *Fish Res.* 175: 24-34.

308 Merrett N, Roe HSJ. 1974. Patterns and selectivity in the feeding of certain mesopelagic
309 fishes. *Mar Biol.* 28(2): 115-126.

310 Moore TA. 2014. Trophic Dynamics and Feeding Ecology of the Southeast Florida Coastal
311 Pelagic Fish Community. Master's Thesis. Nova Southeastern University. Retrieved from
312 NSU Works, Oceanographic Center. http://nsuworks.nova.edu/occ_stu/d/3

313 Oxenford HA. 1999. Biology of the dolphinfish (*Coryphaena hippurus*) in the western central
314 Atlantic: a review. *Sci Mar.* 63(3-4): 277-301.

315 Oxenford HA, Hunte W. 1999. Feeding habits of the dolphinfish (*Coryphaena hippurus*) in the
316 eastern Caribbean. *Sci Mar.* 63(3-4): 303-315.

317 Perissinotto R, Mayzaud P, Nichols PD, Labat JP. 2007. Grazing by *Pyrosoma*
318 *atlanticum* (Tunicata, Thaliacea) in the south Indian Ocean. *Mar Ecol Prog Ser.* 330:1-11.

319 Pusch C, Hulley PA, Kock KH. 2004. Community structure and feeding ecology of
320 mesopelagic fishes in the slope waters of King George Island (South Shetland Islands,
321 Antarctica). *Deep-Sea Res Part I: Oceanogr Res Pap.* 51(11): 1685-
322 1708.

323 R Core Team (2017) R: A language and environment for statistical computing. R Foundation for
324 Statistical Computing, Vienna, Austria.

325 Rudershausen PJ, Buckel JA, Edwards J, Gannon DP, Butler CM, Averett TW. 2010. Feeding
326 ecology of blue marlins, dolphinfish, yellowfin tuna, and wahoos from the North Atlantic
327 Ocean and comparisons with other oceans. *T Am Fish Soc.* 139(5): 1335-1359.

328 Richardson TL, Jackson GA. 2007. Small phytoplankton and carbon export from the
329 surface ocean. *Science*, 315(5813): 838-840.

330 Ricklefs RE, Nealen P. 1998. Lineage-dependent rates of evolutionary diversification: analysis
331 of bivariate ellipses. *Funct Ecol.* 12(6): 871-885.

332 Riebesell U, Schulz KG, Bellerby RGJ, Botros M, Fritsche P, Meyerhöfer M, Neill C, Nondal G,
333 Oschlies A, Wohlers J, Zöllner, E. 2007. Enhanced biological carbon consumption in a
334 high CO₂ ocean. *Nature* 450(7169): 545-548.

335 Robinson, N., Skinner, A., Sethuraman, L., McPartlan, H., Murray, N., Knuckey, I., Smith DC,
336 Hindell J, Talman, S. 2008. Genetic stock structure of blue-eye trevalla (*Hyperoglyphe*
337 *antarctica*) and warehouse (*Serirolella brama* and *Serirolella punctata*) in south-eastern
338 Australian waters. *Mar Freshw Res.* 59(6): 502-514.

339 Sabine CL., Feely RA, Gruber N, Key RM, Lee K, Bullister JL, Wanninkhof R, Wong CS,
340 Wallace DWR, Tilbrook B, Millero FJ, Peng TH, Kozyr A, Ono, T, Rios AF.
341 2004. The oceanic sink for anthropogenic CO₂. *Science.* 305(5682): 367-371.

342 Schaefer HC, Fable Jr WA. 1994. King mackerel, *Scomberomorus cavalla*, mark-recapture
343 studies off Florida's east coast. *Mar Fisher Rev.* 56(3): 13-23.

344 Siegel DA, Buesseler KO, Doney SC, Sailley SF, Behrenfeld MJ, Boyd PW. 2014. Global
345 assessment of ocean carbon export by combining satellite observations and food web
346 models. *Global Biogeochem Cycles.* 28(3): 181-196.

347 Siegel DA, Buesseler KO, Behrenfeld MJ, Benitez-Nelson CR, Boss E, Brzezinski MA, Burd A,
348 Carlson CA, D'Asaro EA, Doney SC, Perry MJ, Stanley RHR, Steinberg, DK. 2016.
349 Prediction of the export and fate of global ocean net primary production: the EXPORTS
350 science plan. *Front Mar Sci.* 3(22)

351 Smith KL, Ruhl HA, Bett BJ, Billett DSM, Lampitt RS, Kaufmann RS. 2009. Climate, carbon cycling,
352 and deep-ocean ecosystems. *Proc Natl Acad Sci USA.* 106(46): 19211-19218.

353 Steinberg DK, Carlson CA, Bates NR., Goldthwait SA, Madin LP, Michaels AF. 2000.
354 Zooplankton vertical migration and the active transport of dissolved organic and
355 inorganic carbon in the Sargasso Sea. *Deep-Sea Res Part I: Oceanogr Res*
356 *Pap.* 47(1):137-158.

357 Sutter III FC., Williams RO, Godcharles MF. 1991. Movement patterns and stock affinities of
358 king mackerel in the southeastern United States. *Fish-B-NOAA*, 89(2): 315-324.

359 Sutton TT, Hopkins TL. 1996. Trophic ecology of the stomiid (Pisces: Stomiidae) fish
360 assemblage of the eastern Gulf of Mexico: strategies, selectivity and impact of a top
361 mesopelagic predator group. *Mar Biol.* 127(2): 179-192.

362 Teffer AK, Staudinger MD, Juanes F. 2015. Trophic niche overlap among dolphinfish and co-
363 occurring tunas near the northern edge of their range in the western North Atlantic. *Mar*
364 *Biol.* 162(9): 1823-1840.

365 Tripp-Valdez A, Galván-Magaña F, Ortega-García S. 2010. Feeding habits of dolphinfish
366 (*Coryphaena hippurus*) in the southeastern Gulf of California, Mexico. *J Appl*
367 *Ichthyol.* 26(4): 578-582.

368 Trueman CN, Johnston G, O'Hea B, MacKenzie KM. 2014. Trophic interactions of fish
369 communities at midwater depths enhance long-term carbon storage and benthic
370 production on continental slopes. *Proc R Soc Biol Sci Ser B.* 281(1787): 20140669

371 Winstanley RH. 1978. Food of the trevalla *Hyperoglyphe porosa* (Richardson) off
372 southeastern Australia (Note). *New Zeal J Mar Fresh.* 12(1):77-79.

373 Wootton JT. 1997. Estimates and tests of per capita interaction strength: diet, abundance, and
374 impact of intertidally foraging birds. *Ecol Monogr.* 67(1): 45-64.
375
376

Table 1: Prey items (to family level) and diet metrics of barrelfish and dolphinfish. %F represents the frequency that a prey type occurred in the total number of stomachs analyzed. %N represents the number of items of a prey type in relation to the total number of prey items. %W represents the percentage by weight of a prey type in relation to the total weight of all prey types. %IRI represents the index of relative importance of a prey type expressed as a percentage of the sum of IRI values for all prey types. UNID = unidentifiable

Consumer Species	Prey Family	%F	%N	%W	%IRI
Barrelfish (n=29)	Pyrosomatidae (Pelagic tunicate)	85.7	47.4	89.4	91.2
	Stomiidae (Viperfishes)	23.8	13.2	0.5	2.5
	Solenoceridae	19	10.5	0.4	1.6
	Sternoptychidae (Hatchetfishes)	4.8	10.5	0.9	0.4
	Tetragonuridae (Squartail)	4.8	5.3	0.1	0.2
	UNID Squid	23.8	13.2	8.8	4.1
Dolphinfish (n=46)	Exocoetidae (Flying fishes)	29	14	28.7	28.6
	Carangidae (Jacks)	16.1	8.1	11.5	7.3
	Clupeidae (Sardines and herrings)	16.1	8.1	8.6	6.2
	Belonidae (Needlefishes)	9.7	3.5	21.4	5.6
	Scombridae (Atl. chub mackerel)	12.9	12.8	0.9	4.1
	Nomeidae (Man-o-war fish)	3.2	10.5	4	1.1
	Hemiramphidae (Ballyhoos)	6.5	2.3	4.4	1.0
	Balistidae (Triggerfishes)	6.5	2.3	2.6	0.7
	Lobotidae (Tripletail)	3.2	1.2	3.7	0.4
	Diodontidae (Porcupinefishes)	3.2	1.2	0	0.1
	UNID Fish	51.6	31.4	5.7	44.2
	UNID Squid	3.2	1.2	8.5	0.7

FIGURE LEGENDS:

Figure 1: Density plot of Bayesian standard ellipse areas (SEA_B) for barrelfish and three epipelagic species. Black dots represent the mode of posterior distribution of SEA_B values with grey boxes presenting 50, 75, and 95% credible intervals.

Figure 2: Stable isotope values ($\delta^{13}C$ and $\delta^{15}N$) of barrelfish and three epipelagic species, along with each species' standard ellipse.



