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**Abstract:** We have used stable isotope ratios of nitrogen ( $\delta^{15}\text{N}$ ) as a validation tool for determining the accuracy of the effective trophic levels computed in network analysis models for Core Sound (NC, USA). Trophic levels and stable isotopes were compared between fishery management areas where shrimp trawling has been restricted for 30 years. Carbon stable isotopes are widely used to trace carbon (C) in food webs to the ultimate source of energy, and stable N ratios are used to estimate trophic level due to fractionation, which is the increase in  $\delta^{15}\text{N}$  that occurs with each trophic transfer in the assimilation of food. We found that measured  $\delta^{13}\text{C}$  sources in the estuarine Core Sound ecosystem in North Carolina (USA) were small (-17 to -22‰) for algal producers (phytoplankton and algae) and enriched (-12‰) for seagrass (*Halodule wrightii*). These producers also had low  $\delta^{15}\text{N}$  isotopic ratios (3.8 - 6.2‰ for algae and 2.9‰ for seagrass), whereas consumers (invertebrates and fishes) had higher values (7.5‰ for zooplankton and 14‰ for high trophic level fish-consumers, like smooth dogfish, Spanish mackerel and bluefish). Linear regression of ETL as a predictor of  $\delta^{15}\text{N}$  isotopic ratio was highly significant ( $R^2 = 0.66$ ), suggesting that  $\delta^{15}\text{N}$  is 2.52‰ per trophic level. This estimate agrees with a recent meta-analysis of nitrogen fractionation estimates. There was also a significant relationship for ETL and  $\delta^{13}\text{C}$ , suggesting that carbon isotope ratios do increase slightly (1.03‰) with trophic level in the Core Sound ecosystem. There was no significant difference between trawling zones, although there were significantly higher  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  in the areas open to trawling for certain species of fish (pinfish, spot, dogfish), squid, and blue crabs. These species had different diets in the two zones, suggesting that they consumed prey at a higher trophic level in the areas open to trawling. The increase was also observed as an increase in the ETL for these species. Atlantic menhaden, which feed on detritus and zooplankton, had much higher  $\delta^{15}\text{N}$  values than the Ecopath ETLs would suggest, pointing out either the model's inaccuracy in the diet specification for that fish or that the detritus consumed was high in organic matter derived from consumers (not producers). We conclude that this Ecopath network model of Core Sound is valid and predicts with good accuracy the shifts and changes in trophic level and diet as measured by stable isotopes and observed in diet studies. The Core Sound network model will be a useful approach when predicting impacts in the ecosystem due to changes in trawling or other fisheries management changes.

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B.D. Fath  
Editor-in-Chief  
*Ecological Modelling*

Dear Dr. Fath,

Please find the attached manuscript, "Validation of Effective Trophic Levels from Core Sound Ecopath Models Using Stable Isotope Analysis," which I am submitting on behalf of my co-authors as an original research paper to *Ecological Modelling*. This manuscript is the first work to come from my doctoral dissertation and is not under consideration for publication elsewhere at this time.

We feel this manuscript would make a worthy contribution to *Ecological Modelling*. Using site-specific field collections and fisheries landings data, we created two Ecopath models for Core Sound, North Carolina, an area where commercial shrimp trawling has been excluded from nursery areas for 30 years. We used stable isotope analysis to validate the effective trophic levels from the Ecopath models, showing that  $\delta^{13}\text{C}$  increased 1.03‰ per trophic level and  $\delta^{15}\text{N}$  increased 2.52‰ per trophic level. Although there was no significant system-wide difference between trawling zones, there were significantly higher  $\delta^{15}\text{N}$  in the areas open to trawling for certain species (Atlantic menhaden, pinfish, spot, blue crabs). These species had different diets in the two zones, suggesting that they consumed prey at a higher trophic level in the areas open to trawling. Atlantic menhaden, which feed on detritus and zooplankton, had much higher  $\delta^{15}\text{N}$  values than the Ecopath ETLs would suggest, pointing out either the model's inaccuracy in the diet specification for that fish or that the detritus consumed was high in organic matter derived from consumers. Overall, we conclude that this Ecopath network model of Core Sound is valid and predicts with good accuracy the shifts and changes in trophic level and diet as measured by stable isotopes and observed in diet studies.

Thank you for your consideration of our manuscript. We look forward to hearing from you.

Sincerely,

Rebecca A. Deehr

Deehr et al., “Validation of Effective Trophic Levels from Core Sound Ecopath Models Using Stable Isotope Analysis”

Highlights:

- We created two Ecopath models for areas open and closed to commercial trawling
- We use stable isotope analysis to validate model-generated effective trophic levels
- There was 2.52‰  $\delta^{15}\text{N}$  and 1.03‰  $\delta^{13}\text{C}$  enrichment per trophic level
- Atlantic menhaden had higher  $\delta^{15}\text{N}$  than the Ecopath models would predict
- These Ecopath models can be useful tools for future fisheries management decisions

1 **Validation of Effective Trophic Levels from Core Sound Ecopath Models**  
2 **Using Stable Isotope Analysis**

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18

19 **Abstract**

20 We used stable isotope ratios of nitrogen ( $\delta^{15}\text{N}$ ) as a validation tool for determining the accuracy  
21 of the effective trophic levels computed in network analysis models for Core Sound, North  
22 Carolina, USA. Effective trophic levels (ETLs) and stable isotopes were compared between  
23 fishery management areas where shrimp trawling has been restricted for 30 years. Carbon stable  
24 isotopes are widely used to trace C in food webs to the ultimate source of energy, and stable N  
25 ratios are used to estimate trophic level due to fractionation, which is the increase in  $\delta^{15}\text{N}$  that  
26 occurs with each trophic transfer in the assimilation of food. We found that measured  $\delta^{13}\text{C}$   
27 sources in the estuarine Core Sound ecosystem were small (-17 to -22‰) for algal producers  
28 (phytoplankton and algae) and enriched (-12‰) for seagrass (*Halodule wrightii*). These  
29 producers also had low  $\delta^{15}\text{N}$  isotopic ratios (3.8 – 6.2‰ for algae and 2.9‰ for seagrass),  
30 whereas consumers (invertebrates and fishes) had higher values (7.5‰ for zooplankton and 14‰  
31 for high trophic level fish-consumers, like smooth dogfish, Spanish mackerel and bluefish).  
32 Linear regression of ETL as a predictor of  $\delta^{15}\text{N}$  isotopic ratio was highly significant ( $R^2 = 0.66$ ),  
33 suggesting that  $\delta^{15}\text{N}$  increases by 2.52‰ per trophic level. This estimate agrees with a recent  
34 meta-analysis of nitrogen fractionation estimates. There was also a significant relationship for  
35 ETL and  $\delta^{13}\text{C}$ , suggesting that carbon isotope ratios do increase (1.03‰) with trophic level in the  
36 Core Sound ecosystem. There was no significant difference between trawling zones, although  
37 there were significantly higher  $\delta^{15}\text{N}$  in the areas open to trawling for certain species of fish  
38 (pinfish, spot, smooth dogfish) and invertebrates (squid, blue crabs). These species had different  
39 diets in the two zones, suggesting that they consumed prey at a higher trophic level in the areas  
40 open to trawling. The increase was also observed as an increase in the ETL for these species.  
41 Atlantic menhaden, which feed on detritus and zooplankton, had much higher  $\delta^{15}\text{N}$  values than

42 the Ecopath ETLs would suggest, pointing out either the model's inaccuracy in the diet  
43 specification for that fish or that the detritus consumed was high in organic matter derived from  
44 consumers (not producers). We conclude that this Ecopath network model of Core Sound is  
45 valid and predicts with good accuracy the shifts and changes in trophic level and diet as  
46 measured by stable isotopes and observed in diet studies. The Core Sound network model will  
47 be a useful approach when predicting impacts in the ecosystem due to changes in trawling or  
48 other fisheries management decisions.

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52 **Keywords**

53 Ecopath; effective trophic level; estuarine ecosystem; shrimp trawling; stable nitrogen isotope;  
54 stable carbon isotope

## 55 **1. Introduction**

56 Ecosystems have been modeled as networks of ecological flows among species or nodes,  
57 following a medium such as carbon as a surrogate for energy. Network models are becoming  
58 more widely used in ecosystem analysis, especially for fisheries management applications. One  
59 popular modeling approach is Ecopath with Ecosim (Christensen et al., 2008), which has been  
60 used for studies on aquaculture (Leloup et al., 2008; Lopez et al., 2008; Byron et al., 2011;  
61 Forestal et al., 2012), marine protected areas (Colléter et al., 2012; Varkey et al., 2012), climate  
62 change (Taylor et al., 2008; Griffiths et al., 2010; Lauria et al., 2010; Wolff et al., 2012),  
63 eutrophication/pollution (Patrício and Marques, 2006; Han et al., 2011), and the collapse of  
64 fisheries (Bundy, 2005; Arreguin-Sanchez et al., 2008; Morissette et al., 2009; Vargiu et al.,  
65 2009; Downing et al., 2012). Models about changes in fisheries practices, management and  
66 policy exploration are the most numerous in recent years (Ainsworth et al., 2008; Tsehaye and  
67 Nagelkerke, 2008; Heymans et al., 2009; Libralato et al., 2010; Cisneros-Montemayor et al.,  
68 2012; Fouzai et al., 2012; Gascuel et al., 2012; Wang et al., 2012).

69 One thing that is apparent in these ecosystem network modeling efforts is that trophic  
70 levels of species within the system can change and that trophic level is being used as a metric of  
71 ecosystem change due to fishing practices (Pauly et al., 1998; Jackson et al., 2001). Organisms  
72 in a food web are assigned a relative trophic position based on their feeding relationships to other  
73 organisms in the system, with primary producers assigned to trophic level 1. Early work by  
74 Lindeman (1942) assigned integer-level trophic positions to organisms, with herbivores at  
75 trophic level 2 and primary carnivores at trophic level 3. However, many organisms eat from  
76 multiple trophic levels; Odum and Heald (1975) suggested fractional trophic levels to account  
77 for this omnivory. This fractional trophic level is called the effective trophic level (ETL), and is



78 the weighted average of the preys' trophic levels. Network analysis programs, such as Ecopath,  
79 calculate ETLs for nodes in an ecosystem based on the flow of carbon among nodes and known  
80 food web relationships derived from direct observation, stomach contents, and tagging  
81 experiments. These calculated values can be compared with stable isotope data for those nodes  
82 to provide validation for the network model.

83         Stable nitrogen isotopes provide an alternate method for determining trophic positioning  
84 in a food web. Stable isotopes of both nitrogen and carbon ( $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$ ) have been  
85 documented to change with trophic position of the consuming organism, a process referred to as  
86 fractionation, in which stable isotope ratios are enriched from prey to consumers, during the  
87 metabolic processing of the consumed material (Fry and Sherr, 1984; Fry, 2006). In controlled  
88 laboratory experiments, researchers have found that  $\delta^{15}\text{N}$  values of animals reflect the isotopic  
89 values of the prey consumed (DeNiro and Epstein, 1978, 1981; Peterson and Fry, 1987; Wada et  
90 al., 1991), but with an enrichment factor variable that accounts for the observed fractionation.  
91 Trophic fractionation varies geographically within and among species and may be affected by  
92 temperature (Bosley et al., 2002; Barnes et al., 2007; Bloomfield et al., 2011), feeding rate (Olive  
93 et al., 2003), growth rate (DeNiro and Epstein, 1978, 1981; Sakano et al., 2005; Sweeting et al.,  
94 2005; Trueman et al., 2005; Weidel et al., 2011) and developmental stage (Tarboush et al., 2006;  
95 Church et al., 2008; Kurle et al., 2011; Buchheister and Latour, 2011; Weidel et al., 2011).  
96 Another factor that can increase variation in isotopic data is migration of individuals from areas  
97 outside the area of interest (Herzka, 2005). Recent immigrants may reflect a history of feeding  
98 within the habitat from which they emigrated rather than the receiving habitat (Jackson and  
99 Harkness, 1987). Understanding variation in trophic fractionation and how it relates to trophic  
100 position is important because small changes in fractionation may indicate the contribution of

101 different source materials to production (McCutchan et al., 2003).

102 Unlike direct observations of stomach contents, a consumer's isotopic signature is based  
103 on assimilation of the isotope into its tissue, not just the most recent meal (Peterson and Fry,  
104 1987). Thus, stable isotopes represent a time-integrated measure of trophic position (Vander  
105 Zanden and Rasmussen, 1999), which may provide a better idea of an individual's long-term diet  
106 and its relative trophic position in an ecosystem. The amount of time the stable isotope signature  
107 from a particular diet remains within an animal's tissues can vary.

108 Carbon isotopes ( $\delta^{13}\text{C}$ ) have been shown to indicate the origin of a food source, because  
109 fractionation of carbon between trophic levels is very small. Both laboratory and field studies  
110 have found that carbon isotopic compositions of animals reflect their source diet within about  
111 1‰ (DeNiro and Epstein, 1978; Peterson and Fry, 1987; Vander Zanden and Rasmussen, 2001;  
112 Post, 2002; Fry, 2006; Michener and Lajtha, 2007). In a review of more than 100 estimates of  
113  $\delta^{13}\text{C}$ , Post (2002) reported a mean  $\delta^{13}\text{C}$  fractionation rate of  $0.39 \pm 1.3\%$ . Vander Zanden and  
114 Rasmussen (2001) examined aquatic consumers and found  $\delta^{13}\text{C}$  fractionation values of 0.8‰ for  
115 carnivores and 0.4‰ for herbivores. Conversely, one recent study of European sea bass reared  
116 on sandeel and dab by Sweeting et al. (2007) found that  $\delta^{13}\text{C}$  fractionation across trophic levels  
117 was closer to 1.5‰.

118 In trophic studies, nitrogen isotopes ( $^{15}\text{N}$ ) tend to have higher and more variable  
119 fractionation rates than carbon isotopes. Numerous studies report an average per-trophic-level  
120  $\delta^{15}\text{N}$  fractionation of 3-4‰ (Minagawa and Wada, 1984; Vander Zanden and Rasmussen, 2001;  
121 Post, 2002; Sweeting et al., 2007). Vanderkluft and Ponsard (2003) conducted a meta-analysis of  
122 134 studies and found an average enrichment of 2.54‰, which included terrestrial, freshwater  
123 and marine organisms. Similarly, McCutchan et al. (2003) reported an average  $\delta^{15}\text{N}$  value of

124 2.3‰ for terrestrial organisms, with a lower  $\delta^{15}\text{N}$  trophic fractionation rate for consumers raised  
125 on invertebrates (1.4‰) than for consumers raised on high protein diets (3.3‰). DeNiro and  
126 Epstein (1981) reported that lab-reared animals (ranging from brine shrimp to mice) had  $\delta^{15}\text{N}$   
127 increases of -0.5 to 9.2‰ over their diets, but indicated that this range was due to differences in  
128 the types of tissue analyzed as well as the diet composition. Overall, an average  $\delta^{15}\text{N}$  enrichment  
129 of 3-4‰ per trophic level is most commonly used in comparative studies.

130 Thus, the fractionation of stable C and N isotopes should be compared to modeling  
131 measures of trophic position, such as the ETLs provided by Ecopath. If there is good agreement  
132 between stable isotopes and effective trophic position, an Ecopath model and the dietary  
133 composition matrix on which it is based could be validated. Disagreement in the stable isotopic  
134 signatures and modeled trophic position could indicate an incompletely specified model or  
135 unaccounted variation in stable isotope concentration due to environmental, metabolic or  
136 species-specific parameters.

137 Three recent studies have utilized stable isotope analysis to validate ecological network  
138 models for natural, unmanipulated ecosystems. Dame and Christian (2008) used stable isotope  
139 analysis and ecological network analysis to compare four salt marsh ponds (Virginia, USA)  
140 during times of high- and low-stress and following natural disturbance. Navarro et al. (2011)  
141 used stable isotope analysis to make comparisons with the effective trophic levels from a single  
142 Ecopath model of the South Catalan Sea (northwest Mediterranean Sea) marine ecosystem.  
143 Finally, Milessi et al. (2010) found that trophic positions derived from isotope analysis were  
144 highly correlated with Ecopath-calculated trophic levels for a food web of Laguna de Rocha  
145 (Uruguay). These studies found good correlation between Ecopath-calculated trophic levels and  
146 the  $\delta^{15}\text{N}$  levels, especially in higher-trophic level organisms, which indicated that the diet data

147 used for the Ecopath model represented the trophic relations reasonably well.

148         The purpose of this paper is to compare the calculated ETLs from two Ecopath models,  
149 developed for areas managed for commercial trawling since 1978 (closed areas) and areas open  
150 to commercial trawling, in Core Sound, North Carolina, USA, with results from stable isotope  
151 analysis. In addition, we wanted to determine if there was a difference in the stable isotope data  
152 between areas open and closed to trawling. Special attention in our analysis was paid to  
153 mesotrophic predators, those organisms that feed in the middle of the food web, such as pinfish,  
154 spot, Atlantic menhaden and blue crabs. These organisms are also common in the shrimp trawl  
155 bycatch and are discarded thus being consumed by scavengers and recycled within the  
156 ecosystem. The impact of this bycatch on the system's trophic structure was also investigated by  
157 comparing ETL and isotopic fractionation.

## 158 **2. Methods**

### 159 *2.1. Study area*

160         Core Sound is a narrow, relatively shallow body of water (maximum depth  
161 approximately 4 m in navigational channel) approximately 35 km long in Carteret County, North  
162 Carolina. It is bordered to the west by several bays, saltmarshes, forests, agricultural lands and  
163 small residential areas. Core Sound is bordered to the east by sound-side seagrass beds and the  
164 Core Banks, federally-owned lands within the Cape Lookout National Seashore, which protect  
165 Core Sound from the Atlantic Ocean. There is one inlet (New Drum Inlet, or more recently  
166 known as Isabel Inlet) which allows ocean water to enter Core Sound and the adjacent bays. The  
167 influence of tides is limited in the inshore waters of North Carolina, and wind-driven water  
168 movement can be greater than tidal influence because of large fetch (Giese et al., 1979). A

169 NOAA tide station located at Sea Level, NC (operating between January and July 2004)  
170 indicated a mean tidal range of 0.175 m (NOAA Center for Operational Oceanographic Products  
171 and Services [CO-OPS] Observational Data Interactive Navigation).

172 The fishery management areas in Core Sound are called primary, secondary, and special  
173 secondary nursery areas. In primary nursery areas (PNAs), most fishing gears are excluded from  
174 these areas, because this is where post-larval fish and invertebrate development takes place.  
175 Secondary nursery areas (SNAs) are areas utilized by juvenile and sub-adult organisms, and only  
176 trawling is prohibited in these areas. Special Secondary Nursery Areas (SSNAs) differ from  
177 SNAs in that the Director of the NC Division of Marine Fisheries may declare SSNAs open to  
178 trawling for discreet time periods (NCMFC 2005, 15A NCAC 03N .0105). In Core Sound,  
179 PNAs, SNAs and SSNAs are located in Jarrett, Nelson, and Thorofare Bays, as well as the creeks  
180 that feed into the Sound.

181 Twelve study sites (six in closed areas and six in open areas) were selected for this  
182 observational study. The sites included shallow (<2 m) and deep (>2 m) sites within three bays  
183 (closed to trawling) and adjacent Core Sound waters (open to trawling) with approximately  
184 similar bottom types. Since trawling is prohibited in seagrass beds even in open areas, all sites  
185 were selected for their absence of seagrass. See Figure 1 for map of the Core Sound study sites.  
186 Each site was sampled in the spring (April, May, June) and fall (August, September, October) of  
187 2007, before and after peak shrimp trawl activity, respectively.

## 188 2.2. *The Ecopath approach*

189 Ecopath with Ecosim (hereafter referred to as Ecopath) is one of the most widely used  
190 food web modeling and network analysis tools for fisheries and aquatic ecosystems. Ecopath  
191 combines the biomass budget approach of Polovina (1984a, 1984b) with network analysis theory

192 (Ulanowicz, 1986) for analyzing flows between compartments (Christensen et al., 2008). The  
 193 basic input requirements for each compartment include biomass (B), production to biomass ratio  
 194 (P/B), consumption to biomass ratio (Q/B) and ecotrophic efficiency (EE). Ecotrophic efficiency  
 195 is defined as the fraction of total production of a group that is consumed or exported from the  
 196 system. Those four basic input parameters are required for each compartment, but if only three  
 197 are known, then Ecopath can compute the missing parameter (Christensen and Pauly, 1992). A  
 198 diet matrix must also be constructed to account for the trophic interactions (consumption and  
 199 import of food items) of all compartments in the system.

200 Ecopath models are constructed from two master equations for production and  
 201 consumption: 1) Production = catch + predation + net migration + biomass accumulation + other  
 202 mortality, and 2) Consumption = production + respiration + unassimilated food (Christensen and  
 203 Pauly, 1992). A mass-balanced system sets production equal to consumption, combining the  
 204 above equations into:

$$205 \quad B_i \cdot (P/B)_i \cdot EE_i = Y_i + \sum B_j \cdot (Q/B)_j \cdot DC_{ji} + BA_i + NM_i \quad (1)$$

206 where  $B_i$  and  $B_j$  are biomasses of prey (i) and predators (j), respectively;  $P/B_i$  is the  
 207 production/biomass ratio of group  $I$ ;  $EE_i$  is the ecotrophic efficiency of group  $I$ ;  $Y_i$  is the fisheries  
 208 catch per unit area and time of group  $I$ ;  $Q/B_j$  is the food consumption per unit biomass of group  $I$ ;  
 209  $DC_{ji}$  is the contribution of group  $I$  to the diet of predator  $j$ ;  $BA_i$  is the biomass accumulation of  
 210 group  $I$  (positive or negative); and  $NM_i$  is the net migration of group  $I$  (emigration less  
 211 immigration). Once a system is balanced, system-wide and compartment-specific indices are  
 212 calculated and provide important information about the size, organization, development and  
 213 trophic dynamics of the ecosystem.

214 2.3. *Model construction and parameterization*

215 The Ecopath with Ecosim 6 software package was utilized to create two models of the  
216 Core Sound networks: one for areas open to trawling, the other for areas closed to trawling. To  
217 construct Ecopath models of Core Sound, compartments encompassing everything from detritus  
218 to birds were sampled. The “currency” for these models was grams of carbon per square meter  
219 ( $\text{g C/m}^2$ ) for biomasses and grams of carbon per square meter per year ( $\text{g C/m}^2/\text{yr}$ ) for flows. For  
220 this study, biomass was measured directly for most compartments, and a diet matrix was partially  
221 constructed from the diet data obtained by Hart (2008) for a limited number of fish species.

222 2.3.1. *Methods for biomass sampling*

223 At each of the 12 sites, benthic cores (inside diameter of 9.5 cm) were collected by  
224 SCUBA divers and pushed manually into the substrate to a depth of 10 cm. A total of 12 cores  
225 were collected at each site to obtain biomass measurements for most benthic compartments  
226 (macrofauna and meiofauna).

227 2.3.1.1. *Detritus*

228 Detritus samples were collected from each core using a 1-cm diameter syringe pushed to  
229 a depth of 1 cm and stored on ice in a dark cooler then frozen until processed in the laboratory.  
230 Loss on ignition (LOI) was used to determine the ash-free dry mass of organic matter (Allen,  
231 1989; Hirota and Szyper, 1975; Nelson and Sommers, 1996). Since the sample potentially  
232 included numerous sources of organic matter, values of sediment microalgae, sediment bacteria  
233 and meiofauna biomasses (also calculated for this study) were subtracted from the LOI-obtained  
234 measurement of organic carbon. Dry weights were converted to g C by multiplying by 0.58

235 (Allen 1989).

#### 236 2.3.1.2. *Benthic macrofauna and meiofauna*

237 Three cores each were combined to form one sample that was processed for benthic  
238 macrofauna; triplicate samples were collected in this manner. Samples were passed through a  
239 500- $\mu\text{m}$  sieve in the field, and all retained specimens were preserved in 10% buffered formalin  
240 with Rose-Bengal stain until processed in the laboratory. All specimens were identified to the  
241 lowest taxonomic level (Fox and Bynum, 1975; Morris and Clench, 1975; Fauchald, 1977;  
242 Fauchald and Jumars, 1979; Ubelacker and Johnson, 1984; Williams, 1984; Fox and Rupert,  
243 1985), dried at 60°C for 48 hr, weighed, and then converted to carbon by multiplying dry weight  
244 by 0.40 using Jørgensen et al. (1991) and Ricciardi and Bourget (1998).

245 The remaining three benthic cores were sub-sampled for meiofauna. Meiofauna were  
246 collected from each core with a 2-cm diameter syringe plunged to a depth of 3 cm, and preserved  
247 in 10% buffered formalin with Rose-Bengal stain. Meiofauna were separated from sediments  
248 using Ludox, following the method of Burgess (2001), passed through stacked 500- $\mu\text{m}$  and 63-  
249  $\mu\text{m}$  sieves (to exclude macroinvertebrates), and all specimens retained on the 63- $\mu\text{m}$  sieve were  
250 identified to lowest taxonomic level using Higgins and Thiel (1988) and Giere (1993). All  
251 individuals (by taxa) were converted to g C from wet weight/individual and/or g C/individual  
252 from several sources (Goodman, 1980; Van Damme et al., 1980; Widbom, 1984; Bessière et al.,  
253 2007; Nascimento et al., 2012).

#### 254 2.3.1.3. *Infaunal mollusks*

255 A clam rake was used to collect mollusks from sites in shallow water. Four 2.32- $\text{m}^2$   
256 transects were raked at the six shallow sites. Mollusks were stored on ice until returned to the



257 laboratory for positive identification and measurements. All specimens were removed from the  
258 shells and dried in an oven at 60°C for 48 hr. Dry weight mass was converted to g C by  
259 multiplying by 0.40 (Jørgensen et al., 1991).

#### 260 2.3.1.4. *Benthic primary producers (microalgae, macroalgae, seagrasses and drift algae)*

261 Benthic microalgae was sampled from each core using a 1-cm diameter syringe plunged  
262 to a depth of 1 cm. Benthic microalgal biomass was measured using fluorometry (Strickland and  
263 Parsons, 1972) as the amount of chlorophyll *a* content in the sample. Chlorophyll *a* was  
264 converted to g C by multiplying by 0.47 (de Jonge, 1980). Samples were only collected during  
265 the spring for both open and closed sites.

266 The biomass of other primary producers (macroalgae, seagrasses, and drift algae) was  
267 measured using various techniques. Seagrass biomass estimates were obtained from an ongoing  
268 submerged aquatic vegetation study in Jarrett Bay using 0.15-m cores and quadrats, as well as  
269 remote sensing, and video and acoustic methods (Luczkovich et al., unpublished). Data from a  
270 site in the area closed to trawling in Jarrett Bay were collected from June – September 2010; the  
271 values for seagrass biomass are only from the closed areas, but those values were also used for  
272 the open areas of the Core Sound model. Drift algae and macroalgae biomass estimates were  
273 calculated from algae collected in otter trawls for sites open and closed to trawling, but data were  
274 only collected in the fall. Otter trawl distances were obtained from a digital echo-sounder (see  
275 Nekton below).

#### 276 2.3.1.5. *Phytoplankton*

277 Water samples were collected at each site to measure phytoplankton. Carboys (1 L<sup>3</sup>)  
278 were filled with surface water at each station and stored on ice in a cooler until returned to the

279 laboratory. In the laboratory, water was filtered through glass microfiber filters (47 mm, GF/C).  
280 Pigment extraction was done with a mixture of 45% acetone/45% methanol/10% deionized  
281 water, then kept in a freezer for 12-24 hr, using the methods of Strickland and Parsons (1972), as  
282 modified by L. Clough. Initial readings were done on the fluorometer, then 10% HCl was added,  
283 to correct for pheophytin pigments, and then read again. Chlorophyll *a* values were then  
284 converted to g C by multiplying by 0.47 (de Jonge, 1980).

#### 285 2.3.1.6. *Zooplankton*

286 Three replicates of zooplankton samples were collected at each site using 90- $\mu$ m mesh  
287 bongo plankton nets (net diameter of 28 cm), towed for 1 min at a constant speed. A General  
288 Oceanics flow meter with the low-speed rotor was attached to the bongo net to measure the  
289 volume of water towed. All zooplankton samples were fixed in 10% buffered formalin for  
290 storage until processing. Any ctenophores or other large gelatinous zooplankton were removed  
291 before fixing. To estimate the abundance of ctenophores, separate 1-min tows were conducted.  
292 Any ctenophores collected in the tows were counted and recorded on the boat. Total counts of  
293 ctenophores were converted to dry weight biomass then g C (Jørgensen et al., 1991) for use in  
294 the Ecopath models. In the laboratory, all large zooplankton specimens ( $\geq 500 \mu\text{m}$ ) were  
295 counted and dried at 60°C for 48 hr to measure dry mass, which was converted to g C by  
296 multiplying by 0.40 (Jørgensen et al., 1991). Using a Folsom splitter, samples were split three  
297 times, and the 1/8 sample was suspended in 500 mL of water. Five 10-ml subsamples were  
298 taken with Hensen-Stempel pipettes and passed through a series of sieves (425  $\mu\text{m}$ , 250  $\mu\text{m}$ , 150  
299  $\mu\text{m}$ , and 75  $\mu\text{m}$ ). The contents of each sieve were counted, identified to lowest taxonomic level  
300 (using Young et al., 2002 and Johnson and Allen, 2005), summed and total counts were  
301 multiplied by 80 to obtain the whole sample count. This method subsampled at least 100-300

302 individuals at a time, an amount recommended by several sources to avoid potential errors  
303 associated with repetitive Folsom splitting of samples (Van Guelpen et al., 1982; Griffiths et al.,  
304 1984; Mallin, 1991; Johnson and Allen, 2005). The entire contents of each sieve were dried at  
305 60°C for 48 hr to calculate dry mass, and then converted to g C by multiplying by 0.40  
306 (Jørgensen et al., 1991).

#### 307 2.3.1.7. Nekton

308 To sample fishes and other forms of nekton, an otter trawl similar to the one used by the  
309 North Carolina Division of Marine Fisheries (NCDMF) was deployed. The otter trawl had a  
310 headrope of 3.2-m, a body net stretch mesh of 1-cm, a cod-end stretch mesh of 0.5-cm, a tickler  
311 chain, and trawl doors measuring 90 cm by 46 cm. Trawls were deployed for 2 min at a constant  
312 speed, three times at each site. Trawl tow lengths were determined using a scientific echo-  
313 sounder operated simultaneously with the trawl deployment. The BioSonics DTX echo-sounder  
314 was used to assess bathymetry, bottom substrate, and fish abundance in front of the trawl. The  
315 echo-sounder was interfaced with a JVC GPS receiver and a Panasonic Toughbook CF-29 laptop  
316 computer so that precise trawl tracks and depths were recorded to a hard drive (Hart, 2008). All  
317 specimens retained by the trawls were euthanized and preserved in 10% buffered formalin for  
318 identification and measurement in the laboratory. When necessary, some samples were weighed  
319 in the field using spring scales. In the laboratory, all specimens were identified, measured for  
320 length and wet weight, and stomachs of selected fishes were removed for diet analyses. All  
321 biomass measurements were converted to dry weight and g C by multiplying by 0.15 (Jørgensen  
322 et al., 1991).

323 Experimental gill nets were used to collect larger, faster fishes not captured by the otter  
324 trawl. Five 23-m panels of different stretch mesh (8.9 cm, 10.2 cm, 11.5 cm, 12.7 cm and 13.9

325 cm) were deployed for upwards of six hours and checked at least every two hours. All  
326 specimens were euthanized, tagged and stored on ice in a cooler until brought back to the  
327 laboratory or field processing site. Specimens were identified, measured and stomachs were  
328 removed for diet analyses. All biomass measurements were converted to g C by multiplying by  
329 0.15 (Jørgensen et al., 1991).

330 Additional fish and shellfish data were obtained from the NCDMF Program 120 Juvenile  
331 Trawl Survey (Katy West, personal communication). Trawl surveys have been conducted in the  
332 spring in nursery areas to inform management decisions on the opening and closing dates of  
333 various fisheries. Data for several species of fish and shrimps were included in the construction  
334 of the models in this study.

#### 335 2.3.1.8. *Fisheries data*

336 Unpublished NCDMF Trip Ticket data from April-June 2006 and 2007 (averaged to  
337 represent Spring) and August-October 2006 and 2007 (averaged to represent Fall) for six fishing  
338 gears (shrimp trawls, skimmer trawls, pound nets, crab pots, haul seines and gill nets) were  
339 included in the models for this study. The area of Core Sound waters was reported by Cheuvront  
340 (2002) as 72,000 acres (291,272,662 m<sup>2</sup>). The average catch (in wet weight pounds) was  
341 converted to grams of wet weight then multiplied by 0.15 (Jørgensen et al., 1991) to convert g C  
342 dry weight, and finally divided by the area of Core Sound (resulting in g C/m<sup>2</sup> for each species  
343 by gear type). Because trawlers cannot operate in closed areas or in known seagrass beds, the  
344 area for calculating shrimp trawl and skimmer trawl catches was reduced by 50% (145,686,831  
345 m<sup>2</sup>). These values represent the biomass of each species that was added to our own data  
346 collections (from juvenile trawls and gill nets). To calculate fisheries trip averages (for fisheries  
347 landings data in Ecopath), we used the pounds/trip average of the time periods listed above and

348 calculated g C for those data. To convert fisheries trip averages to g C/m<sup>2</sup>, we estimated the area  
349 fished by each gear type, based on our knowledge of the gears, the information provided by the  
350 NCDMF, and shrimp trawl and skimmer trawl bycatch studies.

351 Information about shrimp and skimmer trawl landings were incorporated only in the  
352 model representing areas open to trawling. Data about the landings of the other four gears were  
353 split 10% in the Closed model and 90% in the Open model, based on the relative areas of closed  
354 and open waters in the study, respectively.

355 Bycatch from trawls only was also included in the open model for this study. Bycatch  
356 data were available from local studies conducted in/near Core Sound by Johnson (2003, 2006)  
357 for otter trawls, and by Coale (1993), Coale et al. (1994) and Hines et al. (1999) for skimmer  
358 trawls. While bycatch is known to occur with the other four gear types, studies reporting bycatch  
359 statistics for gill nets, pound nets, haul seines and crab pots were insufficient for inclusion in this  
360 study.

#### 361 2.3.1.9. *Large vertebrates*

362 Visual surveys were conducted for groups such as birds, dolphins and turtles. Bird  
363 surveys were conducted for 30 min at each site within an area of 500 m<sup>2</sup>, similar to the methods  
364 used by Christian and Luczkovich (1999). Bird biomasses were estimated from the Cornell Lab  
365 of Ornithology online database (<http://www.allaboutbirds.org/guide>). Loggerhead sea turtles  
366 (*Caretta caretta*) were occasionally observed while sampling. The biomass of any loggerhead  
367 sea turtles near the study sites was estimated by visual estimates of carapace length and width  
368 (and literature: Epperly et al., 1995; Sasso et al., 2007; NMFS NOAA website  
369 <http://www.nmfs.noaa.gov/pr/species/turtles/loggerhead.htm>) rather than capture. Any  
370 bottlenose dolphins (*Tursiops truncatus*) observed near study sites were counted, and estimates

371 of biomass were made from literature values (Hansen and Wells, 1996; Foster, 2000).

### 372 2.3.2. *Energetics data*

373 Information on production:biomass (P/B) and consumption:biomass (Q/B) ratios were  
374 collected from literature. In particular, several studies were utilized to parameterize the  
375 energetics data for the models in this study, especially the trawl bycatch study in Core Sound by  
376 Johnson (2003, 2006), and several publications from the Neuse River estuary ModMon project  
377 (Luettich et al., 2000; Baird et al., 2004; Christian et al., 2004; Christian et al., 2009). Most Q/B  
378 ratios for fish were obtained through FishBase (Froese and Pauly, 2009). Additional sources of  
379 information from other network models included: Baird and Ulanowicz (1989), Christian and  
380 Luczkovich (1999), Sellner et al. (2001), Okey et al. (2004), Christensen et al. (2009), and  
381 Harvey et al. (2010). Ecotrophic efficiencies were calculated by Ecopath in the models.

### 382 2.3.3. *Diet matrix*

383 To construct a diet matrix, diet data were collected using stomach content analysis for  
384 seven fish species collected in Core Sound (Hart 2008). A sieve fractionation method (modified  
385 by Luczkovich and Stellwag [1993] from Carr and Adams [1973]) and used by Baird et al.  
386 (1998), Luczkovich et al. (2002) and Chagaris (2006) was used in this study. Stomach content  
387 analysis was conducted on individual fishes collected from open and closed areas during the  
388 spring and the fall, including Atlantic menhaden (*Brevoortia tyrannus*), Atlantic croaker  
389 (*Micropogonias undulatus*), bluefish (*Pomatomus saltatrix*), pigfish (*Orthopristis chrysoptera*),  
390 pinfish (*Lagodon rhomboides*), spot (*Leiostomus xanthurus*), smooth dogfish (*Mustelus canis*)  
391 and cownose rays (*Rhinoptera bonasus*). For all other compartments in the models, diet  
392 information was gathered from literature (see summary in Deehr, 2012). For compartments that

393 represented highly mobile species or species/organisms that are only present in Core Sound  
394 estuarine waters for part of the year, diet data included imported prey.

#### 395 2.3.4. *Final model compartments*

396           Given field collections and NCDMF data, each model contained the same 65  
397 compartments, including two non-living groups, five primary producer groups, 25 invertebrate  
398 groups, 24 fish groups, two large vertebrate groups, and five bird groups. In order to maintain  
399 the same number of compartments for each model, a very small placeholder biomass value ( $1 \times$   
400  $10^{-5}$  g C/m<sup>2</sup>) was used for compartments where no individuals of the representative taxa were  
401 collected by field methods. The 65 compartments and their constituent groups are listed in Table  
402 1, and the sources for diet information are listed in Deehr (2012). Some compartments represent  
403 aggregated organisms, particularly lower trophic level organisms. Several benthic invertebrates  
404 groups (namely polychaetes, bivalves, and gastropods) were grouped together in the isotrophic  
405 classes used by Christian and Luczkovich (1999) using regular equivalence (Luczkovich et al.,  
406 2003). While no two species have the exact same relationships to predators and prey, regular  
407 equivalence groups together “trophically analogous” species (Johnson et al., 2001), species that  
408 share similar relationships to both predators and prey of similar trophic groups. Regular  
409 equivalence was effectively used to aggregate taxa (Luczkovich et al., 2003; Chagaris, 2006),  
410 and has been shown to provide better aggregations than Euclidean distance and Bray-Curtis  
411 similarity (Metcalf et al., 2008).

#### 412 2.3.5. *Balancing the Models*

413           We followed the general guidelines for balancing Ecopath models reported by  
414 Christensen et al. (2008). An Ecopath model is considered balanced when the ecotrophic

415 efficiency (EE) of all compartments is less than 1.0. If  $EE > 1$ , the consumption of the  
416 compartment is greater than its production and therefore not mass-balanced. Following an initial  
417 run, manual balancing adjustments were made according to the following guidelines we utilized  
418 for the construction of the Core Sound models: 1) balance each compartment with  $EE > 1$   
419 individually; 2) adjust diets first, maintaining binary relationships, but adjust percentage of prey  
420 items depending on biomass availability; 3) avoid changing diets of fishes reported by Hart  
421 (2008) as much as possible, using as a guide the prey biomass availability; 4) adjust the diets of  
422 predator compartments with large biomasses, because they exert the strongest force on their  
423 prey; 5) utilize the predation mortality spreadsheet, an Ecopath output, to modify predator diets;  
424 6) import portions of diets based on migratory habits of the organism (percentage of time spent  
425 out of system should have imported diet), using Nelson et al. (1991) for fish and invertebrates  
426 and Christian and Luczkovich (1999) for birds; 7) allow cannibalism, but only up to 10%; 8)  
427 double check gross efficiency (production:consumption ratio), because P/B and Q/B were  
428 borrowed from literature, they may need to be adjusted; 9) gross efficiency values should be  
429 around 0.1 – 0.3 for most compartments, but maybe lower for top predators and higher for very  
430 small organisms (Christensen et al. 2008); 10) adjust biomass of a compartment, beginning with  
431 the lowest-confidence compartments, particularly those deemed under-sampled (e.g., forage fish  
432 such as Atlantic silversides and anchovies, which are under-sampled by trawls). We used an  
433 iterative process for the latter, adjusting biomass values by 10% at a time.

434         A model was deemed balanced when EE for all compartments was less than 1. If, after  
435 following the guidelines listed above, the EE was still greater than 1, we set the EE to a value  
436 less than 1 (generally 0.95 or 0.99) and allowed Ecopath to calculate one of the other parameters,  
437 generally P/B.



438 2.4. *Stable isotopes*

439 In order to validate the Core Sound Ecopath models, representative species from as many  
440 compartments as possible were collected for stable isotope analysis, for both spring and fall and  
441 for areas open and closed to trawling. Carbon and nitrogen isotope data were obtained from 232  
442 samples representing 28 compartments (four producers, 10 invertebrates and 14 fishes) from the  
443 Core Sound models. Many of these organisms were collected during the spring and fall 2007  
444 sampling efforts; however, some additional samples were collected in early June 2010. All  
445 organisms collected for stable isotope analysis were collected using trawls and gill nets, and all  
446 vertebrates were handled according to the protocols approved by the East Carolina University  
447 Institutional Animal Care and Use Committee.

448 Water samples were filtered to separate zooplankton from phytoplankton, and then  
449 filtered through ashed 47 mm glass fiber filters (GF/F) before being frozen until processed. For  
450 invertebrates, organisms were identified, recorded, hard parts (mollusk shells, crustacean  
451 exoskeletons) were removed and then the remaining soft tissues were frozen until processed.  
452 Seagrass, drift algae, and macroalgae were thoroughly rinsed and scraped to remove non-plant  
453 tissue before being frozen.

454 Pinnegar and Polunin (1999) indicated that white muscle is less variable in  $^{15}\text{N}$  levels  
455 than red muscle, liver or heart tissue, so care was taken to remove only white muscle from fishes  
456 for this study. For fishes, all individuals were identified to species and recorded before a section  
457 of dorsal white muscle tissue was removed and frozen until processed. All stable isotope tissue  
458 samples were freeze-dried for 24 hrs before being ground to a fine powder with a mortar and  
459 pestle, then stored in scintillation vials.

460 The stable carbon and nitrogen isotope composition of all filters and ground, freeze-dried

461 samples were measured using a ThermoFinnigan Delta V Advantage isotope ratio mass  
462 spectrometer coupled to a Costech elemental analyzer via the Conflo III combustion interface in  
463 the Environmental Geochemistry Laboratory, Department of Geology, Bates College. Stable  
464 isotope data are expressed in parts per thousand (‰) deviation from international standards using  
465 the following equation:

466

$$467 \quad X = (R_{\text{sample}} / R_{\text{standard}} - 1) \times 1000, \quad (2)$$

468

469 where  $X = {}^{15}\text{N}$  or  ${}^{13}\text{C}$ , and  $R$  = ratio of heavy/light isotope content ( ${}^{15}\text{N}/{}^{14}\text{N}$  or  ${}^{13}\text{C}/{}^{12}\text{C}$ ). The  
470 standard for carbon is PeeDee Belemnite limestone, and the standard for nitrogen is atmospheric  
471 nitrogen gas. Internal standards (acetanilide, caffeine and fish muscle) were run every 8 to 10  
472 samples. The reproducibility, as determined by the standard deviation of the internal standards,  
473 was  $\pm 0.2\text{‰}$  for both  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$ .

#### 474 2.5. Comparisons of effective trophic levels and stable isotope analysis

475 The effective trophic levels (ETLs) of the two 65-compartment Core Sound models were  
476 calculated by Ecopath (Table 2). Ecopath uses equation (3) to compute ETLs:

477

$$478 \quad \text{ETL} = \left( \sum_{i=1}^S p_i * TL_i \right) + 1 \quad (3)$$

479

480 where  $p_i$  is the proportion of prey  $i$  in the diet of the predator compartment,  $TL_i$  is the trophic  
481 level of prey  $i$  and  $S$  is the total number of prey types in the diet.

482 To compare stable isotope data with ETLs, generalized linear models (GLM) and  
483 MANOVAs were conducted. We also calculated trophic position (TP) using equation (4) from

484 Minagawa and Wada (1984) and Milessi et al. (2010):

485

$$486 \quad TP = \lambda + (\delta^{15}\text{N}_{\text{organism}} - \delta^{15}\text{N}_{\text{base of the food web}}) / 3.4 \quad (4)$$

487

488 where  $\delta^{15}\text{N}_{\text{organism}}$  is measured, and 3.4 is the parts per thousand (‰) average  $\delta^{15}\text{N}$  enrichment  
489 per trophic position (Vander Zanden and Rasmussen, 2001). The  $\delta^{15}\text{N}_{\text{base of the food web}}$  is the  $\delta^{15}\text{N}$   
490 of an organism that is a sessile herbivore, therefore providing an isotopic baseline for estimating  
491 higher trophic level consumers; in this study, this organism is the benthic filter-feeding hard  
492 clam (*Mercenaria mercenaria*), which has  $\lambda = 2.0$ . The calculated TP was then compared to the  
493 Ecopath-calculated ETL using t-tests and regressions. To determine if the stable isotope data  
494 increased with effective trophic level, the  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  of each sample was paired with the  
495 appropriate compartment and its effective trophic level from one of the Core Sound models  
496 (Open or Closed). The regression line provides information about the trophic enrichment of both  
497  $^{13}\text{C}$  and  $^{15}\text{N}$ , which will be compared with other published literature. Additionally, Kruskal  
498 Wallis test was used to detect differences between ETLs and  $^{15}\text{N}$  for spot, pinfish, Atlantic  
499 menhaden and blue crabs, mesopredators that are common shrimp trawl bycatch species.

### 500 **3. Results**

#### 501 *3.1. Core Sound Ecopath model effective trophic levels*

502 The Ecopath model was used to produce effective trophic levels (ETLs) for all 65  
503 compartments modeled in open and closed trawling areas. Producers (phytoplankton, benthic  
504 microalgae, benthic macroalgae, seagrasses and drift algae) had ETLs of 1.0 (Table 2).  
505 Consumers had varying levels of ETLs ranging from herbivores and detritivores such as benthic

506 and aquatic bacteria (2.0), hard clams (2.02), deposit-feeding polychaetes (in open areas  
507 ETL=2.48), omnivorous fishes such pinfish (in open areas ETL=2.55) and spot (in closed areas  
508 ETL=2.64). Atlantic menhaden were low on the trophic spectrum in this model, with an ETL  
509 =2.1, based on the gut analysis data from this study that suggested they were eating large  
510 amounts of detritus (Hart 2008). White shrimp were relatively low in trophic position, with ETL  
511 = 2.14 in closed and 2.16 in open areas, consuming mostly detritus and benthic micro- and  
512 macroalgae. In contrast, the brown shrimp occupied a higher trophic position, with ETL = 3.06  
513 in closed trawl areas and 3.11 in open trawling areas. Pink shrimp was similar to brown shrimp,  
514 with ETL= 3.1 in closed areas and in open areas. These shrimp species were omnivores,  
515 consuming meiofauna (ETL=2.08-2.13), polychaetes (ETL= 2.2-2.51), juvenile crabs  
516 (ETL=2.87-2.98), other shrimps (ETL=2.61-2.64), pericaridean crustaceans (ETL=2.2) and  
517 detritus (ETL = 1). These three shrimps were the target of the trawl fishery in Core Sound.

518       Trophic level three species were mostly fishes, including fish species like  
519 zooplanktivorous bay and striped anchovies (ETL=3.07), Atlantic silversides (ETL=3.1), benthic  
520 carnivores like pigfish (ETL=2.97-3.06), harvestfish/butterfish (ETL=3.15), Florida pompano  
521 (ETL=3.34-3.59), and cownose rays (ETL=3.26-3.29) that consumed primarily mollusks  
522 (ETL=2.05-2.2). Trophic level three species also included fish-and-invertebrate consumers like  
523 weakfish (ETL=3.4), spotted seatrout (ETL=3.49-3.67), which shift through several ontogenetic  
524 feeding stages as they grow, starting with zooplankton (ETL=2.1) as larvae, consuming benthic  
525 invertebrates (ETL=2.2 – 3.11) as juveniles, and feeding on smaller fishes like striped mullet  
526 (ETL=2) anchovies, silversides, pinfish, spot and Atlantic croaker (ETL=2.7) as adults.  
527 Piscivorous fishes included Spanish mackerel (ETL=3.48-3.55), black drum (ETL = 3.39-3.57),  
528 red drum (ETL = 3.71-3.77), bluefish (ETL = 3.59), Paralichthid flounders (ETL = 3.42-3.55),

529 and smooth dogfish (ETL=3.78-3.93). Invertebrate animals that were high-trophic level  
530 predators included blue crabs (ETL=2.92-2.98) that consumed fishes discarded from trawls  
531 (bycatch), jellyfish (ETL=3.11-3.14) and ctenophores (ETL=3.31) that consumed zooplankton,  
532 and Atlantic brief squid (ETL=3.5), which consumed fishes. The birds ranged from ETL = 3.36  
533 (shorebirds and waders) to double-crested cormorants (ETL=3.79-3.83). Sea turtles (loggerhead  
534 sea turtles) were relatively high trophic level species (ETL=3.57-3.62) consuming fishes and  
535 jellyfish. The bottlenose dolphin and Atlantic sharpnose sharks were top predators with ETLs of  
536 4.01-4.21.

537 To visualize the entire ecosystem C flows, the two trawling area models were displayed  
538 as node-and-edge flow diagrams with nodes arranged in the vertical dimension by ETL, with  
539 edge thickness proportional to C flow and node size scaled by C biomass (Figure 2A shows the  
540 flow diagram for areas closed to trawling and Figure 2B shows the flows that are open to  
541 trawling). Generally, the model flow diagrams show a decrease in the compartment's biomass as  
542 ETL increases, with species such as sharks and birds having small biomasses near the top of flow  
543 diagrams, and large biomasses for producers (seagrass, phytoplankton, and algae) at the base of  
544 the flow diagram. Detritus and bycatch are non-living compartments and thus are designated  
545 trophic level 1 in the Ecopath modeling approach; these appear at the bottom of the flow  
546 diagram.

547 Most compartments had greater biomass in the open area, including sea turtles, bluefish,  
548 weakfish, spotted seatrout, Spanish mackerel, Atlantic menhaden, pinfish, hard clams,  
549 suspension feeding bivalves, blue crabs, brown, pink and white shrimp, polychaetes, sea  
550 cucumbers, and brittlestars (Table 2). In contrast, detritus, drift algae, meiofauna, zooplankton,  
551 and Atlantic croaker have more biomass in the areas closed to trawling.

552 Flows of C in Core Sound were dominated by consumption of detritus by benthic  
553 bacteria, meiofauna, and higher trophic levels species. Table 3 shows that more C flows from  
554 detritus to all predators in the closed area ( $365.84 \text{ gC/m}^2/\text{yr}$ ) than in the open trawling areas  
555 ( $262.67 \text{ gC/m}^2/\text{yr}$ ). Most of this flow is from detritus to consumers at Lindeman Trophic level II  
556 (i.e., detritivores). However, the energy transfer efficiency from detritus was higher in the open  
557 trawling areas: Lindeman transfer efficiency from detritus to trophic levels II-IV for open areas  
558 was 11.6% and only 4.6% Lindeman transfer efficiency in closed trawling areas. This was also  
559 the case with primary producers, which had higher transfer efficiency in the open areas (8.3% in  
560 open areas vs. 4.5% in closed areas) and total system efficiency (11.1% versus 4.8%). It appears  
561 that the open trawling areas have less detritus but higher trophic efficiency.

562 Generally, the ETLs for each node were similar between the open and closed models  
563 (Table 2), reflecting the similar nature of the diet matrices used to build the models. Diet matrix  
564 data and Ecopath ETLs were different for some fish compartments (pinfish, spot, smooth  
565 dogfish, bluefish, pigfish, Atlantic croaker and cownose rays) that were collected for stomach  
566 content analysis in the two areas (Hart, 2008; Deehr, 2012). For example, pinfish had an ETL =  
567 2.55, which was higher in the open trawling areas than in closed areas (ETL= 2.29). This was  
568 because they consumed more plant material (43% of stomach contents by mass was benthic  
569 microalgae and seagrass in the closed areas) and less plant material (32% of diet) in the areas  
570 open to trawling (Hart, 2008). For Atlantic menhaden, there was little observable difference in  
571 the stomach content analysis from open and closed areas in Core Sound (Hart, 2008), with  
572 unidentifiable material labeled here as “detritus” found to be dominant (45% by dry mass) food  
573 item. Atlantic menhaden diet similarity between trawling areas was reflected in the nearly  
574 identical diet matrix and Ecopath ETL estimates.

575           The Ecopath ETLs for compartments with dietary data derived from the literature  
576 differed between the two trawling areas due to the measured differences in the availability of  
577 prey and the modeled flow between nodes. In Ecopath, a steady-state balanced model assumes  
578 that total flow into and out of each node are equal, with inflow being proportional to available  
579 prey in the absence of dietary data (see Ecopath balancing guidelines 3 and 4 in Section 2.3.5).  
580 Bottlenose dolphins and Atlantic sharpnose sharks were at the highest trophic levels in both  
581 trawling areas, but bottlenose dolphins had a slightly greater ETL in the areas closed to trawling.  
582 Bottlenose dolphins were parameterized in the diet matrix as consumers of both paralichthid  
583 flounders and black drum (high-trophic level species) from both trawling areas. However, the  
584 model of the closed trawling area included a greater proportion of flounder and black drum, and  
585 less spot and Atlantic menhaden (low-trophic level species) than in open areas, which resulted in  
586 a greater ETL in the closed area model. Some bird groups had higher trophic position in open  
587 areas, including pelicans, terns, and shorebirds/waders. For example, brown pelicans were  
588 modeled as consuming 29% more spot and 18% more Atlantic menhaden in open areas, due to  
589 their high availability in those areas, which raised the ETL relative to closed trawling areas.  
590 Other fish species showed similar patterns, for example, smooth dogfish, pigfish, pompano,  
591 flounders (*Paralichthys* sp.), and black drum had higher ETLs in the areas open to trawling  
592 because of higher contributions by prey with high ETLs. Blue crabs, deposit-feeding  
593 polychaetes, and meiofauna were computed to have higher effective trophic levels in the open  
594 trawling due to the high availability of trawling discard [bycatch observed from the Core Sound  
595 trawling fisheries was predominantly fishes, Johnson (2006)]. Conch/whelks, predatory  
596 gastropods, suspension feeding bivalves also had higher ETLs in closed trawling areas. Shrimps  
597 (brown, pink and white) had slightly higher ETLs in open area, but they were not significantly

598 different.

### 599 3.2. Stable isotope measurements in Core Sound

600 In general, the  $\delta^{13}\text{C}$  of producers varied between -22.81‰ for drift algae and -12.27‰ for  
601 seagrass (Table 4). The  $\delta^{13}\text{C}$  of consumers varied between  $-20.94 \pm 1.63\text{‰}$  for tunicates and -  
602 14.14‰ for pigfish. The  $\delta^{15}\text{N}$  values of producers varied between 2.93‰ for seagrass and 6.30  
603  $\pm 0.62\text{‰}$  for drift algae. The  $\delta^{15}\text{N}$  values of consumers varied between 6.51‰ for bryozoans and  
604 14.53‰ for bluefish. The biplot of  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  (Figure 3, left panel) shows that primary  
605 producers (macroalgae, microalgae, seagrass, and drift algae) had low  $\delta^{15}\text{N}$  and low  $\delta^{13}\text{C}$   
606 signatures, with consumers exhibiting high  $\delta^{15}\text{N}$  and high  $\delta^{13}\text{C}$  values; thus, the enrichment of C  
607 and N was associated with an increase in trophic position. These isotopes signatures were within  
608 the measured ranges of published values for other estuaries in the southeast USA (Figure 3, right  
609 panel).

### 610 3.3. Comparison between Ecopath ETL and stable isotopes

611 The average values of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  for the open and closed trawling areas were  
612 calculated by compartment to discern any differences in food web dynamics between the open  
613 and closed sites and to facilitate comparisons with Ecopath ETL (Table 4). In general, there was  
614 a positive relationship between the ETL and the stable isotope fractionation of both nitrogen  
615 (Figure 4) and carbon (Figure 5). There was an overall nitrogen enrichment of 2.52‰ per  
616 trophic level and carbon enrichment of 1.03‰ per trophic level (Tables 5 and 6, respectively).

617 We wished to estimate the relationship between Ecopath ETL and trawling management  
618 areas. To directly compare ETL and stable isotope fractionation in this ecosystem, and to  
619 measure the enrichment factors as regression coefficients, we performed a general linear model



620 regression of  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  isotopic signatures on the Ecopath ETL (trophic level effect) with  
621 factors for trawling management area (trawling effect) and an interaction term (ETL x trawling  
622 area) using paired points for each of the taxa sampled for isotopic analysis. The results of these  
623 univariate analyses are given in Tables 5 and 6. The effective trophic levels from the Ecopath  
624 models were good predictors of  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$ , explaining a large proportion of the variance for  
625  $\delta^{15}\text{N}$  ( $F_{1,218} = 221.18$ ,  $p < 0.00001$ ,  $R^2 = 0.53$ , Table 5), but yet very little of the variance in  $\delta^{13}\text{C}$   
626 ( $F_{1,218} = 19.947$ ,  $p = 0.000013$ ,  $R^2 = 0.095$ , Table 6). There was not a significant trawling area  
627 effect (open area versus closed area) for either of these isotopes (for  $\delta^{15}\text{N}$ :  $F_{1,218} = 0.2842$ ,  $p =$   
628  $0.5945$ , Table 5; for  $\delta^{13}\text{C}$ :  $F_{1,218} = 2.314$ ,  $p = 0.1296$ , Table 6).

629 A MANOVA was also done to jointly assess the differences between trawling  
630 management areas and ETL. In this analysis, a significant trawling area and ETL effect was  
631 observed (Table 7). The trawling area effect on both stable isotopes was significant (MANOVA,  
632 Wilks's Lambda = 0.97,  $F_{2,218} = 3.1297$ ,  $p = 0.0456$ ), with both  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  more enriched in  
633 the open areas. The enrichment was small for each isotope (an increase of 0.34‰ for  $\delta^{15}\text{N}$  and  
634 0.64‰ for  $\delta^{13}\text{C}$ ).

635 A significant difference in nitrogen stable isotope signatures was observed for benthic-  
636 feeding middle trophic level species (pinfish ETL = 2.29 in closed areas, ETL = 2.55 in open  
637 trawling areas; spot ETL = 2.54 in closed areas and ETL = 2.64 in open areas; blue crabs, ETL =  
638 2.92 in closed areas and ETL = 2.98 in open areas). These species had sufficient sample sizes  
639 for  $\delta^{15}\text{N}$  statistical comparisons. Stable isotope data showed significant enrichment for these  
640 three species (Kruskal-Wallis test:  $U = 1.5$ ,  $p = 0.006$  for blue crabs;  $U = 29.0$ ,  $p = 0.0227$  for  
641 pinfish;  $U = 14.0$ ,  $p = 0.0024$  for spot; Figure 6). There was no significant difference for  
642 Atlantic menhaden. However, these results suggest that ETL changes are small and not always

643 higher in the open trawling areas. This was especially true for spot, which had a higher ETL in  
644 the closed areas, but higher  $\delta^{15}\text{N}$  in the open areas.

645 Using hard clams as the reference organism, we calculated trophic position (TP) using the  
646 equation from Minagawa and Wada (1984). A paired t-test indicated that there was a significant  
647 difference between TP and Ecopath ETL ( $t = 4.6536$ ,  $df = 34$ ,  $p = .0000481$ ). A linear regression  
648 of ETL on TP (Figure 7) indicated an increase of ETL with TP, but the line did not go through  
649 the origin:  $\text{ETL} = 0.6377 \text{ TP} + 1.3473$  ( $F_{1,33} = 22.3$ ,  $p = 0.0004166$ ,  $R^2 = 0.3852$ ).

## 650 **4. Discussion**

### 651 *4.1. Do the stable isotope data validate the Ecopath ETLs?*

652 The stable isotope data from this study match well with the Ecopath-calculated ETLs  
653 from the two Core Sound models. First, the linear regression between  $\delta^{13}\text{C}$  and ETL indicated a  
654 trophic enrichment of 1.03‰ per trophic level, which is higher than the value of  $0.39 \pm 0.13\%$   
655 reported in a review study by Post (2002), but within the range of trophic enrichment (between 0  
656 and 1.5‰) reported by others (DeNiro and Epstein, 1978; Peterson and Fry, 1987; Vander  
657 Zanden and Rasmussen, 2001; Fry, 2006; Michener and Lajtha, 2007; Sweeting et al., 2007).  
658 Second, the linear regression between  $\delta^{15}\text{N}$  and ETL indicated an enrichment of 2.52‰ per  
659 trophic level, which is comparable to other studies, where trophic enrichment ranged from 1.3‰  
660 (Minagawa and Wada, 1984) to 9.2‰ (DeNiro and Epstein, 1981). Numerous other studies  
661 report average trophic enrichment of  $\delta^{15}\text{N}$  around 2.5‰ to 3.5‰ (Vander Zanden and  
662 Rasmussen, 2001; Post, 2002; McCutchan et al., 2003; Sweeting et al., 2007). In fact, the meta-  
663 analysis of  $^{15}\text{N}$  conducted by Vanderklift and Ponsard (2003) revealed an average  $\delta^{15}\text{N}$  trophic  
664 enrichment of 2.54‰. This indicates that the diet matrices we constructed for the Core Sound

665 models reliably reflect the carbon and nitrogen tissue signatures of organisms within the system  
666 as a whole.

667         There are some exceptions to the predicted trophic position of certain species in the  
668 models, especially the Atlantic menhaden and anchovies. These species were detritus-  
669 consuming zooplanktivores, based on the model's dietary data. Thus, the ETL was 2.1 for  
670 menhaden, which consumed 60-80% of its diet from detritus in Core Sound (Hart 2008), with the  
671 rest coming from meiofauna and zooplankton, and the ETL was 3.1 for anchovies, based on their  
672 published diets of 57% from zooplankton (mostly calanoid copepods), 33% from meiofauna, and  
673 5% detritus and 5% from other invertebrates (Christensen et al., 2009). However, the stable  
674 isotopic signatures for menhaden were 11.59‰ in the closed areas and 11.91‰ in the open areas,  
675 whereas the predicted  $\delta^{15}\text{N}$  was 9.26‰, a difference of 2.32 and 2.64‰, or approximately a  
676 whole trophic level higher than the Ecopath ETL. Likewise, the anchovies stable isotope  
677 signatures were predicted to be 11.71‰, but the measured  $\delta^{15}\text{N}$  was 13.04‰ and 13.29‰, or a  
678 difference of 1.33‰ and 1.58‰. Thus the Ecopath model underestimated the trophic position  
679 for these two species. One reason for these anomalies may have to do with the detritus prey  
680 category, which may be animal material, and not plant-based, and thus not at trophic level 1,  
681 which the Ecopath model assumes. Other possible reasons include nitrogen enrichment at the  
682 base of the food web from producers outside the Core Sound system and an incorrect diet  
683 specification in the model.

684         There are two ways to evaluate an ecosystem model: 1) using an independent measure of  
685 a computed model output with which to compare; and 2) sensitivity analysis of the model  
686 components, varying them one at a time to see which has a large impact on a computed model  
687 output. Others (Dame and Christian, 2008) have used both approaches. We chose the first

688 method here, comparing the Ecopath-calculated ETL with changes in stable isotope ratios. Our  
689 comparison yielded a general agreement between the ETL and the stable isotope fractionation  
690 ( $\delta^{15}\text{N}$  of 2.52‰ and  $\delta^{13}\text{C}$  of 1.03‰ per trophic level), with effect sizes that are in near perfect  
691 agreement with the published meta-analysis means for unit trophic level increases (2.3‰ per  
692 trophic level for  $\delta^{15}\text{N}$  and 1‰ per trophic level for  $\delta^{13}\text{C}$ ; McCutchan et al., 2003). Although the  
693 regression and MANOVA results suggest the relationships were significant and linear, there was  
694 not a perfect relationship as predicted in the literature, with ETL explaining only 50-60% of the  
695 variation in  $\delta^{15}\text{N}$  stable isotopes, and even less (1%) in  $\delta^{13}\text{C}$ . A good deal of the variation  
696 occurred among individual animals living in the estuary, inside and outside of the trawl  
697 management areas. This variation is unexplained, but as the stable isotope literature  
698 demonstrates, such variation can be due to the local differences in biogeochemistry and sources  
699 of enriched N from pollution sources (Bucci et al., 2007). Comparison with the basal group  $\delta^{15}\text{N}$   
700 and  $\delta^{13}\text{C}$  signatures is important to assess such variation.

701         The MANOVA results suggest a small but significant enrichment of both  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$   
702 was observed when open trawl management areas are compared to those of the closed areas,  
703 particularly in organisms occupying higher trophic levels. Enriched  $\delta^{15}\text{N}$  values in the open  
704 areas may be due to a size effect (pinfish and blue crabs tended to be larger in the open areas;  
705 however, spot were larger in the closed areas yet had enriched  $\delta^{15}\text{N}$  in the open areas). This is a  
706 possible trawling impact, where nitrogen is enriched because of an increase trophic position of  
707 scavengers and predators due to the consumption of discards from the trawls. Other explanations  
708 include migrating fishes ate carbon or nitrogen from sources outside of Core Sound, closer  
709 proximity to *Spartina* marsh resources (such as detritus or marsh-dependent species) in the  
710 closed areas, or open ocean effects on N and C particularly in the open to trawling areas. The

711 significance of this may be that the trawling ban has reduced the enrichment for these two  
712 isotopes, or that trawling enriches the carbon and nitrogen isotope signatures by adding fractional  
713 trophic levels to the open trawling ecosystem. This enrichment may occur due to the bycatch  
714 subsidy, which has been described previously by multiple authors. Fish discards from trawling  
715 are known to be consumed by blue crabs (Johnson 2003), birds (Navarro et al., 2009; Wickliffe  
716 and Jodice, 2010; Jodice et al., 2011), other fishes, amphipods, isopods, ophiuroids, cephalopods  
717 (Bozzano and Sardà, 2002), polychaetes (Groenewold and Fonds, 2000; Sanchez et al., 2000)  
718 and bottlenose dolphins (Broadhurst, 1998; Zollett and Read, 2006). Because of direct evidence  
719 of groups consuming bycatch in our system (personal observation and Johnson, 2003), we  
720 included aquatic and sediment bacteria, predatory gastropods, conch and whelks, blue crabs,  
721 other crabs, gulls, and sharpnose sharks as fish bycatch consumers. Further explorations of the  
722 subsidy provided by trawl discards, the impact of discard subsidy on stable isotope  $\delta^{15}\text{N}$  levels,  
723 and the influence of trawling on the ETL and trophic structure of Core Sound and other heavily  
724 fished ecosystems is warranted by our results. Analysis of stomach contents would corroborate  
725 or refute the importance of bycatch in the open trawl areas.

726         Other researchers have chosen to use a different formula for assessing the relationship  
727 between ETL and  $\delta^{15}\text{N}$ . Some authors have used a correlation approach for assessing the  
728 relationship between ETL and  $\delta^{15}\text{N}$  (Navarro et al., 2011), not making any assumption about  
729 which is a predictor and which is a response variable. A unique stable-isotope trophic position  
730 metric, TP, which computes an index for each species using the standardized difference from the  
731  $\delta^{15}\text{N}$  of an herbivorous species (Minagawa and Wada, 1984), has been used by various authors  
732 (Kline and Pauly, 1998; Dame and Christian, 2008; Milessi et al., 2010). The Minagawa and  
733 Wada formula uses a sessile herbivorous species as a basis of comparison for higher trophic

734 position species, adds 2 (accounting for the trophic position of herbivore base species) to the  
735 difference in  $\delta^{15}\text{N}$  values divided by a  $\delta^{15}\text{N}$  enrichment factor, estimated from previous studies  
736 (typically 3.4‰). In addition, most of the authors using the Minagawa and Wada (1984) method  
737 chose to predict ETL from  $\delta^{15}\text{N}$ , rather than the other way around. There is no clear reason why  
738 either one or the other should be the predictor rather than a response variable in the regression  
739 analysis. If the goal is to predict the ETL from  $\delta^{15}\text{N}$  measurements alone, without the  
740 construction of new models in the future, then the approaches chosen by these authors is  
741 appropriate. If the goal is to assess the validity of the model ETLs and determine the magnitude  
742 of the fractionation factor increases in  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  associated with a unit change in trophic  
743 level, then our approach is appropriate. In addition, it is a result that ignores variation in the  
744  $\delta^{15}\text{N}$  producer base species (a typical non-mobile herbivore is selected instead, but which  
745 herbivore is left to the investigator) and uses a fractionation enrichment factor for  $\delta^{15}\text{N}$  in the  
746 denominator of the formula that is assumed to be correct based on previous analysis. The  
747 fractionation enrichment factor has been changed by the various authors from the original 3.4‰  
748 per TL (Kline and Pauly, 1998; Kline, 1999) to 2.3‰ per TL (Dame and Christian, 2008) or to  
749 varied enrichment factors for different consumers (Nilsen et al., 2008). We think that the  
750 Minagawa and Wada approach is circular in its reasoning (one must know the trophic enrichment  
751 factor per trophic level to compare it to ETL). We did calculate TP using that equation, but  
752 found that there was poor agreement between TP and Ecopath-calculated ETL, particularly  
753 because the regression line does not pass through the origin (Figure 7). Atlantic menhaden may  
754 be a cause for the disagreement; the ETL is much lower than what would be predicted by the TP.  
755 This may be due to the diet matrix used in the models. Previous diet data by Hart (2008)  
756 indicated that detritus was a large proportion of the diet, and Ecopath assigns detritus to trophic

757 level 1. The treatment of detritus will be addressed shortly.

758           There was, however, good agreement between the stable isotope data and the Ecopath  
759 ETLs. We chose to directly compute the fractionation factor for  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  as the beta  
760 coefficient in our regression models using ETL as the predictor and stable isotope signatures as  
761 the response variable. The resulting effect size for each regression factor is the slope of the  
762 regression line (beta coefficients), providing an interpretable result in units of change in  $\delta^{15}\text{N}$  and  
763  $\delta^{13}\text{C}$  ‰. We obtained results that are reasonable and in agreement with published meta-analysis  
764 values, especially Vanderklift and Ponsard (2003). The Minagawa and Wada method is not  
765 recommended and should be interpreted with caution, as the fractionation factor is assumed to be  
766 true yet varies among published studies.

#### 767 *4.2. Effective trophic levels of bycatch and detritus*

768           Another confounding factor is the treatment of detritus and bycatch in Ecopath models.  
769 It was suggested by Cousins (1987) that detritus should not be considered trophic level 1;  
770 however, Ecopath assigns detritus, a non-living compartment, to trophic level 1. Bycatch,  
771 similarly, is also assigned to trophic level 1. Clearly, the bycatch species of shrimp trawls in  
772 Core Sound have ETLs greater than 1 and are being consumed by crabs and birds (Johnson,  
773 2006), allowing greater recycling of both C and N in the areas open to trawling. Both  $\delta^{15}\text{N}$  and  
774  $\delta^{13}\text{C}$  should increase for each consumer of bycatch as well as their predators. However, Ecopath  
775 ETLs will not reflect or agree with the stable isotopic composition of those organisms, since  
776 bycatch has been assigned to trophic level 1.

777           We believe it would be more appropriate to assign both detritus and bycatch to a trophic  
778 level greater than 1, taking into account the trophic level of the source organisms that make up

779 those compartments (Burns, 1989). For instance, in Core Sound, Johnson (2006) reported  
780 percentages of bycatch species from shrimp trawling. We calculated that the weighted average  
781 of those bycatch organisms (fish and invertebrates) could be as high as 2.78, nearly two trophic  
782 levels greater than that assigned by Ecopath. Thus, the ETL of any bycatch-consumer would be  
783 lower than what stable isotope analysis would predict. Detritus is often assumed to be composed  
784 of decaying plant matter, but may also include decomposing animal matter as well (all dead  
785 organisms). It may be more accurate to assign detritus to a higher trophic level to account for the  
786 source composition. Some groups of species exhibited a poor fit on the relationship between  
787  $\delta^{15}\text{N}$  and ETL. The most flagrant of these was the Atlantic menhaden, which had a very high  
788  $\delta^{15}\text{N}$  (11.59‰ in the closed model and 11.91‰ in the Open model) relative to the calculated  
789 Ecopath ETL (2.10 in Closed model and 2.09 in Open model). This discrepancy between the  
790 ETL and the stable isotope data draws attention to the treatment of detritus in Ecopath. Based on  
791 the stomach content analysis from the Core Sound ecosystem by Hart (2008), a sizeable portion  
792 of the menhaden diet comes from detritus, which is assigned to trophic level 1 in Ecopath. It has  
793 been previously observed that when detritus is a major component of a consumer's diet, then the  
794 Ecopath-calculated ETL will be lower than the  $\delta^{15}\text{N}$  (Gaedke and Straile, 1997; Dame and  
795 Christian, 2008; Milessi et al., 2010; Navarro et al., 2011). This is because detritus is most likely  
796 a mixture of producers and some higher trophic position consumer groups, and thus the mean  
797  $\delta^{15}\text{N}$  for detritus would be expected to be greater than the producers. The Ecopath assumption  
798 was that all these groups have the same trophic level (1.0), which may be a poor assumption. If  
799 the detritus were assigned a trophic level that reflected the origin of the material (plant, benthic  
800 invertebrate, or fish), then an increased ETL of detritus may bring the two methods of estimating  
801 trophic position into better alignment.



802 4.3. *Is there a difference in  $\delta^{15}\text{N}$  between areas open and closed to trawling?*

803 The comparison of  $\delta^{15}\text{N}$  values for the mesotrophic species (blue crabs, pinfish and spot)  
804 indicated that values were higher in areas open to trawling. In the open areas, these organisms  
805 have more access to shrimp trawl bycatch, so scavengers such as blue crabs can subsidize their  
806 diets with the bycatch. This result was previously demonstrated for blue crabs by Johnson  
807 (2006). For both the pinfish and the spot, stomach content analysis conducted by Hart (2008)  
808 showed that pinfish and spot ate more plant and seagrass in the closed areas and more epifauna  
809 and infauna in the open areas. This is consistent with our stable isotope results.

810 **5. Conclusions**

811 The stable isotope analyses of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  show good agreement with the Ecopath-  
812 calculated effective trophic levels of the four Core Sound Ecopath models. The results of this  
813 work indicate a  $\delta^{13}\text{C}$  trophic enrichment of 1.03‰ and a  $\delta^{15}\text{N}$  trophic enrichment of 2.52‰,  
814 which is similar to a host of studies comparing stable isotope analysis and effective trophic level.  
815 We believe that this is strong evidence to show that the stable isotope analysis has validated the  
816 Ecopath models for Core Sound. Overall, there was no significant difference in the  $\delta^{15}\text{N}$  values  
817 between open and closed areas. However, a closer inspection of three mesotrophic predators  
818 (blue crabs, pinfish and spot) indicated that those species did have higher  $\delta^{15}\text{N}$  values in the open  
819 areas, which suggests that shrimp trawling may have an effect on the diets of those consumers.

820 We believe that further work should be conducted to determine the diet of detritus-  
821 consumers in Core Sound, especially Atlantic menhaden. The discrepancy between Ecopath  
822 ETL and the stable isotope data is significant, and may require specialized studies focusing on  
823 diet and N metabolism of menhaden. Such studies may include laboratory feeding experiments

824 for diets of salt marsh and seagrass detritus, and zooplankton diets. There may also be  
825 microbiota in the Atlantic menhaden gut that may be adding a trophic level in terms of  $\delta^{15}\text{N}$ . We  
826 believe that experimental testing of these models (temporary closures/openings of open and  
827 closed areas, respectively) is a necessary next step to further explore differences in these  
828 management areas.

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1217

1218 **Figure Captions**

1219 Figure 1. Map of study sites in Core Sound, NC. There are six stations in the Closed to trawling  
1220 area (averaged for the Closed Ecopath model), and there are six stations in the Open to trawling  
1221 area (averaged for the Open Ecopath model). TCS = Thorofare Closed Shallow, TCD =  
1222 Thorofare Closed Deep, TOS = Thorofare Open Shallow, TOD = Thorofare Open Deep, NCS =  
1223 Nelson Closed Shallow, NCD = Nelson Closed Deep, NOS = Nelson Open Shallow, NOD =  
1224 Nelson Open Deep, JCS = Jarrett Closed Shallow, JCD = Jarrett Closed Deep, JOS = Jarrett  
1225 Open Shallow, JOD = Jarrett Open Deep.

1226

1227 Figure 2A. Ecopath flow diagram for the Closed trawling area model. Each compartment is  
1228 represented by a circle node that is scaled to biomass in  $g\ C/m^2$ . The nodes are labeled by  
1229 compartment name. Each arch represents flow between nodes, and the thickness of the line is  
1230 scaled to flow in  $g\ C/m^2/yr$ . The y-axis represents the Effective Trophic Level (ETL), with  
1231 producers, detritus and bycatch assigned to trophic level 1. Higher level consumers are found at  
1232 the top of the diagram.

1233

1234 Figure 2B. Ecopath flow diagram for the Open trawling area model. Each compartment is  
1235 represented by a circle node that is scaled to biomass in  $g\ C/m^2$ . The nodes are labeled by  
1236 compartment name. Each arch represents flow between nodes, and the thickness of the line is  
1237 scaled to flow in  $g\ C/m^2/yr$ . The y-axis represents the Effective Trophic Level (ETL), with  
1238 producers, detritus and bycatch assigned to trophic level 1. Higher level consumers are found at  
1239 the top of the diagram.

1240

1241 Figure 3. Biplots of  $\delta^{13}\text{C}$  (‰) and  $\delta^{15}\text{N}$  (‰) for samples collected in the open and closed to  
1242 trawling areas in Core Sound (left diagram) and for information taken from the literature (right  
1243 diagram). Solid circles represent samples collected in areas closed to trawling, and open circles  
1244 represent samples collect in areas open to trawling. Solid squares represent information taken  
1245 from the literature (Peterson & Howarth, 1987; Couch, 1989; Fogel et al., 1989; Bunn et al.,  
1246 1995; Currin et al., 1995; Deegan & Garritt, 1997; Bucci et al., 2007; Winemiller et al., 2007;  
1247 Jaschinski et al., 2008; Buchheister & Latour, 2010 and 2011).

1248  
1249 Figure 4. Regression of Ecopath-calculated Effective Trophic Level (ETL) versus  $\delta^{15}\text{N}$  (‰).  
1250 Solid circles represent samples from areas closed to trawling; open circles represent samples  
1251 from areas open to trawling.

1252  
1253 Figure 5. Regression of Ecopath-calculated Effective Trophic Level (ETL) versus  $\delta^{13}\text{C}$  (‰).  
1254 Solid circles represent samples from areas closed to trawling; open circles represent samples  
1255 from areas open to trawling.

1256  
1257 Figure 6. Comparison of  $\delta^{15}\text{N}$  (‰) for four species of mesopredator (blue crab, Atlantic  
1258 menhaden, pinfish and spot) from areas in Core Sound that are closed (black) and open (white)  
1259 to trawling. Error bars represent standard error of the mean.

1260  
1261 Figure 7. Regression of Trophic Position (TP) versus Ecopath-calculated Effective Trophic  
1262 Level (ETL). Solid triangles represent samples from areas closed to trawling; solid squares  
1263 represent samples from areas open to trawling.

**Table 1.** Compartment numbers, names and representative species/pooled taxa for the Core Sound Ecopath models.

Compartment Number and Name	Species or pooled taxa	
1	Phytoplankton	Multiple unidentified species
2	Microalgae_benthic	Multiple unidentified species
3	Macroalgae_benthic	<i>Codium, Ruppia, Ulva</i>
4	Drift algae	<i>Gracilaria, Sargassum</i>
5	Seagrass	<i>Zostera, Halodule</i>
6	Bacteria_aquatic	Multiple unidentified species
7	Bacteria_benthic	Multiple unidentified species
8	Meiofauna	harpacticoid copepods, foraminifera, nematodes, platyhelminths, tardigrades, ostracods, kinorhynchs, polychaetes, oligochaetes, amphipods
9	Zooplankton	Calanoid and cyclopoid copepods, holoplankton, meroplankton, other zooplankton
10	Jellyfish	<i>Aurelia aurita, Chrysaora quinquecirrha, Cyanea capillata</i>
11	Ctenophores	<i>Mnemiopsis leidyi</i>
12	Polychaetes_depfd	Families: Capitellidae, Cirratulidae, Maldanidae, Opheliidae, Orbiniidae, Paraonidae, Pectinariidae, Terebellidae, Syllidae
13	Polychaetes_suspdf	Families: Poecilochaetidae, Sabellidae, Spionidae
14	Polychaetes_pred	Families: Amphinomidae, Eucinidae, Glyceridae, Goniadidae, Lumbrineridae, Phyllodocidae, Nereididae, Nemertea
15	Bivalves_suspdf	Genera <i>Aesthenothaerus, Chione, Gemma, Lucina, Macoma, Nucula, Parvilucina, Tagelus, Tellina</i> , Family Lasaeid
16	Bay scallop	<i>Argopecten irradians</i>
17	Hard clam	<i>Mercenaria mercenaria</i>
18	Gastropods_depfd	<i>Astyris</i> sp., <i>Acteocina canaliculata</i>
19	Gastropods_pred	Genera <i>Eulimastoma, Polinices, Turbonilla</i> , Family Nassarid
20	Conchs/whelks	<i>Busycon</i> sp., <i>Pleuroploca gigantea</i>
21	Atl brief squid	<i>Lolliguncula brevis</i>
22	Bryozoans	<i>Bugula</i> sp., <i>Zoobotryon verticillatum</i>
23	Tunicates	<i>Styela</i> sp.
24	Sea cucumber	<i>Sclerodactyla briareus</i>
25	Brittlestars	<i>Ophioderma</i> sp.
26	Pericaridean crustaceans	caprellid and gammarid amphipods, isopods and cumaceans
27	Blue crabs	<i>Callinectes sapidus, C. similis</i>
28	Crabs_other	small crabs in Brachyurid Superfamilies: Majoidea, Portunoidea, Xanthoidea, Pinnotheroidea, and Paguroidea

Compartment Number and Name	Species or pooled taxa
29	Brown shrimp <i>Farfantepenaeus aztecus</i>
30	Pink shrimp <i>Farfantepenaeus duorarum</i>
31	White shrimp <i>Litopenaeus setiferus</i>
32	Shrimps_other mantis, grass, and snapping shrimp
33	Anchovies <i>Anchoa mitchilli</i> , <i>A. hepsetus</i>
34	Atl croaker <i>Micropogonias undulatus</i>
35	Atl menhaden <i>Brevoortia tyrannus</i>
36	Atl silverside <i>Menidia menidia</i>
37	Atl spadefish <i>Chaetodipterus faber</i>
38	Black drum <i>Pogonias chromis</i>
39	Bluefish <i>Pomatomus saltatrix</i>
40	Flounders (Paralichthids) <i>Paralichthys dentatus</i> , <i>P. lethostigma</i> , <i>P. albigutta</i>
41	Harvestfish/Butterfish <i>Peprilus paru</i> , <i>P. triacanthus</i>
42	Striped mullet <i>Mugil cephalus</i>
43	Pigfish <i>Orthopristis chrysoptera</i>
44	Pinfish <i>Lagodon rhomboides</i>
45	Pompano <i>Trachinotus carolinus</i>
46	Red drum <i>Sciaenops ocellatus</i>
47	Sheepshead <i>Archosargus probatocephalus</i>
48	Southern kingfish <i>Menticirrhus americanus</i>
49	Spanish mackerel <i>Scomberomorus maculatus</i>
50	Spot <i>Leiostomus xanthurus</i>
51	Spotted seatrout <i>Cynoscion nebulosus</i>
52	Weakfish <i>Cynoscion regalis</i>
53	Bottlenose dolphins <i>Tursiops truncatus</i>
54	Sea turtles <i>Caretta caretta</i>
55	Atl sharpnose shark <i>Rhizoprionodon terraenovae</i>
56	Smooth dogfish <i>Mustelus canis</i>
57	Cownose rays <i>Rhinoptera bonasus</i>
58	Other rays/skates clearnose skate ( <i>Raja eglanteria</i> ), smooth butterfly ray ( <i>Gymnura micrura</i> ), bullnose ray ( <i>Myliobatis freminvillei</i> ), southern stingray ( <i>Dasyatis americana</i> ), spotted eagle ray ( <i>Aetobatus narinari</i> )
59	Brown pelicans <i>Pelicanus occidentalis</i>
60	Cormorants Double-crested cormorant ( <i>Phalacrocorax auritus</i> )
61	Gulls black-backed ( <i>Larus marinus</i> ), herring ( <i>L. argentatus</i> ), and laughing gulls ( <i>Leucophaeus atricilla</i> )
62	Terns common ( <i>Sterna hirundo</i> ), royal ( <i>Thalasseus maximus</i> ), sandwich ( <i>T. sandvicensis</i> ) and least terns ( <i>Sternula antillarum</i> )

Compartment Number and Name	Species or pooled taxa
63 Shorebirds/waders	great egret ( <i>Ardea alba</i> ), great blue heron ( <i>A. 60erodias</i> ), semipalmated plovers ( <i>Charadrius semipalmatus</i> ), semipalmated sandpipers ( <i>Calidris pusilla</i> ), black-bellied plovers ( <i>Pluvialis squatarola</i> ), green heron ( <i>Butorides virescens</i> ), tri-colored heron ( <i>Egretta tricolor</i> ), black skimmer ( <i>Rynchops niger</i> )
64 Bycatch	Compartments 10,21,27,28, 32-37, 39-45,48-52,56,58
65 Detritus	



**Table 2.** Ecopath balanced model outputs for the open and closed trawling areas in Core Sound, NC, USA. ETL = effective trophic level, P/B = production to biomass ratio, Q/B = consumption to biomass ratio, EE = ecotrophic efficiency.

Group Number and Name	ETL		Biomass (gC/m <sup>2</sup> )		P/B (/yr)		Q/B (/yr)		EE	
	Closed	Open	Closed	Open	Closed	Open	Closed	Open	Closed	Open
1 Phytoplankton	1.00	1.00	3.5	3.405	126.5	126.5			0.043	0.056
2 Microalgae_benthic	1.00	1.00	0.08	0.22	103.3	103.3			0.678	0.740
3 Macroalgae_benthic	1.00	1.00	0.644	1.884	25	25			0.002	0.038
4 Drift algae	1.00	1.00	0.11667	0.05064	25	25			0.001	0.163
5 Seagrass	1.00	1.00	1.8	1.8	9.01	9.014			0.039	0.119
6 Bacteria_aquatic	2.00	2.00	0.1	0.1	33.6	33.55	65.4	65.4	0.836	0.932
7 Bacteria_benthic	2.00	2.00	0.7	0.7	36.5	36.5	71.25	71.25	0.631	0.615
8 Meiofauna	2.08	2.13	7.285	2.18	10	10	40	40	0.152	0.767
9 Zooplankton	2.14	2.11	0.188689	0.13498	22	26.8	67	67	0.280	0.554
10 Jellyfish	3.14	3.11	0.004121	0.03462	0.73	0.73	1.83	1.825	0.222	0.924
11 Ctenophores	3.31	3.31	0.007014	0.0114	6	6	30	30	0.819	0.789
12 Polychaetes_depfd	2.42	2.48	0.220752	0.71178	4.6	4.6	15.9	15.9	0.486	0.416
13 Polychaetes_suspfd	2.20	2.20	0.057198	0.09954	4.6	4.6	15.9	15.9	0.228	0.546
14 Polychaetes_pred	2.50	2.51	0.078893	0.2168	4.6	4.6	15.9	15.9	0.294	0.370
15 Bivalves_suspfd	2.20	2.05	0.219671	0.49266	4.6	4.6	15.9	15.9	0.611	0.852
16 Bay scallop	2.20	2.20	1.00E-05	0.00026	4.5	4.5	22	22	0.271	0.963
17 Hard clam	2.02	2.02	0.509729	2.15055	4.5	4.5	22	22	0.126	0.175
18 Gastropods_depfd	2.06	2.06	0.016443	0.01998	4.6	4.6	15.9	15.9	0.288	0.703
19 Gastropods_pred	3.07	2.98	0.047029	0.20817	4.6	4.6	15.9	15.9	0.261	0.318
20 Conchs/whelks	3.04	2.94	7.83E-05	0.00079	4.5	4.5	22	22	0.548	0.185
21 Atl brief squid	3.51	3.52	0.000172	0.0018	3	3	15	15	0.642	0.476
22 Bryozoans	2.10	2.10	0.205675	0.17101	7	7	27	27	0.014	0.158
23 Tunicates	2.36	2.36	0.002216	0.02564	7	7	27	27	0.018	0.666
24 Sea cucumbers	2.20	2.16	0.013376	0.42909	7	7	27	27	0.002	0.001
25 Brittlestars	2.21	2.21	0.054421	0.3375	7	7	27	27	0.007	0.009
26 Pericaridean crustaceans	2.20	2.20	0.004706	0.01048	7	7	27	27	0.938	0.754
27 Blue crabs	2.92	2.98	0.047824	0.66391	2.4	2.4	8.5	8.5	0.999	0.758

28	Crabs_other	2.89	2.87	0.000637	0.05709	2.4	2.4	8.5	8.5	0.949	0.970
29	Brown shrimp	3.06	3.11	0.00508	0.13129	5.38	5.38	19.2	19.2	0.481	0.431
30	Pink shrimp	3.10	3.11	0.005746	0.07479	5.38	5.38	19.2	19.2	0.324	0.962
31	White shrimp	2.14	2.16	0.003953	0.2683	5.38	5.38	19.2	19.2	0.337	0.317
32	Shrimps_other	2.61	2.64	0.001529	0.02406	5.38	5.38	18.6	19.2	0.590	0.873
33	Anchovies	3.07	3.07	0.005517	0.01198	4.49	3.825	16.65	16.7	0.953	0.985
34	Atl croaker	2.66	2.68	0.25401	0.08387	0.5	1.935741	8.1	8.7	0.162	0.950
35	Atl menhaden	2.10	2.09	0.33786	3.0633	0.83	0.448068	13	13	0.987	0.950
36	Atl silverside	3.10	3.11	0.001742	0.00451	3.13	3.34	15.65	16.7	0.887	0.959
37	Atl spadefish	3.33	3.32	0.000485	0.00758	0.81675	0.8745	4.95	5.3	0.810	0.498
38	Black drum	3.39	3.57	0.001537	0.01756	0.50625	0.55	4.05	4.4	0.913	0.257
39	Bluefish	3.59	3.59	0.013532	0.14971	0.73	0.73	5.62	5.84	0.699	0.557
40	Flounders (Paralichthids)	3.42	3.55	0.014578	0.02606	0.8	0.8	7.6	7.6	0.418	0.706
41	Harvestfish/Butterfish	3.15	3.16	0.004654	0.05543	0.96875	1.66	7.75	8.3	0.992	0.756
42	Striped mullet	2.00	2.00	0.000922	0.018	0.95	1.8	8	6.4	0.922	0.730
43	Pigfish	2.97	3.06	0.011252	0.12835	0.8	0.8	4	4	0.931	0.980
44	Pinfish	2.29	2.55	0.021145	0.08099	1.32	1.85	10.56	14.8	0.486	0.836
45	Pompano	3.34	3.59	0.000489	0.00641	1.38	1.8	11.04	14.4	0.544	0.837
46	Red drum	3.71	3.77	0.000266	0.00295	0.45	0.48	4.5	4.8	0.712	0.394
47	Sheepshead	3.55	3.82	0.001615	0.01804	0.76875	0.9375	6.15	7.5	0.758	0.678
48	Southern kingfish	3.56	3.73	0.006684	0.07741	0.8125	0.875	6.5	7	0.800	0.580
49	Spanish mackerel	3.55	3.48	0.000994	0.03262	0.7	0.7	6	6	0.881	0.835
50	Spot	2.64	2.54	0.749264	1.65863	1.2225	1.32	8.15	8.8	0.416	0.941
51	Spotted seatrout	3.49	3.67	0.014868	0.05627	1.1	1.095	6.94	6.935	0.468	0.860
52	Weakfish	3.42	3.40	0.045473	0.52515	1.1	1.095	6.94	6.935	0.780	0.516
53	Bottlenose dolphins	4.21	4.05	0.00405	0.00405	0.08	0.08	1	1	0.000	0.000
54	Sea turtles	3.57	3.62	0.03798	0.12478	0.08	0.08	1	1	0.000	0.000
55	Atl sharpnose shark	4.01	4.05	0.000494	4.00E-05	0.08	0.08	1	1	0.000	0.033
56	Smooth dogfish	3.78	3.93	0.00145	0.00883	0.08	0.08	1	1	0.000	0.088
57	Cownose rays	3.29	3.26	0.007397	0.02073	0.3	0.3	1	1	0.000	0.000
58	Other rays/skates	3.49	3.53	0.003613	0.00655	0.3	0.3	1	1	0.000	0.012
59	Brown pelicans	3.49	3.78	0.004113	0.00394	5.48	5.475	87.6	87.6	0.000	0.000

60	Cormorants	3.83	3.79	9.00E-05	0.00183	5.48	5.475	87.6	87.6	0.000	0.000
61	Gulls	3.77	3.70	0.000783	0.00078	5.48	5.475	87.6	87.6	0.000	0.000
62	Terns	3.59	3.75	0.000931	0.0007	5.48	5.475	87.6	87.6	0.000	0.000
63	Shorebirds/waders	3.36	3.52	0.003973	0.00013	5.48	5.475	87.6	87.6	0.000	0.000
64	Bycatch	1.00	1.00	1.00E-05	0.6958					0.007	0.395
65	Detritus	1.00	1.00	266.7621	125.9948					0.520	0.368

**Table 3.** Flows from detritus to Lindeman trophic levels in areas open and closed to trawling in Core Sound, NC. Flows are given in gC/m<sup>2</sup>/yr. Imported and exported detrital flows, flows from each trophic level to detritus, flow from detritus to respiration and system throughput at each Lindeman trophic level are also given.

<u>Closed</u>						
Trophic Level	Import	Consumption by predators	Export	Flow to detritus	Respiration	Throughput
VIII		2.68E-08	3E-10	1.777E-07	4.929E-07	6.977E-07
VII		1.8983E-06	2.19E-08	2.34712E-05	6.27615E-05	8.8153E-05
VI		7.43358E-05	1.1158E-06	0.000804539	0.002147072	0.00302706
V		0.002300475	2.9292E-05	0.02051388	0.05336944	0.07621308
IV		0.05376733	0.00028113	0.3860337	0.8525614	1.2926433
III		0.9576154	0.00101195	11.868568	11.878126	24.705322
II		23.467737	0.00049104	169.31525	150.39561	343.17908
Detritus	0	341.35999	316.11447	0	0	657.47449
Sum	0	365.84149	316.11627	181.59119	163.18188	1026.7308

<u>Open</u>						
Trophic level	Import	Consumption by predators	Export	Flow to detritus	Respiration	Throughput
VIII		1.1345E-06	3.73E-08	1.50732E-05	4.12506E-05	5.74955E-05
VII		5.99477E-05	1.74E-06	0.000526691	0.001387832	0.001976209
VI		0.001696868	4.64E-05	0.01115121	0.02852793	0.04142242
V		0.03300074	0.000865	0.1679426	0.3897832	0.5915912
IV		0.4557256	0.008172	1.6344895	3.0525661	5.1509523
III		4.2771468	0.030895	15.153751	19.624256	39.086048
II		36.20908	0.021421	86.832603	108.74488	231.80797
Detritus	0	221.69559	378.3477	0	0	602.4574
Sum	0	262.6723	378.4091	103.80048	131.84145	879.13745

**Table 4.** Average  $\delta^{15}\text{N}$  values and standard error of the mean (SEM) for all samples. n = sample size. Difference is the Open – Closed  $\delta^{15}\text{N}$  means. POM\* = Particulate Organic Material in water included phytoplankton and heterotrophic plankton species smaller than 90  $\mu\text{m}$ .

Trawling area	Closed			Open			Difference
Compartment	n	Mean $\delta^{15}\text{N}$	SEM $\delta^{15}\text{N}$	n	Mean $\delta^{15}\text{N}$	SEM $\delta^{15}\text{N}$	Mean $\delta^{15}\text{N}$
POM*				6	6.19	0.634	
Benthic microalgae	5	4.03	0.197	4	3.67	0.273	-0.36
Benthic macroalgae				7	5.8	0.410	
Drift algae	1	4.39		4	6.3	0.619	1.91
Seagrass ( <i>Halodule</i> )	1	2.93					
Zooplankton	6	7.53					
Hard clam	2	9.52	0.140	2	8.66	0.095	-0.86
Atl brief squid	12	12.81	0.537	2	13.67	1.000	0.86
Bryozoan	1	6.51		4	6.64	0.349	0.13
Tunicate	5	8.38	0.354	5	7.99	0.191	-0.39
Blue crab	12	9.32	0.087	4	10.22	0.260	0.90
Brown shrimp	11	8.67	0.204				
Anchovy	16	13.04	0.303	11	13.29	0.201	0.25
Atl croaker	2	12.26	0.030				
Atl menhaden	12	11.59	0.217	7	11.91	0.394	0.32
Atl spadefish	1	11.41		1	11.43		0.02
Bluefish	1	14.53		4	14.25	0.300	-0.28
Flounder	2	10.76	0.450	2	11.29	0.730	0.53
Pigfish	1	8.82		3	11.17	0.419	2.35
Pinfish	12	10.28	0.210	11	11.07	0.273	0.79
Spot	12	10.78	0.238	10	11.64	0.114	0.86
Atl sharpnose shark	1	12.08		1	12.64		0.56
Sm dogfish	2	12.36	0.715	3	13.61	0.765	1.25
Ray, other	3	10.42	0.306	15	11.43	0.269	1.01

**Table 5.** Generalized linear model regression estimates of effect size for Ecopath effective trophic level and trawling area (Open versus Closed) as predictors of  $^{15}\text{N}$  (‰) stable isotope data from Core Sound, NC. Only compartments that were sampled for  $^{15}\text{N}$  (‰) in both Open and Closed areas were included in this model.

Factor	$^{15}\text{N}$ ‰ Effect size coefficients	df	F-ratio	P – value
Constant	3.912	1		
Ecopath Effective Trophic Level	2.518	1	193.117	<0.000001
Trawling area	0.107	1	0.044	0.835
Effective Trophic Level * Trawling area	-0.043	190	0.057	0.811

**Table 6.** Generalized linear model estimates of effect size for Ecopath effective trophic level and trawling area (Open versus Closed) as predictors of  $^{13}\text{C}$  (‰) stable isotope data from Core Sound, NC.

Factor	$^{15}\text{N}$ ‰ Effect size coefficients	df	F-ratio	P – value
Constant	-20.715	1	1050.31	<0.000001
Ecopath Effective Trophic Level	1.026	1	19.947	0.000013
Trawling area	-0.972	1	2.315	0.130
Effective Trophic Level * Trawling area	0.243	218	1.121	0.291

**Table 7.** Mean values of stable isotopes analyzed in trawling management areas in Core Sound analyzed using MANOVA.

	Closed to Trawling		Open to Trawling	
	$\delta^{15}\text{N}\text{‰}$	$\delta^{13}\text{C}\text{‰}$	$\delta^{15}\text{N}\text{‰}$	$\delta^{13}\text{C}\text{‰}$
Means	10.32	-18.28	10.66	-17.64
Standard Error	0.167	0.227	0.181	0.246

MANOVA Statistic	Value	F-Ratio	df	p-Value
Wilks's Lambda	0.972088	3.129792	2, 218	0.045698
Pillai Trace	0.027912	3.129792	2, 218	0.045698
Hotelling-Lawley Trace	0.028714	3.129792	2, 218	0.045698



Figure1

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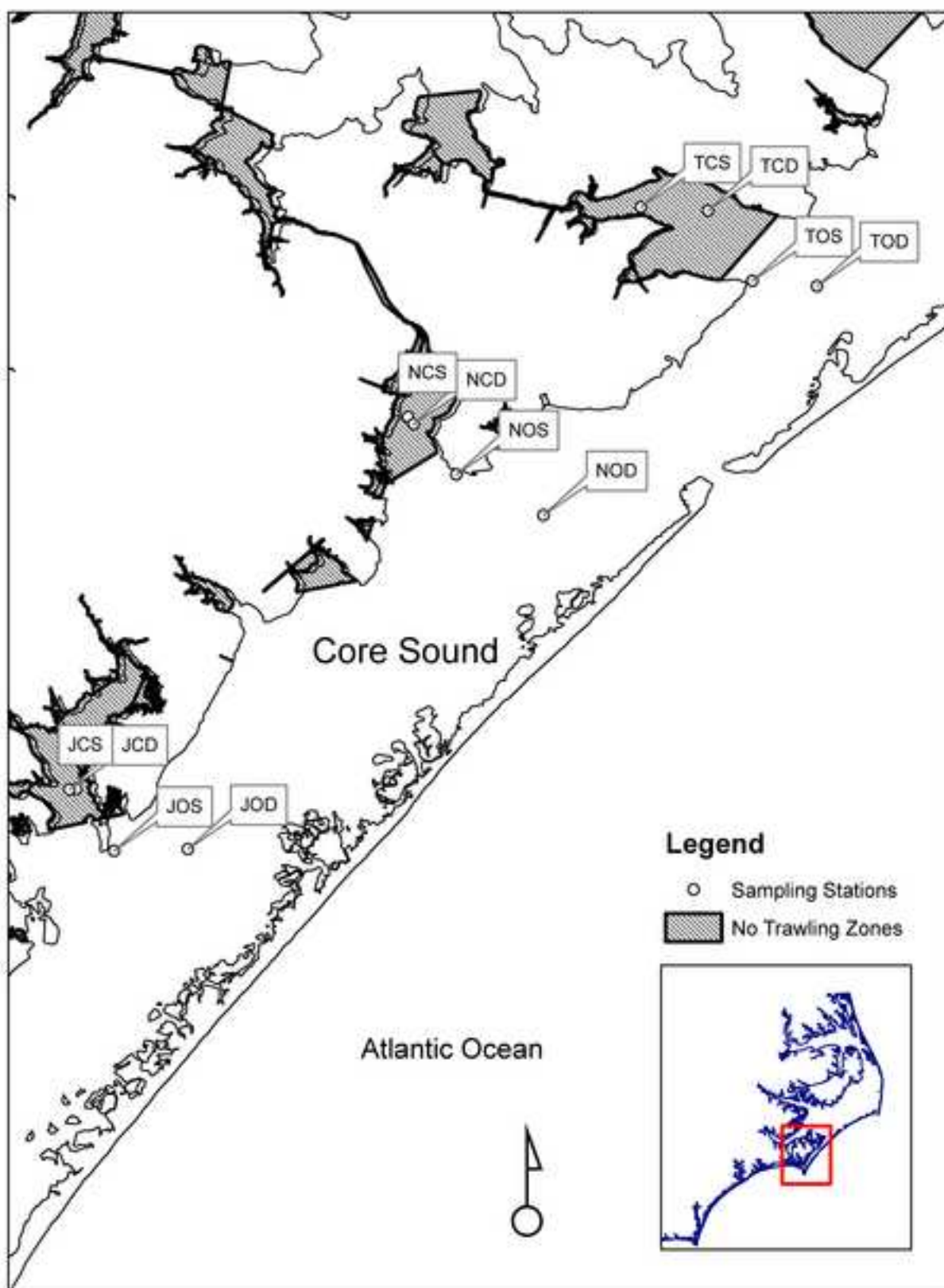








Figure4

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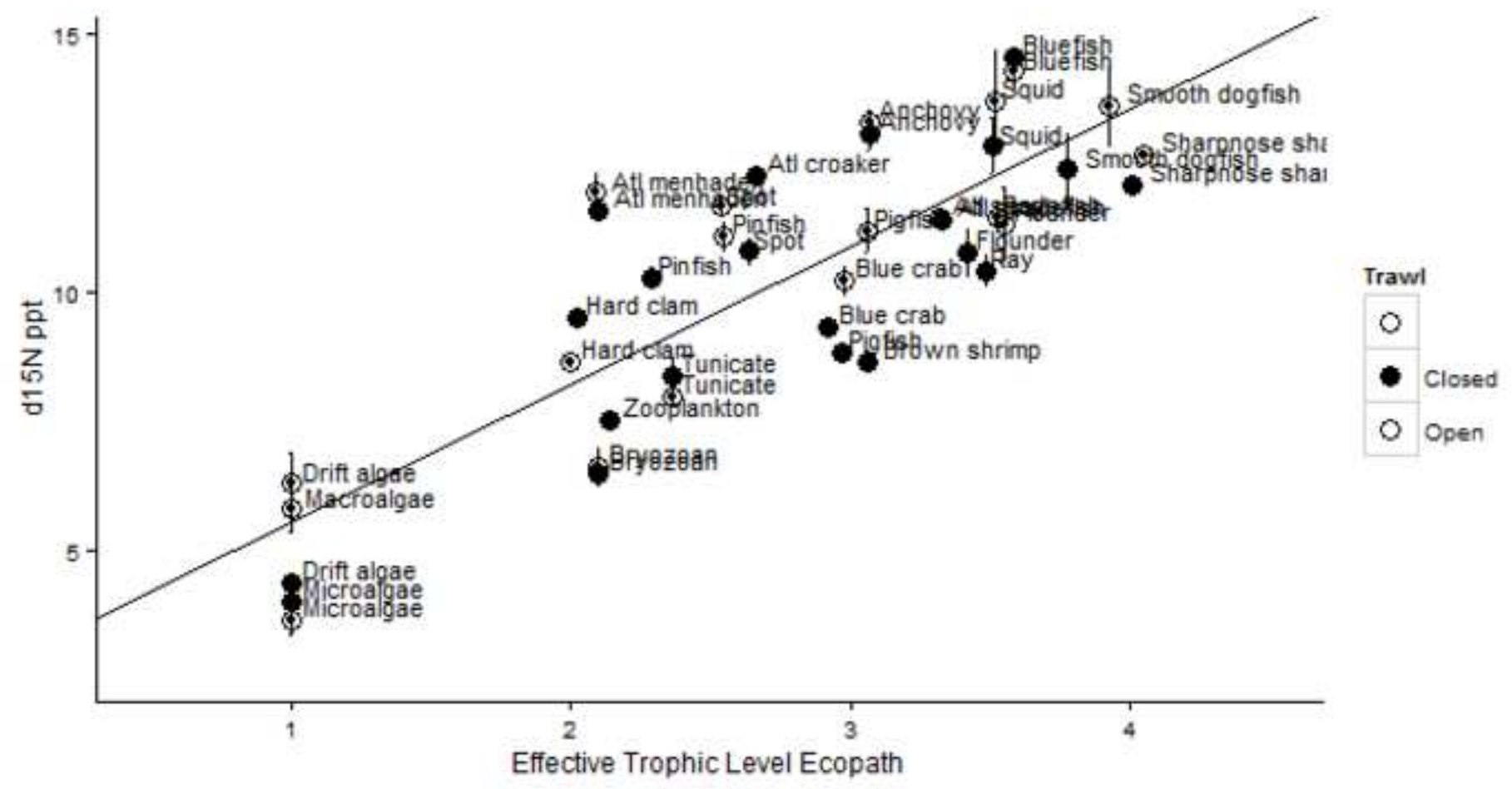


Figure5

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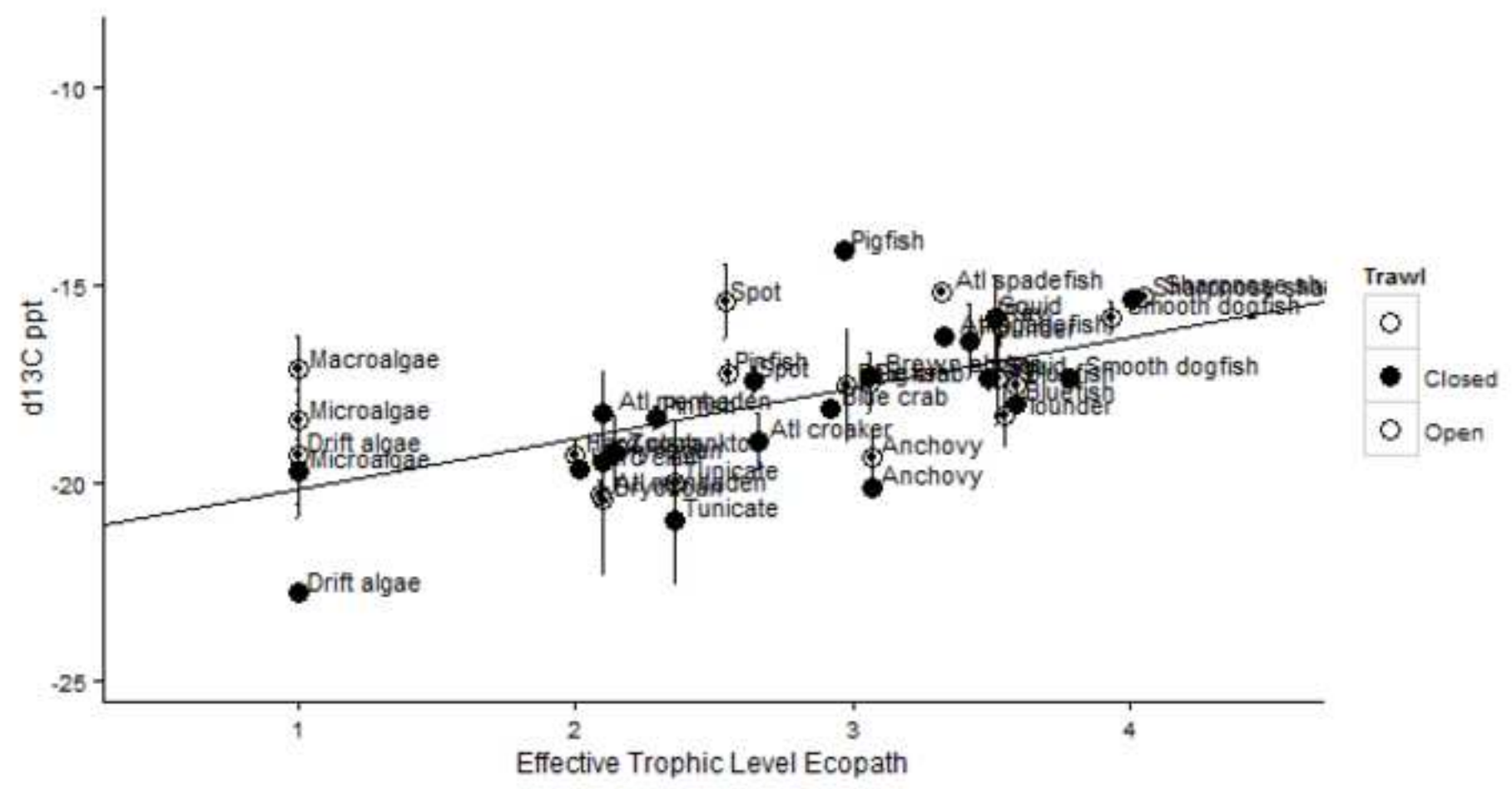


Figure6

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