

1 Cascading Effects of Shrimp Trawling: Increased Benthic Biomass and Increase in Net Primary
2 Production

3
4 Luczkovich, Joseph John¹ East Carolina University, Department of Biology,
5 Institute for Coastal Science and Policy, Greenville, North Carolina, United States, 27858
6 luczkovichj@ecu.edu
7 +01-252-328-9402 (phone)
8 +01-252-328-4265 (fax)

9
10 Deehr, Rebecca A², East Carolina University, Coastal Resources Management Program,
11 Greenville, North Carolina, United States, 27858

12
13 Hart, Kevin J³, East Carolina University, Department of Biology,
14 Greenville, North Carolina, United States, 27858

15
16 Clough, Lisa M⁴, East Carolina University, Department of Biology,
17 Greenville, North Carolina, United States, 27858

18
19 Johnson, Jeffrey C⁵, East Carolina University, Department of Sociology,
20 Institute for Coastal Science and Policy
21 Greenville, North Carolina, United States, 27858

22
23

24 **Running Head:** Cascading Effects of Shrimp Trawling

¹ Corresponding author

² Present Address: Hutchison School, Science, Middle School

Memphis, Tennessee, United States, bdeehr@hutchisonschool.org

³ Present Address: NC Department of Environmental Quality, Coastal Management,
Washington, North Carolina, United States, kevin.hart@ncdenr.gov

⁴ Present Address: Head, Ocean Section, Division of Ocean Sciences

National Science Foundation, Arlington, VA, United States, lclough@nsf.gov

⁵ University of Florida, Anthropology Department, Gainesville, Florida, United States, johnsonje@ufl.edu

25

26 **Abstract**

27 Trawling has been shown to cause high mortality of discarded species (bycatch) and short-term
28 ecological disturbance to bottom communities in coastal systems, resulting in lowered benthic
29 biomass. Here we report evidence of a trawling-induced trophic cascade resulting in an increase
30 in biomass of benthic polychaetes after the end of the shrimp trawling season in areas open to
31 trawling in North Carolina (USA). Using comparative measurements of abundance of bycatch
32 species and benthos in open and closed trawling management areas and Ecopath network
33 modeling, we show that trawling in the open area has led to increases in deposit-feeding
34 polychaetes and decreases in bycatch species (fish and crabs) that are benthic predators on the
35 polychaetes. We conclude that proposed management actions to reduce the shrimp trawl fishery
36 effort will influence other net and trap fisheries for southern flounder and blue crabs indirectly,
37 as revealed by our network models, and the proposed trawling ban may lead to improvements in
38 other valuable fisheries.

39 **Key words:** blue crabs *Callinectes sapidus*, bycatch, ecological network analysis, ecosystem
40 simulation, southern flounder *Paralichthys lethostigma*, polychaetes

41 **Introduction**

42 Globally, bottom trawling is one of the most important types of fishing gear, accounting
43 for 17 % of the global catch of all species in 1990; this is especially true for wild shrimp and
44 prawn fisheries globally, with trawls accounting for 87% of the harvest (1). Trawls have been
45 used since the late 1800's, first on sailing vessels, then on steam-powered vessels, then on
46 motorized vessels with an increasing amount of fishing power or effort (2). Bottom trawling has
47 been shown to alter marine ecosystems by reducing the abundance of trawled species and
48 disturbing bottom habitats (2,3). Previous studies (4–9) suggest that the benthos should be
49 reduced by action of the trawls, which dig into and ride over the bottom, causing a physical
50 bottom disturbance. For example, a meta-analysis of 59 experimental and observational studies
51 (4) revealed that otter trawling should produce on average a 31% decrease in benthic population
52 densities after a single short-term trawling disturbance event, with this effect being habitat-
53 dependent and somewhat larger (57%) in muddy bottom habitats or smaller (21%) in sandy
54 habitats. That same study revealed variation in the response of taxa of benthos to short-term
55 trawling disturbance effects: corals and crustaceans showed the largest (75 %) declines, whereas
56 polychaetes, ophiuroids, holothurians, echinoids, and gastropods showed intermediate (50-75%)
57 declines, bivalves and sponges showed 40% declines, and asteroids and oligochaetes were most
58 resistant to trawling and showed the smallest declines (20-30%); all species examined showed
59 declines, and none showed increases relative to the controls. In contrast with this meta-analysis,
60 here we report an increase in benthic biomass in areas open to shrimp trawling in a North
61 Carolina estuary when compared with no-trawling areas and in open areas after the trawling
62 season has largely ended. In addition, an ecosystem model was developed for examining the
63 effects of shrimp trawling, which simulated this increase in benthos biomass. The model further

64 indicated an increase net primary production, suggesting a previously unrecognized beneficial
65 effect of bottom trawling.

66 The trawling impacts on the benthos are also expected to cause or can be caused by
67 fishing-induced trophic cascades. Trophic cascades are indirect community and ecosystem
68 impacts that occur due to dramatic changes in abundance of a species at one trophic level (i.e.,
69 predator removal) that affect species at two or more trophic levels. Fishing practices, such as
70 trawling, seining, spearing, and even recreational fishing, have been implicated in causing
71 trophic cascades in marine ecosystems (10–16). However, trawling in soft-bottom ecosystems
72 such as North Carolina (USA) estuaries has not been demonstrated previously to cause a trophic
73 cascade. Trawling for shrimp is widely practiced in the southeastern USA and elsewhere (17–
74 21) and has a large potential impacts from sediment re-suspension, removal of bycatch and
75 associated discards, and has great potential to cause trophic cascades.

76 The questions we ask here are what happens to an entire estuarine ecosystem where
77 trawling has taken place over many years? Does the benthos show declines as previously
78 described in short-term trawling experiments? How do the populations of higher trophic level
79 predators respond? Is there a trophic cascade that occurs when shrimp trawling on soft-bottoms
80 is practiced repeatedly? And can we simulate and verify these dynamic processes? We report a
81 200% measured increase in benthos in a heavily trawled area at the end of the shrimp trawling
82 season when it is compared to nearby, otherwise similar, areas closed to shrimp trawling in terms
83 of the density and biomass of benthic polychaete worms. Furthermore, small fish and crab
84 benthos-feeding predators, commonly caught in shrimp trawls and discarded as bycatch, were in
85 lower abundance in trawled areas relative to untrawled areas after the trawling season, which
86 implies that trawls can act like large predator on the by-catch species, removing them, and

87 initiating a trophic cascade. Finally, we used ecosystem trophic network visualizations and
88 simulation models to show that this increase in benthos after trawling is likely to be due to the
89 cumulative effects of a trawling-induced trophic cascade, due to the removal of predators during
90 trawling and a scavenger subsidy effect due to the discarded bycatch from trawling, which feeds
91 the benthos and crabs. This new result shows that discards and trawling disturbance may have
92 different long-term effects than short-term trawling experiments have shown at the whole-system
93 level.

94 **Methods**

95 **Ecopath Modelling Procedures**

96 The ecological network models were built in Ecopath with EcoSim v 6.4 using data that
97 we collected on various species across the trophic spectrum and group biomasses and those
98 biomasses estimated from commercial harvest data. Commercial harvest data were obtained from
99 the North Carolina Division of Marine Fisheries (NCDMF) Trip-Ticket Program database for
100 2006-2008, including all commercial species harvested in the Core Sound Management Area.
101 The NCDMF trip ticket is a form used by fish dealers to report commercial landings information.
102 Trip tickets collect information about the fisherman, the dealer purchasing the product, the
103 transaction date, the number of crew, area fished, gear used and the quantity of each species
104 landed for each trip.

105 Ecopath network models were built for the Core Sound Management Area, using data
106 from 2007 measured in the spring and fall seasons (before and after the shrimp trawling peak in
107 July) for areas open to trawling and during the spring and fall seasons for closed trawling areas, a
108 total of four seasonal models. Two additional annualized models were created, with identical
109 compartments, one for areas open to trawling and one for areas closed to trawling. Each model

110 had 63 living compartments with the biomasses (in g C m^{-2}) of various species (with some
111 compartments comprised of aggregated species groupings) and two compartments with non-
112 living carbon (bycatch and detritus) (Table 2). Bycatch data were obtained from measurements
113 taken as part of an observer program in the shrimp fishery of Core Sound (22). Detritus was
114 directly measured (see below).

115 Table 1. Biomass (g C m^{-2}) of each compartment in the Core Sound Ecopath models. Table
116 arranged by compartment number.

117

118 To construct the Ecopath models of Core Sound, compartments encompassing everything
119 from detritus to birds were sampled. The “currency” for these models was grams of carbon per
120 square meter (g C m^{-2}) for biomasses and grams of carbon per square meter per year ($\text{g C m}^{-2} \text{ yr}^{-1}$)
121 for flows. For this study, biomass was measured directly for most compartments, and a diet
122 matrix was partially constructed from the diet data obtained in Core Sound during the study
123 period by Hart (23) for a limited number of fish species. Samples were collected in the spring,
124 prior to the peak of commercial shrimp trawling, and then again in the fall, after the peak
125 trawling activity ended, in areas open and closed to commercial shrimp trawling. The end result
126 was four models, representing Spring Open, Spring Closed, Fall Open and Fall Closed. Details
127 for all Ecopath modeling, measurements and references provided in the tables listed here are
128 given in Deehr (24)

129 **Measurements of Biomass in Open and Closed Trawling Areas**

130 Organisms’ biomasses or densities were measured at locations in the open and closed
131 trawling areas with similar temperature, salinity, dissolved oxygen, water depth and substrate
132 characteristics at 12 sites in Core Sound, NC (25,24) (Figure 1). We measured dry biomass
133 converted to g C m^{-2} for all benthic groups (macrofauna and meiofauna), zooplankton,

134 seagrasses, algae, small fishes from gill nets (three replicated nets with five 23-m panels of
135 stretch monofilament mesh [8.9 cm, 10.2 cm, 11.5 cm, 12.7 cm and 13.9 cm] were deployed for
136 upwards of six hours and checked at least every two hours) and bottom trawls (head rope of 3.2-
137 m, a body net stretch mesh of 1 cm, a cod-end stretch mesh of 0.5 cm, a tickler chain, and trawl
138 doors measuring 90 cm by 46 cm) deployed for 2 min at a constant speed, three times at each
139 site. All biomass measurements were converted to dry weight and g C by multiplying by 0.15
140 (26).

141

142 *Benthic Macrofauna*

143 At each of the 12 sites, benthic cores (inside diameter of 9.5 cm) were collected by
144 SCUBA divers and pushed manually into the substrate to a depth of 10 cm. Three cores each
145 were combined to form one sample that was processed for benthic macrofauna; triplicate
146 samples were collected in this manner (a total of nine cores at each site). Three additional cores
147 were collected at each site to obtain biomass measurements for meiofauna. Three cores each
148 were combined to form one sample that was processed for benthic macrofauna; triplicate
149 samples were collected in this manner (a total of nine cores). Samples were passed through a
150 500- μ m sieve in the field, and all retained specimens were preserved in 10% buffered formalin
151 with Rose-Bengal stain until processed in the laboratory. All specimens were identified to the
152 lowest taxonomic level using a dissecting microscope, then dried at 60°C for 48 hr, weighed to
153 the nearest 0.00001 g, then converted to carbon by multiplying dry weight by 0.40(26).

154 *Benthic Meiofauna*

155 The remaining three benthic cores were sub-sampled for meiofauna, detritus, benthic
156 microalgae and sediment grain size. Meiofauna were collected from each core with a 2-cm
157 diameter syringe plunged to a depth of 3 cm, and preserved in 10% buffered formalin with Rose-
158 Bengal stain. Meiofauna were separated from sediments using Ludox, following the method of
159 Burgess (2001), passed through stacked 500- μ m and 63- μ m sieves (to exclude
160 macroinvertebrates), and all specimens retained on the 63- μ m sieve were identified to lowest
161 taxonomic level using Higgins and Thiel (27). All individuals (by taxa) were converted to g C
162 from wet weight/individual and/or g C/individual from several sources (24,28).

163 *Benthic Detritus*

164 Detritus samples were collected from each core using a 1-cm diameter syringe pushed to
165 a depth of 1 cm and stored on ice in a dark cooler then frozen until processed in the laboratory.
166 Loss on ignition (LOI) was used to determine the ash-free dry mass of organic matter(29). Since
167 the sample potentially included numerous sources of organic matter, values of sediment
168 microalgae, sediment bacteria and meiofauna biomasses (also calculated for this study) were
169 subtracted from the LOI-obtained measurement of organic carbon. Dry weights were converted
170 to g C by multiplying by 0.58(26).

171 *Benthic Microalgae*

172 Similarly, benthic microalgae biomass was sampled from each core using a 1-cm
173 diameter syringe plunged to a depth of 1 cm. Benthic microalgal biomass was measured using
174 fluorometry as the amount of chlorophyll *a* content in the sample. Chlorophyll *a* was converted
175 to g C by multiplying by 0.47(26). Only the samples collected during the spring (for open and

176 closed sites) were processed in the laboratory; thus, there is no seasonal difference between
177 benthic microalgae biomass.

178 *Infaunal Mollusks*

179 A clam rake was used to collect mollusks from sites in shallow water. Four 2.32-m²
180 transects (total area of 9.29 m²) were raked at the six shallow sites. Mollusks were stored on ice
181 until returned to the laboratory for positive identification and measurements. All specimens were
182 removed from the shells and dried in an oven at 60°C for 48 hr. Dry weight mass was converted
183 to g C by multiplying by 0.40(26).

184 *Benthic Primary Producers*

185 The biomass of primary producers (macroalgae, drift algae, seagrasses) was measured
186 using various techniques. Seagrass biomass estimates were obtained from an ongoing
187 submerged aquatic vegetation study in Jarrett Bay using 0.15-m cores and quadrats, as well as
188 remote sensing, and video and acoustic methods. Data from a site in the area closed to trawling
189 in Jarrett Bay were collected from June – September 2010; thus, seagrass measurements for this
190 project differ by season, but not by area. The values for seagrass biomass are only from the
191 closed areas, but also used for the open areas of the Core Sound models. Drift algae and
192 macroalgae biomass estimates were calculated from algae collected in otter trawls for sites open
193 and closed to trawling, but data were only collected in the fall. Thus, there are no seasonal
194 differences in biomass for the models (the same values for fall were used for spring). Otter trawl
195 distances were obtained from a digital echo-sounder (see Nekton below).

196 *Zooplankton*

197 Three replicates of zooplankton samples were collected at each site using 90- μ m mesh
198 bongo plankton nets (net diameter of 28 cm), towed for 1 min at a constant speed. Continuous
199 GPS locations throughout the tows were recorded to avoid crossing previous tow tracks and to
200 obtain the tow distances. A General Oceanics flow meter with the low-speed rotor was attached
201 to the bongo net to measure the volume of water towed. All zooplankton samples were fixed in
202 10% buffered formalin for storage until processing. Any ctenophores or other large gelatinous
203 zooplankton were removed before fixing. To estimate the abundance of ctenophores, separate 1-
204 min tows were conducted. Any ctenophores collected in the tows were counted and recorded on
205 the boat. Total counts of ctenophores were converted to biomass [assumed one ctenophore had
206 wet weight of 1 g, multiply by 0.20 to convert to dry weight then g C] for use in the Ecopath
207 model. In the laboratory, all large zooplankton specimens ($\geq 500 \mu\text{m}$) were counted and dried at
208 60°C for 48 hr to measure dry mass, which was converted to g C by multiplying by 0.40. Using
209 a Folsom splitter, the remainder of the samples were split three times, and the 1/8 sample was
210 suspended in 500 mL of water. Five 10-ml subsamples were taken with Hensen-Stempel
211 pipettes and passed through a series of sieves (425 μm , 250 μm , 150 μm , and 75 μm). The
212 contents of each sieve were counted in a Ward wheel, identified to lowest taxonomic level,
213 summed and total counts were multiplied by 80 to obtain the whole sample count. This method
214 subsampled at least 100-300 individuals at a time, an amount recommended by several sources to
215 avoid potential errors associated with repetitive Folsom splitting of samples. The entire contents
216 of each sieve were dried at 60°C for 48 hr to calculate dry mass, and then converted to g C by
217 multiplying by 0.40 (26).

218 *Phytoplankton*

219 Water samples were collected at each site to measure phytoplankton. Carboys (1 L³)
220 were filled with surface water at each station and stored on ice in a cooler until returned to the
221 laboratory. In the laboratory, water was filtered through glass microfiber filters (47 mm, GF/C).
222 Pigment extraction was done with a mixture of 45% acetone/45% methanol/10% deionized
223 water, then kept in a freezer for 12-24 hr, using the methods of Strickland and Parsons (30).
224 Initial readings were done on the fluorometer, then 10% HCl was added, to correct for
225 pheophytin pigments, and then read again. Chlorophyll *a* values were then converted to g C by
226 multiplying by 0.47(26).

227 *Nekton*

228 To sample fishes and other forms of nekton, an otter trawl similar to the one used by NC
229 DMF was deployed. The protocols that follow are from Hart (23). The otter trawl had a
230 headrope of 3.2-m, a body net stretch mesh of 1-cm, a cod-end stretch mesh of 0.5-cm, a tickler
231 chain, and trawl doors measuring 90 cm by 46 cm. Trawls were deployed for 2 min at a constant
232 speed, three times at each site. Trawl tow lengths were determined using a scientific echo-
233 sounder operated simultaneously with the trawl deployment. The BioSonics DTX echo-sounder
234 was used to assess bathymetry, bottom substrate, and fish abundance in front of the trawl. The
235 echo-sounder was interfaced with a JVC GPS receiver and a Panasonic Toughbook CF-29 laptop
236 computer so that precise trawl tracks and depths were recorded to a hard drive (23). All
237 specimens retained by the trawls were euthanized and preserved in 10% buffered formalin for
238 identification and measurement in the laboratory. When necessary, some samples were weighed
239 in the field using spring scales. In the laboratory, all specimens were identified, measured for

240 length and wet weight, and stomachs of selected fishes were removed for diet analyses. All
241 biomass measurements were converted to dry weight and g C by multiplying by 0.15 (26).

242 Experimental gill nets were used to collect larger, faster fishes not captured by the otter
243 trawl. Five 23-m panels of different stretch mesh (8.9 cm, 10.2 cm, 11.5 cm, 12.7 cm and 13.9
244 cm) were deployed for upwards of six hours and checked at least every two hours. All
245 specimens were euthanized, tagged and stored on ice in a cooler until brought back to the
246 laboratory or field processing site. Specimens were identified, measured and stomachs were
247 removed for diet analyses. All biomass measurements were converted to g C by multiplying by
248 0.15 (26).

249 Additional fish and shellfish data were obtained from the North Carolina Division of
250 Marine Fisheries (NCDMF) Program 120 Juvenile Trawl Survey (Katy West, personal
251 communication, NCDMF, 3441 Arendell St, Morehead City, NC 28557 USA). Trawl surveys
252 have been conducted in the spring in nursery areas to inform management decisions on the
253 opening and closing dates of various fisheries. Data for several species of fish and shrimps were
254 included in the construction of the models in this study.

255 *Fisheries Data*

256 Unpublished NCDMF Trip Ticket data from April-June 2006 and 2007 (averaged to
257 represent Spring) and August-October 2006 and 2007 (averaged to represent Fall) for the six
258 fishing gears described in Chapter One (shrimp trawls, skimmer trawls, pound nets, crab pots,
259 haul seines and gill nets) were included in the models for this study. If a landings report was
260 made but unavailable (due to confidentiality), an average of years 2001-2005 for that gear type,
261 species and month (in 2006 or 2007) was used. The area of Core Sound waters was estimated to
262 be 72,000 acres (291,272,662 m²). The average catch (in wet weight pounds) was converted to

263 grams of wet weight then multiplied by 0.15 (26) to convert g C dry weight, and finally divided
264 by the area of Core Sound (resulting in g C/m² for each species by gear type). Because trawlers
265 cannot operate in closed areas or in known seagrass beds, the area for calculating shrimp trawl
266 and skimmer trawl catches was reduced by 50% (145,686,831 m²). These values represent the
267 biomass of each species that was added to our own data collections (from juvenile trawls and gill
268 nets). To calculate fisheries trip averages (for fisheries landings data in Ecopath), we used the
269 pounds/trip average of the time periods listed above and calculated g C for those data. To
270 convert fisheries trip averages to g C/m², we estimated the area fished by each gear type, based
271 on our knowledge of the gears, the information provided by the NCDMF, and shrimp trawl and
272 skimmer trawl bycatch studies (**Error! Reference source not found.**).

273 Information about shrimp and skimmer trawl landings were incorporated only in the
274 models representing areas open to trawling. Data about the landings of the other four gears were
275 split 10% in the Closed models and 90% in the Open models, based on the relative areas of
276 closed and open waters in the study, respectively.

277 Bycatch from trawls was also included in the models for this study. Bycatch data for
278 shrimp and skimmer trawls were available from local studies conducted in and near Core Sound
279 (17,22,31). These data are included in (**Error! Reference source not found.**). While bycatch is
280 known to occur with the other four gear types, studies reporting bycatch statistics for gill nets,
281 pound nets, haul seines and crab pots were insufficient for inclusion in this study.

282 Trip ticket landings data were organized using six fishery gear types (crab pots, haul
283 seines, pound nets, gill nets, skimmer trawls and shrimp trawls) that were included in the
284 Ecopath models as fishing fleets. Inclusion of the NCDMF Trip-Ticket data in the Ecopath
285 model required us to increase the biomass in the open trawling areas relative to the closed

286 trawling areas, because most of the trip-ticket landings in Core Sound were reported from
287 trawling gear. We determined that >90 % of the commercial harvest in Core Sound came from
288 open trawling areas. Because trawling gear is not allowed in closed trawling areas (NCDMF
289 designated Primary or Secondary Nursery Areas) all trip-ticket data from trawling gear was
290 included in the open-trawling Ecopath model only. In contrast, for other fishing gear types
291 (pound nets, gill nets, haul seines, and crab pots), which can be used in either open-trawling
292 areas and the Secondary Nursery Areas (but not Primary Nursery Areas), we made the
293 assumption that 90% of the Trip-Ticket catch (in pounds converted to Ecopath biomass per unit
294 area g C m^{-2}) originated in the open trawling areas, based on the relative size of Secondary
295 Nursery Areas (10% of the total area of Core Sound). Biomass estimates from some of our field
296 measurements were insufficient to account for reported landings, as indicated by Ecotrophic
297 Efficiencies > 1 in Ecopath, and the carbon energy required by the commercial fisheries of Core
298 Sound could not be met by production of lower trophic levels.

299 **Ecosim simulation modelling**

300 Ecosim is a module of Ecopath that allows time-dynamic simulations of balanced Ecopath
301 models (38). EcoSim was run after balanced EcoPath models were achieved. Default settings
302 for vulnerability were used (2% of each prey population was available for predator consumption
303 at any given time), and the system was calibrated with historical catch and effort data. The
304 Ecopath model used was the Annualized Open trawling model for the simulation (SI Tables 4-8).
305 We drove the model effort statistics for each year for the fishing fleets (Table SI 10) as reported
306 on Trip Tickets to the NCDMF for the shrimp trawling fishery in the Core Sound Management
307 Area for the years 2001-2007. The model was fit to time series of annual catches of brown
308 shrimp, white shrimp, pink shrimp, blue crabs, flounders, spot, pinfish, and other species for
309 each fish gear (Table SI 9) . In Ecosim, vulnerabilities are parameters that assign a value for

310 each species or node indicating the proportion of that node's population that is available to
311 preyed upon by other consumers. A vulnerability of 0.0 would indicate that all biomass in that
312 node would be immune from any predation, whereas $V = 100.0$ or greater would indicate that all
313 the individuals and their biomass are vulnerable to predation. The vulnerabilities were kept
314 initially at the default values of 2.0. The vulnerabilities are essential in maintaining the model
315 within stable boundaries, and provide a degree of refugia for each of the nodes. We used the
316 Ecosim module "fit to time series" to estimate vulnerability parameters that minimize the sum of
317 squares between predicted and observed values ($SS = 112.1313$, Akaike Information Criterion,
318 $AIC = 435.5736$). Our model effort time series reflected the real trawling and other fishing gear
319 relative fishing effort during the historical time period for which harvest data were available, and
320 this served as a basis for simulating the trawling effort reduction. Next, a "trawl ban" was
321 simulated by setting the shrimp trawling effort = 0 trips per month for the years 2008-2026.
322 Other gears were left with a relative fishing effort of 1.0 over this same period, (i.e., effort levels
323 as reported in 2007, the base year for which our Ecopath models were developed). The runs of
324 the model with the "trawl ban" were reported for 18 years after trawling effort ceased and are
325 reported here.

326

327 **Visualization of the Trophic Networks**

328 To visualize the food web, we plotted each of the 65 nodes plus the 6 fleets using the log-
329 10 transformed biomass (or catch) of each node and the consumption ($Q_{i,j}$) matrices from
330 Ecopath, where prey i is consumed by predator j , and the consumption in $\text{gC m}^{-2} \text{yr}^{-1}$ of i by j is
331 given in each cell. Consumption matrices for each model from Fall 2007, areas open and closed
332 to trawling, were analyzed for similarity in trophic roles using regular equivalence (REGE,

333 (32,33) as a measure of similarity. The REGE coefficients were plotted in a 2-D
334 multidimensional scaling coordinates with in UCI Net 6.361 and Pajek64 3.12 (34,32,35). The
335 algorithm takes any real-valued $N \times N$ (species-by-species) matrix X as input, and returns a
336 species-by-species matrix R of coefficients (ranging from 0 to 1) which records, for each pair of
337 species, the extent of (maximal) regular equivalence. The essence of the algorithm is as follows:

- 338 0. Set $r_{ij} = 1$ for all i and j (i.e., let all species be 100% equivalent to start)
- 339 1. For each species i and j ,
 - 340 A. For each species k eaten by i , find species m eaten by j that is most equivalent
341 to k and which is eaten in the most similar proportion as k is eaten by i , in other
342 words, which maximizes the quantity $z_k = r_{km} * \text{Min}(x_{ik}, x_{jm}) / \text{Max}(x_{ik}, x_{jm})$
 - 343 B. For each k which eats i , find species m that eats j that is most equivalent to k and
344 which eats j in the most similar proportion as k eats i , in other words which
345 maximizes the quantity $y_k = r_{km} * \text{Min}(x_{ki}, x_{mj}) / \text{Max}(x_{kj}, x_{mj})$
 - 346 C. Set r_{ij} and $r_{ii} = \sum z_k + \sum y_k$
- 347 2. Repeat Step 1 until no more changes in r_{ij} or maximum iterations exceeded. The
348 maximum iterations = N species or compartments.

349 The resulting coefficients r_{ij} have ordinal properties.

350 Trophic roles are thought to be most similar in this analysis when the REGE coefficient
351 r_{ij} is large between any pair of nodes, indicating a similar trophic niche (predator's with similar
352 trophic roles or niches and prey with similar trophic roles or niches, but not the exact same
353 predator or prey). The REGE algorithm is iterative; a minimum of 50 iterations were used to
354 obtain the REGE coefficients for each trophic network model, and as nodes were assessed for
355 trophic similarity at each iteration, the REGE coefficients from the previous iteration were used

356 to assess trophic similarity in the next iteration. All nodes begin in one group at the first iteration
357 (REGE is set at 100 % similarity for all nodes), and trophic role similarity was used to establish
358 the REGE coefficients at each iteration of the algorithm, finding the nodes that are least similar
359 to the group and giving them a new, lower REGE coefficient.

360 After running the REGE algorithm on each of the seasonal and trawling area closure
361 networks (65 Ecopath compartments plus 4 closed trawling area or 6 open trawling area fishing
362 gears as nodes in the network), a clustering strategy was applied [Johnson's hierarchical
363 clustering strategy in UCINET (36)] to the resulting matrix (71 x 71 node by node matrix for open
364 trawling areas and 69 x 69 nodes for closed trawling areas) of REGE coefficients. Because it is
365 appropriate for ordinal data, we used Johnson's hierarchical linkage clustering, which yields a
366 dendrogram and a set of nested partitions.

367 To simplify interpretation of the results, a hierarchical clustering of the output matrix E
368 from the REGE algorithm was also performed, yielding a dendrogram. For display purposes, one
369 partition within the hierarchical clustering was selected to classify compartments. The particular
370 choice of partition was based on a series of regressions designed to measure cluster adequacy.
371 Since an ideal clustering of the E matrix would locate the largest values of E within clusters and
372 the smallest values of E between clusters, we can measure the extent to which a given clustering
373 is optimal via an analysis of variance in which the cases are pairs of nodes, the dependent
374 variable is the REGE coefficient for each pair, and the independent variable is a dummy variable
375 coded 1 if the pair are in the same cluster and 0 if they are in different clusters. The resulting R-
376 square (or η^2 as it is called in the ANOVA context) is then interpreted as a measure of cluster
377 adequacy. By necessity, R-square is a non-decreasing function of the number of clusters. By
378 plotting R-square against the number of clusters we obtain a scree plot which can be examined

379 for inflection points. A clustering with k classes is chosen if it provides a sizeable increase in R-
380 square over the next simplest clustering (i.e., with $k-1$ clusters), yet explains nearly as much
381 variance as the next most complicated clustering ($k+1$ clusters).

382 The cluster adequacy scree plots [η^2 plotted versus cluster partition group size; η^2 is a
383 measure of within-cluster versus between-cluster variance (37)] was plotted for the four models
384 are shown in Figure 2. The plot shows that when all nodes are grouped as one large cluster (on
385 left side of plot), η^2 is low. Conversely, when each node is assigned to its own individual cluster
386 partition group (resulting in 69 - 71 clusters, on the right side of the plot), η^2 is also very low.
387 When η^2 is maximal, the clustering partitioning is most adequate at capturing the within group
388 variance in REGE coefficients. The four models had slightly different η^2 maxima for number of
389 cluster groups (Spring Open $\eta^2 = 0.75$, Spring Closed $\eta^2 = 0.75$, and Fall Closed $\eta^2 = 0.76$
390 occurred at 15 clusters; Fall Open was maximal $\eta^2 = 0.75$ at 9 clusters), and these groups with
391 maximal within group REGE coefficients were used to assign color classes to nodes with high
392 REGE similarity.

393 In food web these visualizations, if two nodes have similar REGE coefficients, they are
394 likely to have similar trophic roles and will plot near one another on the MDS coordinates.
395 Node size on each food web visualization was scaled by log-10 biomass: in addition, we plotted
396 the difference in log-10 biomass measured between open and closed areas in fall (2007), thus
397 providing node-by-node a ratio of the open: closed biomass, and closed: open biomass.

398

399 **Results**

400 **Benthic Biomass in the Closed and Open Trawling Areas**

401 In Core Sound, North Carolina, shrimp trawling starts in March and runs through October
402 (39). After the peak of the shrimp trawling season in the fall of 2007, benthic deposit-feeding
403 polychaetes biomass (Figure 3) was higher in the open trawling areas than in closed trawling
404 areas [Table 1, repeated-measures ANOVA between trawling areas: total macrobenthic
405 invertebrates ($F_{1,34} = 6.210$, $p = 0.018$), deposit-feeding polychaetes ($F_{1,34} = 7.894$, $p = 0.008$)
406 and predatory polychaetes ($F_{1,34} = 6.339$, $p = 0.017$)]. Deposit-feeding polychaetes are
407 scavengers and consume dead fishes, organic material and smaller bacteria and microbes.

408 **Bycatch Biomass in the Closed and Open Trawling Areas**

409 The three species most commonly caught as bycatch in shrimp trawls are blue crabs
410 (*Callinectes sapidus*, Portunidae), pinfish (*Lagodon rhomboides*, Sparidae), and spot
411 (*Leiostomus xanthurus*, Sciaenidae) (17). These were collected in our own replicated trawl
412 samples (using a smaller version of the otter trawls used by shrimpers, with smaller mesh liner
413 and shorter headrope) to capture these bycatch species at the start of and after the shrimp season
414 (spring and fall 2007) at the same stations as the benthic samples were taken above. There was
415 significantly greater biomass of the three main bycatch species in the closed trawling areas at the
416 end of the trawling season (Figure 4, Wilcoxon test, blue crab: $W = 945$, $p > 0.00001$, pinfish:
417 $W = 832$, $p > 0.04$, spot: $W = 1062$, $P > 0.00001$, $n = 36$ trawls/trawling area in each case). Stomach
418 content analysis and stable isotope estimates of the spot and pinfish diets showed that they
419 consumed predominantly polychaetes, among many other invertebrate prey, algae and plants.
420 Thus, predation by these bycatch fish species on deposit-feeding polychaetes was likely to be far
421 lower in the open trawling areas, especially at the end of the shrimp trawling season, and these
422 data were included in the Ecopath models that we constructed next.

423 **Ecopath and Food Web Model of Core Sound**

424 The food web network models of the open and closed shrimp trawling areas of Core
425 Sound after the shrimping season was over (in the fall months) showed a dramatic change in the
426 benthos (Figure 5). The trophic levels of all compartments in open and closed areas are given in
427 supplementary information (species names Table SI-2; dietary sources in SI-3; effective trophic
428 levels Table SI-4; biomass values in Table SI-5; production/biomass ratios Table SI-6;
429 consumption/biomass ratios in Table SI-7; ecotrophic efficiencies in Table SI-8). To make these
430 visualizations of the Ecopath network models, we used a method based on graph theory (regular
431 equivalence algorithm, or REGE (37)) to assess the trophic role similarity in each fishery
432 management area. These food web flow diagrams are based on a two-dimensional
433 multidimensional scaling of the nodes, and thus nodes with similar REGE coefficients (and
434 trophic roles) plot close to one another, with high similarity indicated by the same color class (no
435 two species had identical REGE coefficients; color classes with high-within class REGE
436 similarity were determined using a clustering algorithm (Figure 2), along with species ID codes
437 (Table 4). The position of each node in the vertical and horizontal dimensions of these plots is
438 interpreted as depicting a trophic role for each species that is influenced not only by the
439 relationship to the producers (39, 43, 55) and detritus (28) at the bottom of the plots, but also
440 their relationships to their predators. Thus apex predators, including the various fishery gears
441 [crab pots (25), gill nets (33), haul seines (37), pound nets (51), shrimp trawls (58), and skimmer
442 trawls (60) appear near the top of the plots.

443 The nodes in Figure 5 are scaled by \log_{10} biomass (g C/m^2). The food web of Core
444 Sound is detritus-based. Detritus (28) was considered a non-living compartment and designated
445 trophic level 1 in the Ecopath modelling approach; this very large-biomass node appears at the
446 bottom and in a central position on the flow diagrams in Figure 5. A general decrease in

447 biomass is apparent as the trophic position of each species increases, with species apex predators
448 such as various fishes [southern flounders (*Paralichthys lethostigma*) and other Paralichthidae
449 (30), bluefish (*Pomatomus saltatrix*, 15), red drum (*Sciaenops ocellatus*, 52), sharks and rays (6,
450 25, 42, 61), birds (18,57,67) and sea turtles (54) having small biomasses and plotting near the top
451 of flow diagram. Producers [seagrasses (55), phytoplankton (43), and benthic macroalgae (39)
452 have large biomasses and plot near the bottom of the diagram. Note that biomass of bycatch (21)
453 is small in the closed areas (from some legal fisheries in the no-trawling management areas), but
454 a very large amount of bycatch biomass is present in the open areas. This bycatch biomass is the
455 basis of a scavenger food web [the benthic bacteria (10), meiofauna (40), deposit-feeding
456 polychaetes (47), and indirectly the blue crabs (14).

457 After the shrimp trawling season was largely over, in the fall of 2007, more detritus was
458 found in the closed areas than in the open areas of Core Sound. Flows of C in Core Sound were
459 dominated by consumption of detritus by benthic bacteria (10), meiofauna (40), and higher
460 trophic levels species (Table 2). More C flowed from detritus to all predators in the closed area
461 ($365.84 \text{ gC m}^{-2} \text{ yr}^{-1}$) than in the open trawling areas ($262.67 \text{ gC m}^{-2} \text{ yr}^{-1}$). Most of this flow is
462 from detritus to consumers at Trophic level II (i.e. detritivores). Most modeled compartments
463 had greater biomass in the open trawling area after the end of the shrimp season (Figure 6, top)
464 including bluefish (*Pomatomus saltatrix*, 15), weakfish (*Cynoscion regalis*, 69), spotted seatrout
465 (*C. nebulosus*, 65), Spanish mackerel (*Scomberomorus maculatus*, 63), Atlantic menhaden
466 (*Brevoortia tyrannus*, 5), spot (64), pinfish (45), hard clams (*Mercenaria mercenaria*, 35),
467 suspension feeding bivalves (12), blue crabs (*Callinectes sapidus*, 14), brown (*Farfantepenaeus*
468 *aztecus*, 19), pink shrimp (*F. duorarum*, 46), white shrimp (*Litopenaeus setiferus*, 70),
469 polychaetes (47-49), sea cucumbers (53), and brittlestars (17). In contrast, detritus (28), drift
470 algae (29), meiofauna (40), phytoplankton (43), zooplankton (71), and Atlantic croaker

471 (*Micropogonias undulatus*, 4) have more biomass in the areas closed to trawling (Figure 6,
472 bottom).

473 The node-specific log-biomass differences (ratios) displayed in Figure 6 are based on
474 single biomass estimates used to create balanced steady-state Ecopath models. For each species
475 or node, a biomass was estimated from all of our samples and the North Carolina Division of
476 Marine Fisheries (NCDMF) harvest data, one estimate/node for open trawling areas and one
477 estimate/node for closed trawling areas. The steady-state network models, balanced to achieve
478 steady-state conditions (see SI for method used for steady-state model balancing), were then used
479 to perform Ecosim simulations. Biomass estimates for fishery species are based on modelled
480 parameters derived from fisheries harvest data reported to NCDMF, and subdivided into the open
481 and closed areas (e.g., no commercial trawl harvest data were assigned to closed areas, but other
482 gear types were allowed in the closed trawl areas; these were proportionally divided by relative
483 amount of fished areas), which means that there are no statistical uncertainties associated with
484 these estimates. For biomasses of the benthos, where these were directly measured with
485 replication, see Table 1 and results displayed Figure 3.

486 **Simulation modelling in EcoSim**

487 Ecopath was used to simulate the closure of Core Sound to shrimp trawling using the
488 EcoSim simulation module. We used an Ecopath open trawling area annual model (Deehr *et al.*
489 2014) that was verified with stable isotope measurements and included a time series of fisheries
490 harvest data for Core Sound (SI Table 9) to calibrate the Ecosim model along with fishing effort
491 (annual trips SI Table 10) by gear type reported to the NCDMF from 2001-2007. During that
492 period, trawling effort declined 76.5 %: average annual reported trawling trips declined from
493 5,546 trips/year in 2001 to 1,303 trips/year in 2007, a decline in relative fishing effort from 4.26
494 to 1.0 (Figure 7). After calibration, we ran an EcoSim scenario beginning in 2001, incorporating
495 the historical shrimp trawl fishery effort and catches reported to NCDMF from 2001-2007, and
496 simulated a complete shrimp trawl ban (0% trawling effort) in 2008, ending in 2026 (a 25-year
497 run). A trawl ban in estuarine waters has been recently proposed in North Carolina, and is under
498 consideration at the current time by the North Carolina Fishery Commission, so this simulation is
499 timely and reflects what could happen if a trawl ban were enacted. Time series and predictions
500 from the Ecosim simulations are shown for some key fishery species (Figure 7) that are the most
501 valuable fishery species in North Carolina (\$13.3 million for pink, brown, and white shrimp
502 combined, \$21.8 million for blue crabs, \$4.5 million for southern flounder (*Paralichthys*
503 *lethostigma*) in 2012, NCDMF commercial landings data (40).

504 Consistent with our hypothesized trawling-induced trophic cascade, the closure of the
505 shrimp trawling areas is predicted to cause some species to increase (spot and pinfish) and others
506 to decline (deposit-feeding polychaetes and Penaeidae shrimp) after the simulated trawling ban.
507 There was an increase (0.7175 g C m⁻² biomass) in deposit-feeding polychaetes during year 2003
508 when trawling was at its peak in the historical time series. Our simulation model shows that the
509 biomass of this scavenger group would decline after trawling cessation, reaching background

510 relative biomass (0.7099 gC m^{-2}) in 2009, a decline of 1.3% in biomass (Figure 7). This
511 predicted decline after the simulated trawling ban is concurrent with a shrimp trawling effort
512 decline and the increase of brown shrimp, other penaeid shrimp, and the bycatch species
513 (primarily spot *Leiostomus xanthurus* and pinfish *Lagodon rhomboides* in Figure 7), all of which
514 feed on polychaetes. These dramatic changes to the benthos and the fishes that feed on the
515 benthos is due to the cessation of a trawling-induced trophic cascade, which depleted brown
516 shrimp to 0.96 relative biomass during the peak of trawling effort (2001-2002). Thus, our
517 simulation model appears to predict the direction of change in the standing stock of deposit-
518 feeding polychaetes biomass, although not the magnitude of the difference in our measurements
519 taken in open and closed trawling areas (Table 1).

520 It is notable in the trawl ban scenario on key fisheries in North Carolina: southern
521 flounders and others in the family Paralichthyidae, after declining to 0.0256 gC m^{-2} due to
522 trawling impacts in year 3 (2004), are predicted to return to the pre-trawling biomass of 0.0265
523 gC m^{-2} by year 6, due to declining fishing effort, then reach a peak biomass 15 years after a trawl
524 ban, with only a 2% increase relative to 2001. This suggests that trawling ban would increase
525 slightly the southern flounder stocks; this is a desirable effect, as the flounder stock is currently
526 depleted. Spot (0.5%) and pinfish (0.9%) and brown shrimp (0.8%) would also increase slightly
527 over 25 years. Finally, a trawl ban would actually cause decrease in the stocks of brown, pink
528 and white shrimps, perhaps because of the increase in predation by other predators (flounders).
529 There would be negligible increase of blue crabs (0.9% increase relative to 2001 biomass)
530 followed by a slight decline (0.6673 gC m^{-2}). The largest increase in biomass occurred in
531 flounders, which are at the highest trophic levels of these key fishery species. Thus, a shrimp
532 trawling ban is predicted to reverse the trophic cascade allowing biomass to pass back up the
533 food web.

534 Fisheries managers in North Carolina are faced with a difficult choice based on these
535 interacting fisheries: a trawl ban may cause a relatively large increase in in the biomass of the
536 shrimp stocks, but this would be transfer energy to higher trophic level species, resulting in a
537 slight increase the blue crab and larger increase southern flounder stocks. Shrimp would no
538 longer be harvested by the trawlers, and any increase in their stocks would simply feed high
539 trophic level fishes like the southern flounder, with the system reaching an equilibrium after
540 2018, a recovery period of 10 years. The fisheries for blue crabs, flounder, and shrimp are thus
541 interconnected, directly by being harvested in the same gear (trawls) and indirectly through the
542 food web network in this ecosystem, and cannot be easily managed separately. Note that this is
543 true for the other fisheries (haul seines, gill nets, pound nets, crab pots) as well, which are still
544 included in our ecosystem network models, but here modeled as having unchanging effort.
545 These other fisheries may show increased fishing effort after a trawl ban, and increased harvests
546 of these species, because fishermen will be likely to switch to the alternative gears (e.g., use
547 more gill nets to catch increased flounder stocks) to target the same species, but this is not a
548 scenario we have modeled.

549

550 **Discussion**

551 Contrary to previous studies (cite them), there was more benthic scavenger biomass
552 (deposit-feeding polychaetes) in the areas open to trawling after the shrimp season ended in the
553 estuarine ecosystem in Core Sound. Further, in contrast to the earlier studies measuring acute
554 trawling impacts on the benthos, the areas measured in the current study have been subjected to
555 trawling for over thirty years. These findings are consistent with a long-term trawling-induced
556 indirect effect or trophic cascade, which has been observed due to fishing in other ecosystems

557 elsewhere (10–13,41) and as revealed by simulations in our ecosystem models. In a trophic
558 cascade, the removal of a high-trophic-level species causes an increase in its prey species, which
559 then decreases the abundance of that species' prey. Shrimp trawling is a high-trophic level
560 fishery (ETL=3.87)(21) that, as we observed, has reduced the abundance of benthic-feeding
561 fishes (bycatch in the fishery is mostly pinfish and spot), and we suggest that their prey (deposit-
562 feeding polychaetes) have increased as an indirect effect in the areas open to trawling, due to
563 reduced fish predation, as a result of a trophic cascade.

564 What is unique about the trophic cascade in our system is that we now have a
565 confirmation of a time-series based simulation model that mimics in a qualitative way the
566 measurements of the prey's difference in biomass between benthic samples taken in a marine
567 protected area (closed trawling area) and a fished area (open trawling area). This system has
568 been repeatedly trawled over thirty years and the discarded bycatch has been returned to the
569 system (rather than exported to markets) and subsidized the detrital food web and benthos. This
570 bycatch subsidy has resulted in an even greater difference in biomass of deposit-feeding
571 polychaetes. It is important to note that other factors, such as water conditions in the closed
572 areas (pollution for land run-off) and lack of mixing of the sediments by trawlers (20) after the
573 no trawling areas were established in the 1970's, could have resulted in environmental conditions
574 that may contributed to of the difference in deposit-feeding polychaete biomass.

575 This trawling-induced trophic cascade hypothesis requires further experimental testing.
576 The increase in benthos that has resulted directly from the trawling-induced trophic cascade
577 influenced the whole ecosystem that produces the brown, pink and white shrimp of Core Sound
578 because 1) the shrimp trawlers remove and return to the sea much of the juvenile fish biomass as
579 dead discards, and harvest of penaeid shrimps and blue crabs reduces the overall predation on the

580 benthos; and 2) the discard of the bycatch fishes as non-living carrion feeds the scavenger guild
581 of Core Sound. The bycatch is fed upon by decomposing bacteria, microbes, polychaetes,
582 penaeid and other shrimp, snails, and blue crabs and other crabs in these models. Indeed, other
583 work suggests that δN^{15} is enriched the primary bycatch species pinfish and spot in the open
584 trawling areas of Core Sound (25). In addition, this same study revealed an increase in the
585 effective trophic levels for these bycatch species in the open trawling area Ecopath models (21).
586 Our measurements of greater biomass of deposit-feeding polychaetes and lowered biomass of
587 bycatch species (pinfish and spot), which were taken after the trawling season, in conjunction
588 with the Ecopath/Ecosim simulation results, suggest that a trawling-induced trophic cascade has
589 occurred in the study area. The observation that pinfish and spot in the open trawling areas were
590 enriched in δN^{15} ratios after the trawling season suggests that a trophic subsidy occurred as well,
591 due to carrion returned to the system, which added a partial increase in trophic level. The
592 combined effect of the trophic cascade due trawling and the increase in biomass of the deposit-
593 feeding polychaetes suggests a pronounced effect of shrimping on the whole ecosystem.
594 Importantly, these measured shrimp-trawling impacts provide empirical verification of the
595 Ecosim simulation model, which has not been accomplished previously.

596 There is a clear effect of shrimp trawling on the Core Sound ecosystem, causing a
597 trawling-induced trophic cascade. The question remains if this is detrimental to the ecosystems'
598 functioning, and if societal goals for beneficial uses of Core Sound are being met. Based on the
599 general perceived negative impact of trawling discards on these ecosystems, both in the USA and
600 in Europe, North Carolina is considering enacting a shrimp trawl ban in estuaries. Our results
601 call into question the general negative impact of trawl discards. Discards may in fact benefit
602 particular trophic groups in the benthos, subsidizing their growth and production of polychaetes.
603 This trawling-induced trophic cascade and potential bycatch subsidy to the benthos is eventually

604 returned to the ecosystem as a pulse of carbon, stimulating energy and productivity of the
605 benthos, which cascades up the food web and results in more spot, pinfish and southern flounder,
606 albeit after many years, after the trawling virtually ceased in our Ecosim simulations.

607 Whether the nursery areas should be expanded to completely close trawling in the estuary
608 remains a significant management concern. We could use our existing models to explore
609 trawling policy options, simulating an expansion of the nursery areas using the Ecospace module
610 in Ecopath, and following the approach of (42); however, this would require better spatially
611 referenced harvest data for Core Sound. We recommend that fishery managers should proceed
612 with caution and conduct an experiment, perhaps they should close some currently open trawling
613 areas, and open some of currently closed the nursery areas to trawling, to see if this trophic
614 cascade and bycatch stimulus effect can be measured. This should be considered as a temporary,
615 and experimental, management option, with proper experimental protocols established to
616 monitor the plankton, benthos, seagrasses, fishes, and larger vertebrates in an experimental
617 design. We would recommend that long-term trawling closure-opening experiments be
618 conducted with cooperation of the fishing industry, so the effects of shrimp trawling can be
619 directly observed with rigorous before and after control and impact (BACI) study.

620

621 **Acknowledgements**

622 The Coastal Resources Management Doctoral Program, the Institute for Coastal Science and
623 Policy and the Department of Biology provided support for two of the authors (R. Deehr and K.
624 Hart) financially while they were students at East Carolina University. We obtained support to
625 conduct the field research and data analysis from North Carolina Sea Grant, project R/BS-1. We

626 also thank Kyle Regensburg (Department of Biology at East Carolina University) for laboratory
627 processing of benthic meiofauna samples; Cecilia Krahforst (Department of Biology at East
628 Carolina University) for field collection help. Jill Luczkovich was a bird observer during our
629 field studies. Robert Christian (Department of Biology at East Carolina University) reviewed an
630 earlier draft of the manuscript. Finally, we are indebted to Carl Walters (University for British
631 Columbia) helped us with Ecosim modelling advice.

632

633 References

- 634 1. Watson R, Revenga C, Kura Y. Fishing gear associated with global marine catches. II.
635 Trends in trawling and dredging. *Fish Res.* 2006;79(1–2):103–11.
- 636 2. Thurstan RH, Brockington S, Roberts CM. The effects of 118 years of industrial fishing
637 on UK bottom trawl fisheries. *Nat Commun* [Internet]. Nature Publishing Group;
638 2010;1(2):15. Available from: <http://dx.doi.org/10.1038/ncomms1013>
- 639 3. Olsgard F, Schaanning MT, Widdicombe S, Kendall M a., Austen MC. Effects of bottom
640 trawling on ecosystem functioning. *J Exp Mar Bio Ecol* [Internet]. Elsevier B.V.;
641 2008;366(1–2):123–33. Available from: <http://dx.doi.org/10.1016/j.jembe.2008.07.036>
- 642 4. Collie JS, Hall SJ, Kaiser MJ, Poiner IR. A quantitative analysis of fishing impacts on
643 shelf-sea benthos. *J Anim Ecol.* 2000;69:785–98.
- 644 5. Auster PJ, Malatesta RJ, Langton RW, Watling L, Valentine PC, Donaldson CLS, et al.
645 The impacts of mobile fishing gear on seafloor habitats in the Gulf of Maine (Northwest
646 Atlantic): implications for conservation of fish populations. *Rev Fish Sci.* 1996;4:185–
647 202.
- 648 6. Sparks-McConkey PJ, Watling L. Effects on the ecological integrity of a soft-bottom
649 habitat from a trawling disturbance. *Hydrobiologia.* 2001;456:73–85.
- 650 7. Watling L, Norse EA. Special section: Effects of mobile fishing gear on marine benthos.
651 *Conserv Biol.* 1998;12:1178–9.
- 652 8. Watling L, Findlay RH, Mayer LM, Schick DF. Impact of a scallop drag on the sediment
653 chemistry, microbiota, and faunal assemblages of a shallow subtidal marine benthic
654 community. *J Sea Res.* 2001;46:309–24.
- 655 9. Watling L. The global destruction of bottom habitats by mobile fishing gear. *Mar Conserv*
656 *Biol Sci Maint Sea’s Biodiversity Isl Press* Washington, DC. 2005;198–210.
- 657 10. Frank KT, Petrie B, Choi JS, Leggett WC. Trophic cascades in a formerly cod-dominated
658 ecosystem. *Science* (80-). 2005;308:1621–3.
- 659 11. Daskalov GM, Grishin AN, Rodionov S, Mihneva V. Trophic cascades triggered by
660 overfishing reveal possible mechanisms of ecosystem regime shifts. *Proc Natl Acad Sci.*
661 2007;104:10518–23.
- 662 12. Daskalov GM. Overfishing drives a trophic cascade in the Black Sea. *Mar Ecol Prog Ser.*
663 2002;225:53–63.
- 664 13. Pinnegar JK, Polunin NVC, Francour P, Badalamenti F, Chemello R, Harmelin-Vivien
665 ML, et al. Trophic cascades in benthic marine ecosystems: lessons for fisheries and
666 protected-area management. *Environ Conserv.* 2000;27:179–200.
- 667 14. Mumby PJ, Dahlgren CP, Harborne AR, Kappel C V, Micheli F, Brumbaugh DR, et al.
668 Fishing, trophic cascades, and the process of grazing on coral reefs. *Science.*
669 2006;311(5757):98–101.
- 670 15. Altieri AH, Bertness MD, Coverdale TC, Herrmann NC, Angelini C. A trophic cascade
671 triggers collapse of a salt-marsh ecosystem with intensive recreational fishing. *Ecology*
672 [Internet]. Ecological Society of America; 2012 Jun 1;93(6):1402–10. Available from:
673 <http://dx.doi.org/10.1890/11-1314.1>

- 674 16. Casini M, Blenckner T, Mollmann C, Gardmark a., Lindegren M, Llope M, et al. From
675 the Cover: Predator transitory spillover induces trophic cascades in ecological sinks. Proc
676 Natl Acad Sci. 2012;109(21):8185–9.
- 677 17. Coale JS, Rulifson R a, Murray JD, Hines R. Comparisons of shrimp catch and bycatch
678 between a skimmer trawl and an otter trawl in the North Carolina inshore shrimp fishery.
679 North Am J Fish Manag. 1994;14(4):751–68.
- 680 18. Murray JD, Bahen JJ, Rulifson RA. Management Considerations for By-catch in the
681 North Carolina and Southeast Shrimp Fishery. Fisheries [Internet]. Taylor & Francis
682 Group; 1992 Jan 9 [cited 2015 May 27];17(1):21–6. Available from:
683 [http://www.tandfonline.com/doi/abs/10.1577/1548-](http://www.tandfonline.com/doi/abs/10.1577/1548-8446(1992)017%253C0021%253AMCFBIT%253E2.0.CO%253B2)
684 [8446\(1992\)017%253C0021%253AMCFBIT%253E2.0.CO%253B2](http://www.tandfonline.com/doi/abs/10.1577/1548-8446(1992)017%253C0021%253AMCFBIT%253E2.0.CO%253B2)
- 685 19. Diamond SL, Cowell LG, Crowder LB. Population effects of shrimp trawl bycatch on
686 Atlantic croaker. Can J Fish Aquat Sci. 2000;57(10):2010–21.
- 687 20. Dellapenna TM, Allison M a., Gill G a., Lehman RD, Warnken KW. The impact of
688 shrimp trawling and associated sediment resuspension in mud dominated, shallow
689 estuaries. Estuar Coast Shelf Sci. 2006;69(3–4):519–30.
- 690 21. Deehr R a., Luczkovich JJ, Hart KJ, Clough LM, Johnson BJ, Johnson JC. Using stable
691 isotope analysis to validate effective trophic levels from Ecopath models of areas closed
692 and open to shrimp trawling in Core Sound, NC, USA. Ecol Modell [Internet]. Elsevier
693 B.V.; 2014;282:1–17. Available from: <http://dx.doi.org/10.1016/j.ecolmodel.2014.03.005>
- 694 22. Johnson GA. The role of trawl discards in sustaining blue crab populations. Raliegh, NC;
695 2003.
- 696 23. Hart KJ. Comparison of abundance and diets of selected fishes in trawling and non-
697 trawling zones in Core Sound, NC, USA. East Carolina University; 2008.
- 698 24. Deehr RA. Measuring the ecosystem impacts of commercial shrimp trawling and other
699 fishing gear in Core Sound, North Carolina, using ecological network analysis. Coastal
700 Resources Management PhD Program. [Greenville, NC]: East Carolina University; 2012.
- 701 25. Deehr RA, Luczkovich JJ, Hart KJ, Clough LM, Johnson BJ, Johnson JC. Using stable
702 isotope analysis to validate effective trophic levels from Ecopath models of areas closed
703 and open to shrimp trawling in Core Sound, NC, USA. Ecol Modell. 2014;282:1–17.
- 704 26. Jorgensen SE, Nielsen SN, Jorgensen LA. Handbook of ecological parameters and
705 ecotoxicology. 1991.
- 706 27. Higgins RP, Thiel H. Introduction to the study of meiofauna. Smithsonian Institution
707 Press; 1988.
- 708 28. Widbom B. Determination of average individual dry weights and ash-free dry weights in
709 different sieve fractions of marine meiofauna. Mar Biol. 1984;84(1):101–8.
- 710 29. Nelson DW, Sommers LE, others. Total carbon, organic carbon, and organic matter.
711 Methods soil Anal Part. 1996;3(3):961–1010.
- 712 30. Strickland JDH, Parsons TR. A manual of sea water analysis. Queen’s Printer; 1965;
- 713 31. Hines KL, Rulifson RA, Murray JD. Performance of Low-Profile Skimmer Trawls in the
714 Inshore Shrimp Fishery of North Carolina. North Am J Fish Manag. 1999;19(2):569–80.
- 715 32. Borgatti SP, Everett MG, Freeman LC. Ucinet for Windows: Software for social network

- 716 analysis. 2002;
- 717 33. Borgatti SP, Everett MG. The class of all regular equivalences: Algebraic structure and
718 computation. *Soc Networks*. 1989;11:65–88.
- 719 34. Luczkovich JJ, Borgatti SP, Johnson JC, Everett MG. Defining and measuring trophic role
720 similarity in food webs using regular equivalence. *J Theor Biol*. 2003;220(3):303–21.
- 721 35. Batagelj V, Mrvar A. *Pajek—analysis and visualization of large networks*. Springer; 2004.
- 722 36. Johnson SC. Hierarchical clustering schemes. *Psychometrika*. 1967;32:241–53.
- 723 37. Luczkovich JJ, Borgatti SP, Johnson JC, Everett MG. Defining and measuring trophic role
724 similarity in food webs using regular equivalence. *J Theor Biol*. 2003;220:303–21.
- 725 38. Christensen V, Walters CJ. *Ecopath with Ecosim: Methods, capabilities and limitations*.
726 *Ecol Modell*. 2004;172(2–4):109–39.
- 727 39. Brown K. *Interstate Fisheries Management Program Implementation for North Carolina:
728 Documentation and Reduction of Bycatch in North Carolina Fisheries; Job 2:
729 Characterization of the inshore commercial shrimp trawl fishery in Pamlico Sound and its
730 tributaries*, Nor. Morehead City, NC; 2010.
- 731 40. North Carolina Division of Marine Fisheries. *Commercial Harvest Statistics [Internet].
732 Commercial Harvest Statistics*. 2014 [cited 2015 Jul 9]. Available from:
733 <http://portal.ncdenr.org/web/mf/marine-fisheries-catch-statistics>
- 734 41. Pace ML, Cole JJ, Carpenter SR, Kitchell JF. Trophic cascades revealed in diverse
735 ecosystems. *Trends Ecol Evol*. 1999;14:483–8.
- 736 42. Walters C, Pauly D, Christensen V. *Ecospace: Prediction of mesoscale spatial patterns in
737 trophic relationships of exploited ecosystems, with emphasis on the impacts of marine
738 protected areas*. *Ecosystems*. 1999;2(6):539–54.
- 739
- 740

741 Table 1. Biomass (g C m⁻²) of each compartment in the Core Sound Ecopath models. Table
742 arranged by compartment number.

Compartment Number and Name	Spring Closed	Spring Open	Fall Closed	Fall Open	Annual Closed	Annual Open	
1	Phytoplankton	2.03	2.36	4.97	4.45	3.500000	3.40500
2	Microalgae, benthic	0.08	0.22	0.08	0.22	0.080000	0.22000
3	Macroalgae, benthic	0.644	1.884	0.644	1.884	0.644000	1.88400
4	Drift algae	0.117	0.051	0.117	0.051	0.116670	0.05064
5	Seagrass	2.4	2.4	1.2	1.2	3.600000	3.60000
6	Bacteria, aquatic	0.1	0.1	0.1	0.1	0.100000	0.10000
7	Bacteria, benthic	0.7	0.7	0.7	0.7	0.700000	0.70000
8	Meiofauna	7.93	2.87	6.64	1.49	7.285000	2.18000
9	Zooplankton	0.20040	0.19995	0.17698	0.07002	0.188689	0.13498
10	Jellyfish	0.00814	0.03507	0.00010	0.03416	0.004121	0.03462
11	Ctenophores	0.01000	0.01667	0.00403	0.00614	0.007014	0.01140
12	Polychaetes, deposit feeder	0.20930	0.49177	0.23220	0.93178	0.220752	0.71178
3	Polychaetes, suspension feeder	0.03518	0.06800	0.07921	0.13108	0.057198	0.09954
14	Polychaetes, predatory	0.05864	0.21389	0.09915	0.21970	0.078893	0.21680
15	Bivalves, suspension feeder	0.28922	0.83462	0.15012	0.15070	0.219671	0.49266
16	Bay scallop	0.00001	0.00001	0.00001	0.00052	0.000010	0.00026
17	Hard clam	0.36562	0.35131	0.65384	3.94980	0.509729	2.15055
18	Gastropods, deposit feeder	0.01642	0.01895	0.01646	0.02101	0.016443	0.01998
19	Gastropods, predatory	0.09304	0.39086	0.00102	0.02547	0.047029	0.20817
20	Conchs, whelks	0.00012	0.00127	0.00004	0.00030	0.000078	0.00079
21	Atlantic brief squid	0.00026	0.00092	0.00008	0.00267	0.000172	0.00180
22	Bryozoans	0.13301	0.00001	0.27834	0.34201	0.205675	0.17101
23	Tunicates	0.00442	0.00282	0.00001	0.04845	0.002216	0.02564
24	Sea cucumbers	0.00001	0.85698	0.02674	0.00121	0.013376	0.42909
25	Brittlestars	0.10883	0.66378	0.00001	0.01122	0.054421	0.33750
26	Amphipods, isopods, cumaceans	0.00665	0.00643	0.00276	0.01453	0.004706	0.01048
27	Blue crabs	0.0395	0.4895	0.0562	0.8384	0.047824	0.66391
28	Crabs, other	0.0012	0.0680	0.0001	0.0462	0.000637	0.05709
29	Brown shrimp	0.0002	0.0156	0.0100	0.2470	0.005080	0.13129
30	Pink shrimp	0.0015	0.1445	0.0100	0.0051	0.005746	0.07479
31	White shrimp	0.0001	0.0002	0.0078	0.5364	0.003953	0.26830
32	Shrimps other	0.0005	0.0135	0.0025	0.0346	0.001529	0.02406
33	Anchovies	0.0042	0.0068	0.0068	0.0172	0.005517	0.01198
34	Atlantic croaker	0.0130	0.0622	0.4950	0.1055	0.254010	0.08387

Compartment Number and Name	Spring Closed	Spring Open	Fall Closed	Fall Open	Annual Closed	Annual Open
35 Atlantic menhaden	0.5244	6.0489	0.1513	0.0777	0.337860	3.06330
36 Atlantic silverside	0.0033	0.0026	0.0002	0.0064	0.001742	0.00451
37 Atlantic spadefish	0.0004	0.0058	0.0006	0.0093	0.000485	0.00758
38 Black drum	0.0016	0.0180	0.0015	0.0171	0.001537	0.01756
39 Bluefish	0.0203	0.2162	0.0067	0.0832	0.013532	0.14971
40 Flounders (Paralichthyidae)	0.0260	0.0117	0.0032	0.0404	0.014578	0.02606
41 Butterfishes (Stromateidae)	0.0052	0.0610	0.0041	0.0498	0.004654	0.05543
42 Striped mullet	0.0006	0.0104	0.0013	0.0256	0.000922	0.01800
43 Pigfish	0.0116	0.1243	0.0109	0.1324	0.011252	0.12835
44 Pinfish	0.0159	0.0414	0.0264	0.1205	0.021145	0.08099
45 Pompano	0.0005	0.0059	0.0005	0.0069	0.000489	0.00641
46 Red drum	0.0003	0.0029	0.0003	0.0030	0.000266	0.00295
47 Sheepshead	0.0016	0.0178	0.0016	0.0183	0.001615	0.01804
48 Southern kingfish	0.0050	0.0574	0.0084	0.0975	0.006684	0.07741
49 Spanish mackerel	0.0013	0.0256	0.0007	0.0397	0.000994	0.03262
50 Spot	0.0791	0.7699	1.4194	2.5473	0.749264	1.65863
51 Spotted seatrout	0.0232	0.0373	0.0065	0.0753	0.014868	0.05627
52 Weakfish	0.0501	0.5756	0.0408	0.4747	0.045473	0.52515
53 Bottlenose dolphins	0.0041	0.0041	0.0041	0.0041	0.004050	0.00405
54 Sea turtles	0.0760	0.0651	0.0000	0.1845	0.037980	0.12478
55 Atlantic sharpnose shark	0.0006	0.0001	0.0004	0.0000	0.000494	0.00004
56 Smooth dogfish	0.0029	0.0069	0.00001	0.0108	0.001450	0.00883
57 Cownose rays	0.0129	0.0368	0.0019	0.0047	0.007397	0.02073
58 Other rays, skates	0.0072	0.0074	0.0000	0.0057	0.003613	0.00655
59 Brown pelicans	0.0042	0.0032	0.0040	0.0047	0.004113	0.00394
60 Cormorants	1.00E-05	1.00E-05	0.0002	0.0037	0.000090	0.00183
61 Gulls	0.0002	1.00E-05	0.0014	0.0016	0.000783	0.00078
62 Terns	0.0011	0.0002	0.0007	0.0012	0.000931	0.00070
63 Shorebirds, wading birds	0.0034	1.00E-05	0.0045	0.0003	0.003973	0.00013
64 Bycatch	1.00E-05	0.3761	1.00E-05	1.0155	0.000010	0.69580
65 Detritus	266.76	125.99	266.76	125.99	266.76210	125.9948

743
744

745 Table 2. Average biomass (g C m⁻²) for total macrobenthic invertebrates and the 14 sub-groups
 746 (± standard error of the mean). Averages calculated by trawling area (Open, Closed), season
 747 (Spring, Fall) and Ecopath model (Spring Closed, Spring Open, Fall Closed, Fall Open).

Groupings	Trawling Area		Season		Model			
	Closed	Open	Spring	Fall	Spring Closed	Spring Open	Fall Closed	Fall Open
Total macrobenthic invertebrates	0.786 ± 0.139	5.044 ± 2.519	2.334 ± 0.714	3.496 ± 2.468	0.964 ± 0.242	3.704 ± 1.349	0.608 ± 0.133	6.385 ± 4.908
Deposit-feeding polychaetes	0.221 ± 0.049	0.712 ± 0.152	0.351 ± 0.086	0.582 ± 0.144	0.209 ± 0.080	0.492 ± 0.148	0.232 ± 0.059	0.932 ± 0.261
Suspension-feeding polychaetes	0.057 ± 0.017	0.100 ± 0.021	0.052 ± 0.012	0.105 ± 0.024	0.035 ± 0.014	0.068 ± 0.019	0.079 ± 0.031	0.131 ± 0.037
Predatory polychaetes	0.079 ± 0.015	0.217 ± 0.049	0.136 ± 0.037	0.159 ± 0.039	0.059 ± 0.017	0.214 ± 0.067	0.099 ± 0.024	0.220 ± 0.072
Suspension-feeding bivalves	0.220 ± 0.066	0.493 ± 0.138	0.562 ± 0.139	0.150 ± 0.050	0.289 ± 0.087	0.835 ± 0.248	0.150 ± 0.088	0.151 ± 0.051
Deposit-feeding gastropods	0.016 ± 0.006	0.020 ± 0.005	0.018 ± 0.005	0.019 ± 0.006	0.016 ± 0.007	0.019 ± 0.006	0.016 ± 0.009	0.021 ± 0.007
Predatory gastropods	0.047 ± 0.020	0.208 ± 0.150	0.242 ± 0.149	0.013 ± 0.013	0.093 ± 0.038	0.009 ± 0.003	0.001 ± 0.001	0.391 ± 0.296
Amphipods, isopods and cumaceans	0.005 ± 0.002	0.010 ± 0.003	0.007 ± 0.002	0.009 ± 0.003	0.007 ± 0.004	0.006 ± 0.003	0.003 ± 0.002	0.015 ± 0.006
Omnivorous shrimps	0.001 ± 0.001	0.001 ± 0.000	0.001 ± 0.001	0.001 ± 0.000	0.001 ± 0.001	<0.000	<0.000	0.001 ± 0.001
Tunicates	0.002 ± 0.002	2.424 ± 2.423	0.004 ± 0.003	2.423 ± 2.423	0.004 ± 0.004	0.003 ± 0.003	<0.000	4.845 ± 4.845
Sea cucumbers	0.013 ± 0.013	0.429 ± 0.428	0.428 ± 0.428	0.014 ± 0.003	<0.000	0.857 ± 0.855	0.027 ± 0.027	0.001 ± 0.001
Brittlestars	0.054 ± 0.054	0.338 ± 0.173	0.386 ± 0.179	0.006 ± 0.006	0.093 ± 0.038	0.009 ± 0.003	0.001 ± 0.001	0.391 ± 0.296
Omnivorous crabs	<0.000	0.083 ± 0.059	0.067 ± 0.058	0.016 ± 0.016	<0.000	0.135 ± 0.115	<0.000	0.031 ± 0.031
Jellyfish	0.004 ± 0.004	0.011 ± 0.008	0.015 ± 0.009	<0.000	0.008 ± 0.008	0.022 ± 0.016	<0.000	<0.000
Bryozoans	0.067 ± 0.067	<0.000	0.067 ± 0.067	<0.000	0.133 ± 0.133	<0.000	<0.000	<0.000

748

749 Table 3 Flow of material in $\text{gC m}^{-2} \text{y}^{-1}$ from detritus (assumed to be trophic level 1) to higher
 750 trophic levels (integrated at each level across species by Ecopath network modelling software)
 751 for the closed and open trawling areas of Core Sound, NC, USA.

Closed to Trawling

Trophic Level	Imported	Consumption by predators	Exported	Flow to detritus	Respiration	Throughput
VIII		2.68×10^{-8}	3×10^{-10}	1.78×10^{-7}	4.93×10^{-7}	6.98×10^{-7}
VII		1.90×10^{-6}	2.19×10^{-8}	2.35×10^{-5}	6.28×10^{-5}	8.82×10^{-5}
VI		7.43×10^{-5}	1.12×10^{-6}	0.0008	0.00215	0.0030
V		0.0023	2.93×10^{-5}	0.0205	0.05337	0.0762
IV		0.0538	0.0003	0.3860	0.8526	1.2926
III		0.9576	0.0010	11.8686	11.8781	24.7053
II		23.4677	0.0005	169.3153	150.3956	343.1791
Detritus	0	341.3599	316.1145	0	0	657.4745
Sum	0	365.8414	316.1163	181.5912	163.18188	1026.7308

Open to Trawling

Trophic level	Imported	Consumption by predators	Exported	Flow to detritus	Respiration	Throughput
VIII		1.13×10^{-6}	3.73×10^{-8}	1.51×10^{-5}	4.13×10^{-5}	5.75×10^{-5}
VII		5.99×10^{-5}	1.74×10^{-6}	0.0005	0.00139	0.0020
VI		0.0017	4.64×10^{-5}	0.0112	0.0285	0.0414
V		0.0330	0.0009	0.1679	0.3898	0.5916
IV		0.4557	0.0082	1.6345	3.0526	5.1510
III		4.2771	0.0309	15.1538	19.6243	39.0860
II		36.2090	0.0214	86.8326	108.7449	231.8080
Detritus	0	221.6956	378.3477	0	0	602.4574
Sum	0	262.6723	378.4091	103.80048	131.84145	879.13745

752

753 Table 4. The species identification codes for food web visualizations shown in Figure 5 and
754 Figure 6.

Code on graph	Ecopath ID	Group name in Ecopath
1	26	Amphipods, isopods, cumaceans
2	33	Anchovies
3	21	Atlantic brief squid
4	34	Atlantic croaker
5	35	Atlantic menhaden
6	55	Atlantic Sharpnose shark
7	36	Atlantic silverside
8	37	Atlantic spadefish
9	6	Bacteria aquatic
10	7	Bacteria benthic
11	16	Bay scallop
12	15	Bivalves, suspension feeding
13	38	Black drum
14	27	Blue crabs
15	39	Bluefish
16	53	Bottlenose dolphins
17	25	Brittlestars
18	59	Brown pelicans
19	29	Brown shrimp
20	22	Bryozoans
21	64	Bycatch
22	20	Conchs, whelks
23	60	Cormorants
24	57	Cownose rays
25		Crab Pots

26	28	Crabs other
27	11	Ctenophores
28	65	Detritus
29	4	Drift algae
30	40	Flounders (Paralichthyidae)
31	18	Gastropods, deposit feeders
32	19	Gastropods, predatory
33		Gill Nets
34	61	Gulls
35	17	Hard clams
36	41	Butterfishes (Stromatiedae)
37		Haul Seines
38	10	Jellyfish
39	3	Macroalgae, benthic
40	8	Meiofauna
41	2	Microalgae, benthic
42	58	Other rays and skates
43	1	Phytoplankton
44	43	Pigfish
45	44	Pinfish
46	30	Pink shrimp
47	12	Polychaetes, deposit feeders
48	14	Polychaetes, predatory
49	13	Polychaetes, suspension feeders
50	45	Pompano
51	46	Pound Nets
52	24	Red drum

53	10	Sea cucumbers
54	54	Sea turtles
55	5	Seagrass
56	47	Sheepshead
57	63	Shorebirds/waders
58		Shrimp Trawls
59	32	Shrimps other
60		Skimmer Trawls
61	56	Smooth dogfish
62	48	Southern kingfish
63	49	Spanish mackerel
64	50	Spot
65	51	Spotted seatrout
66	42	Striped mullet
67	62	Terns
68	23	Tunicates
69	52	Weakfish
70	31	White shrimp
71	9	Zooplankton

755

756

757

758 **Figure legends**

759

760 Figure 1. Fishery management areas in Core Sound, North Carolina, USA. Open and closed
761 trawling areas are defined by rule (15A NCAC 03 in North Carolina Marine Fishery Commission
762 Rules) and have been enforced for 30 years (NC Division of Marine Fisheries NCDMF). No
763 trawling is allowed in primary and secondary nursery areas.

764 Figure 2. Core Sound networks clustering results. Scree plot of cluster group size and η^2 for
765 each of the Core Sound models, based on Johnson's hierarchical clustering procedure of the
766 REGE coefficients from UCINET of the four Core Sound network models.

767 Figure 3. The log-transformed biomass m^{-2} of deposit-feeding polychaetes in Core Sound, NC in
768 areas closed (nursery areas) and open to shrimp trawling. Individual points show the abundance
769 of polychaetes at each of stations sampled during 2007, before (Spring 2007) and after (Fall
770 2007) the shrimping season.

771 Figure 4. The main bycatch species (blue crabs, *Callinectes sapidus*, pinfish, *Lagodon*
772 *rhomboides*, and spot, *Leiostomus xanthurus*) \log_{10} biomass ($g\ m^{-2}$) estimates in open and closed
773 trawling areas before shrimp season has begun (Spring) and after it is over (Fall). The box plots
774 show the median (horizontal lines), 25% and 75% percentiles (upper and lower limits of the
775 box), and the whiskers are $1.5 * \text{the inter-quartile}$ (distance between the upper and lower box
776 limits). Points outside the whiskers are extreme values.

777 Figure 5. The ecological network model of Core Sound shrimping areas, with nodes
778 representing standing stocks (size of node proportional to biomass in C dry mass $g\ m^{-2}$) and

779 flows of carbon ($\text{gC m}^{-2} \text{yr}^{-1}$) shown as arrows. Nodes are arranged according to their similarity
780 of trophic niche, using a non-metric multidimensional scaling (MDS) of the REGE coefficients.
781 Nodes with the same color are similar in trophic niche (>90% similar as judged by a REGE
782 coefficient See clustering results in SI). Top: areas closed to trawling in the fall, after shrimp
783 season (MDS stress=0.099 after 42 iterations); Bottom: areas open to trawling after shrimp
784 season (MDS stress=0.091 after 47 iterations).

785 Figure 6. The Core Sound food web, with nodes arranged using MDS as in Figure 2 bottom
786 (Fall, Open), but with node size scaled as the difference in \log_{10} biomass between open trawling
787 and closed trawling areas (i.e., the ratio of biomasses in the two areas). Top graph: nodes in
788 which $(\log_{10} \text{ open biomass} - \log_{10} \text{ closed biomass}) > 0$, i.e., where the biomass in open trawling
789 areas exceeded closed trawling areas; Bottom graph: nodes in which $(\log_{10} \text{ closed biomass} -$
790 $\log_{10} \text{ open biomass}) > 0$, i.e., where the biomass in closed trawling areas exceeded open trawling
791 areas.

792 Figure 7. Ecosim projections of relative biomass (2001 baseline gC m^{-2}), while simulating the
793 impact of a trawl net ban (after 2008), for the bycatch and key species in Core Sound, NC. Top
794 row, left: trawling trips reported to NCDMF; top row, right: bycatch (discards of all species);
795 second row, left: benthic deposit-feeding polychaetes; second row, right: brown shrimp; third
796 row, left: spot, *Leiostomus xanthurus*; third row, right: pinfish, *Lagodon rhomboides*; bottom
797 left: blue crabs *Callinectes sapidus*, bottom right: southern flounder *Paralichthys lethostigma*
798 and other paralichthid flounders. Dashed line represents the steady-state biomass in 2001 prior to
799 the trawl ban for each compartment.

800

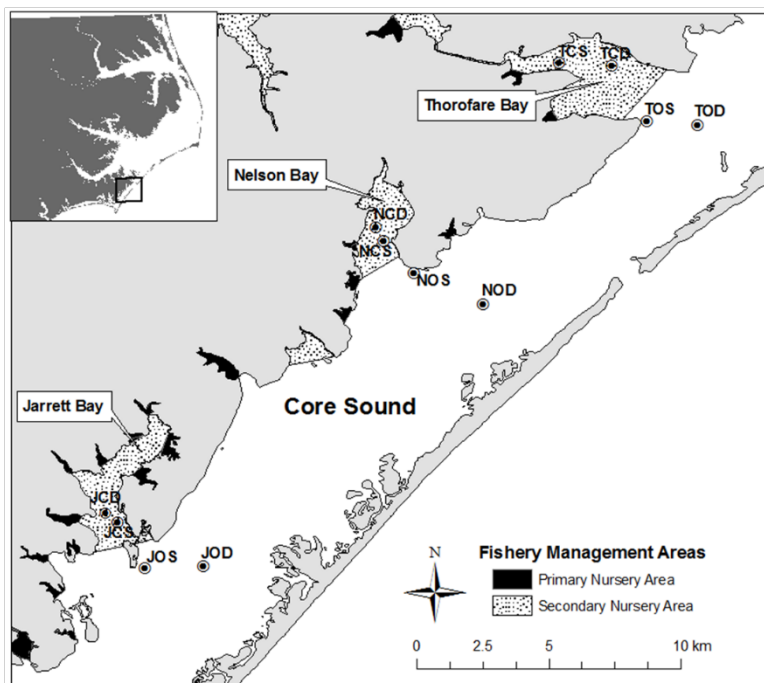


Figure 1

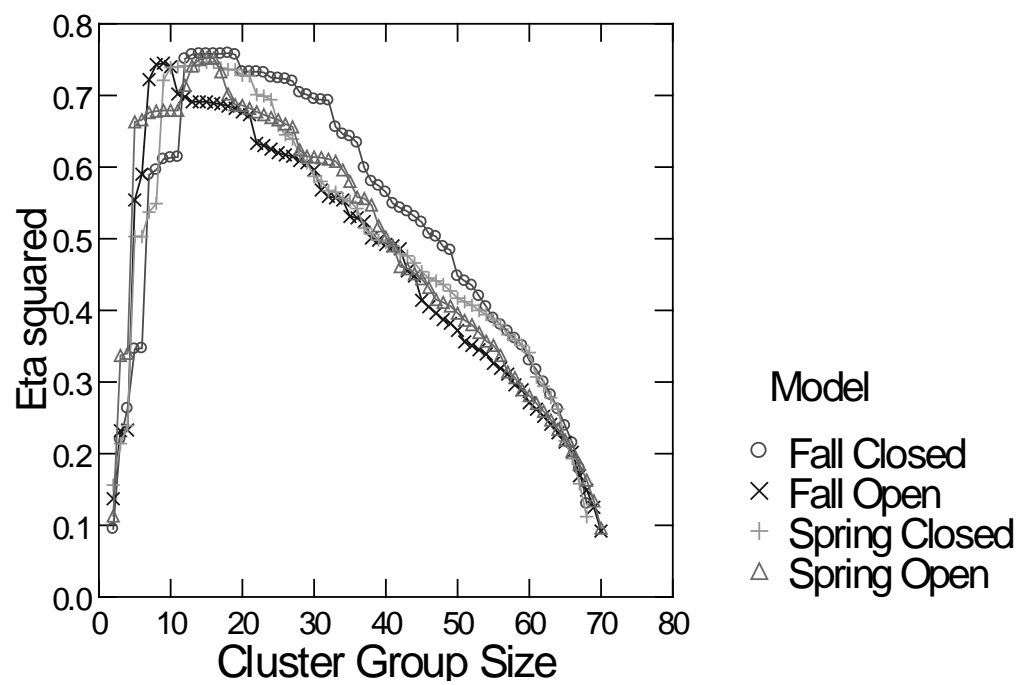


Figure 2

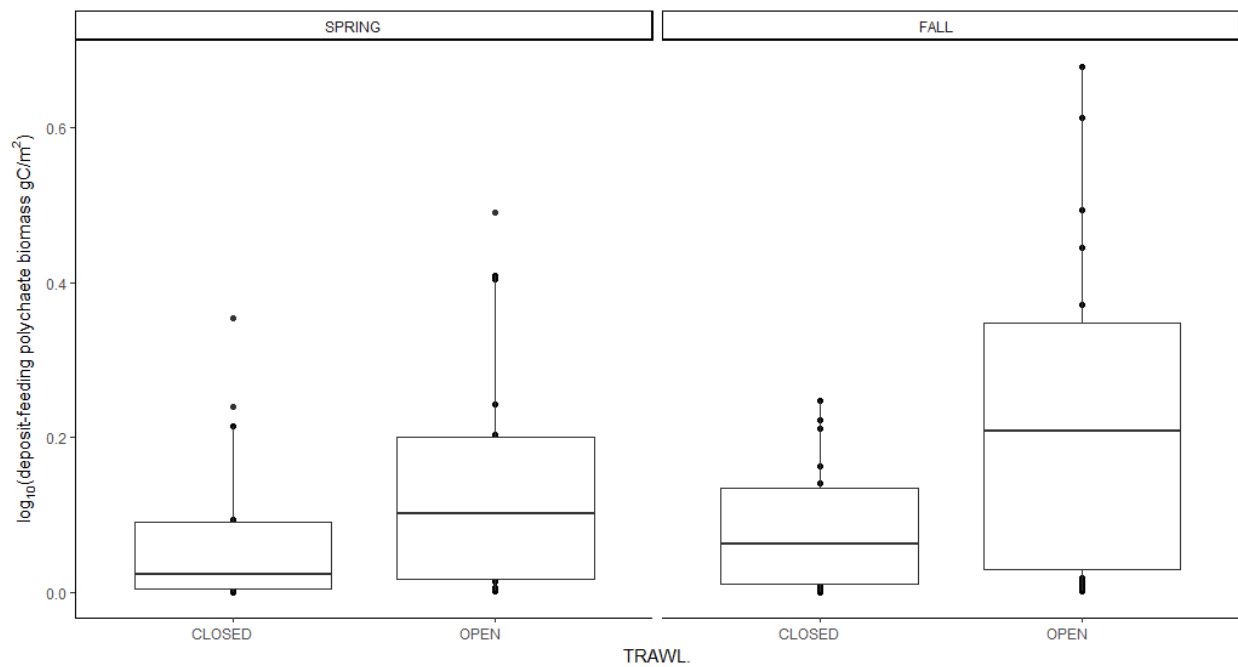


Figure 3

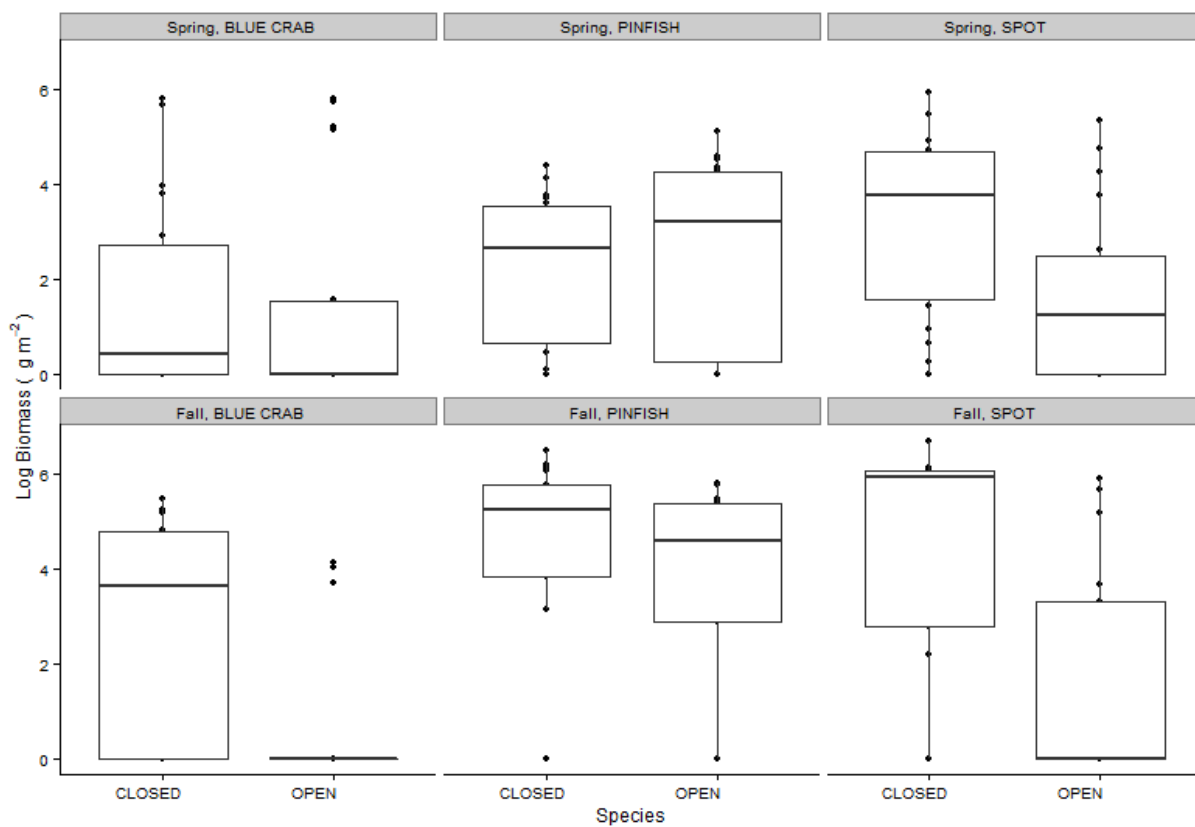


Figure 4

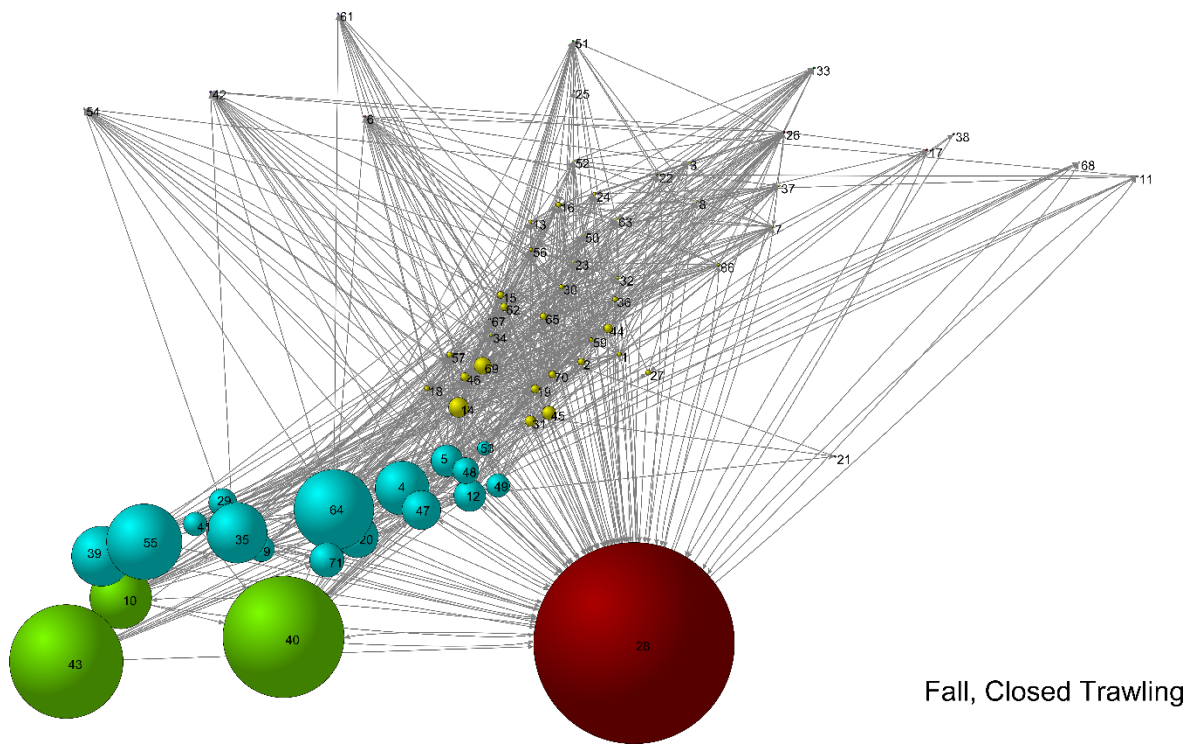


Figure 5.

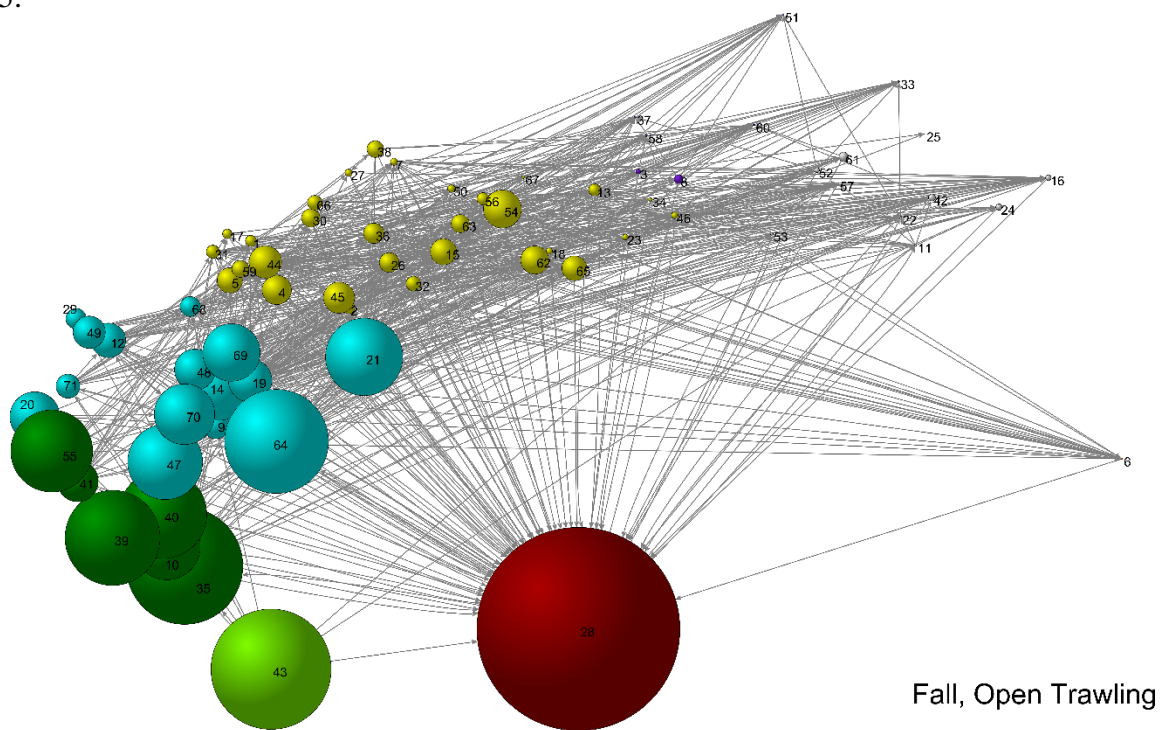
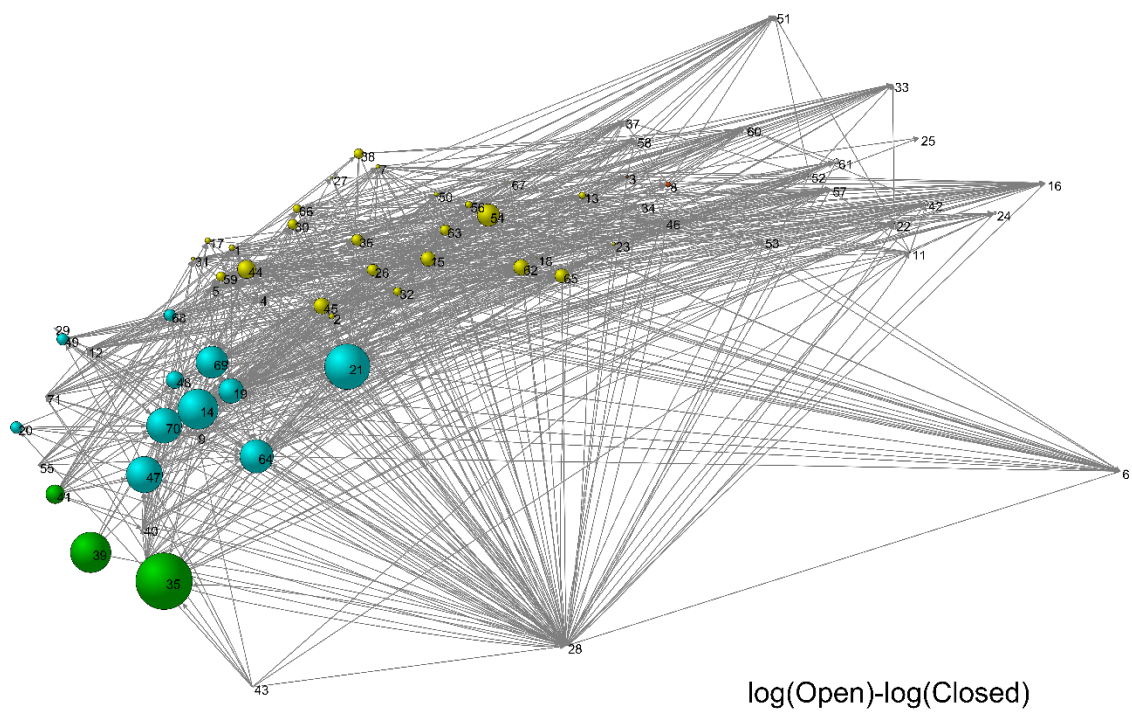
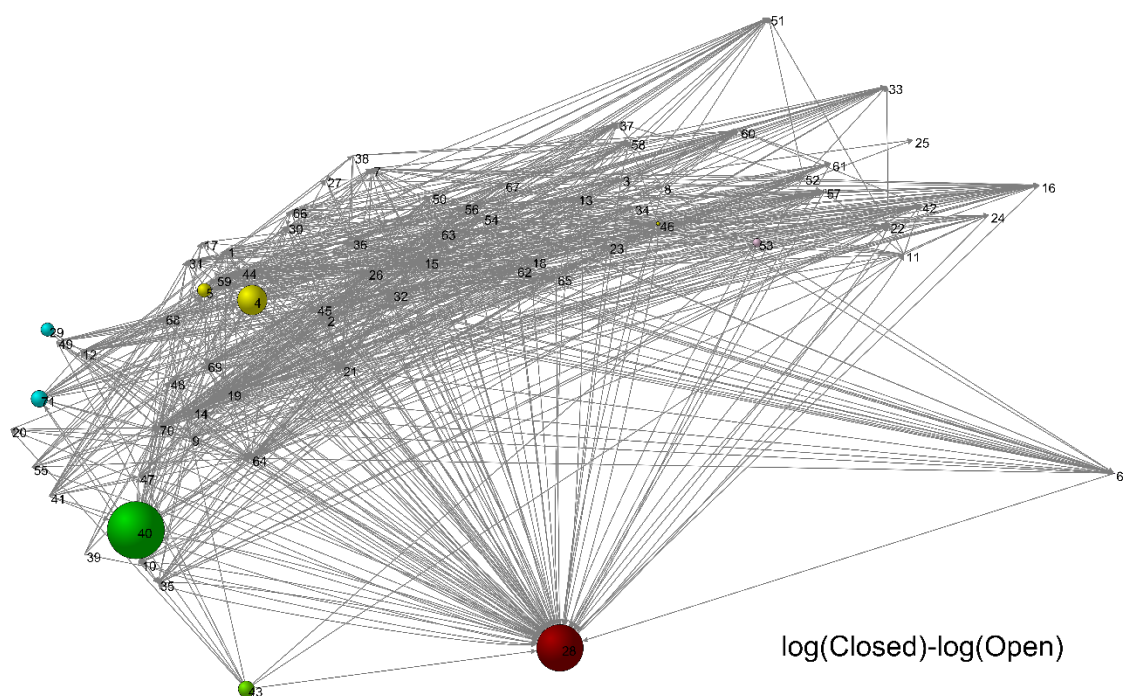


Figure 6



⌘

Figure 7



⌘

Figure 8

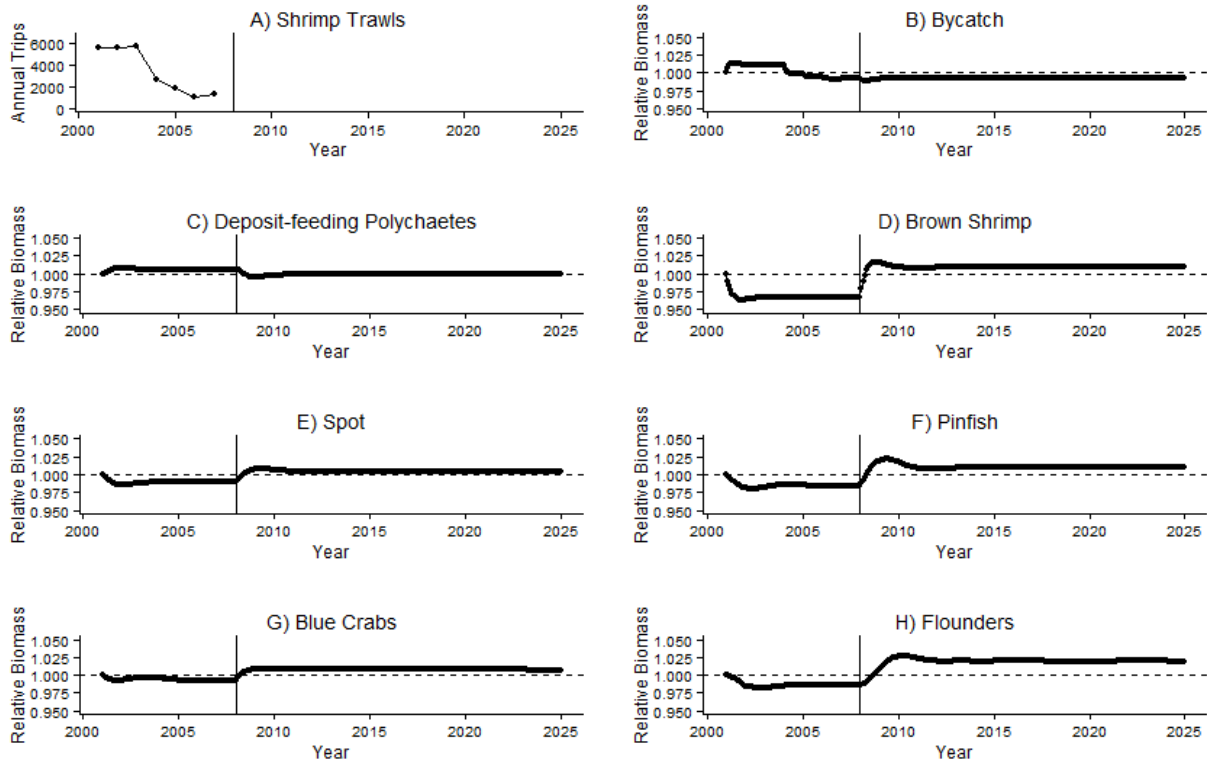
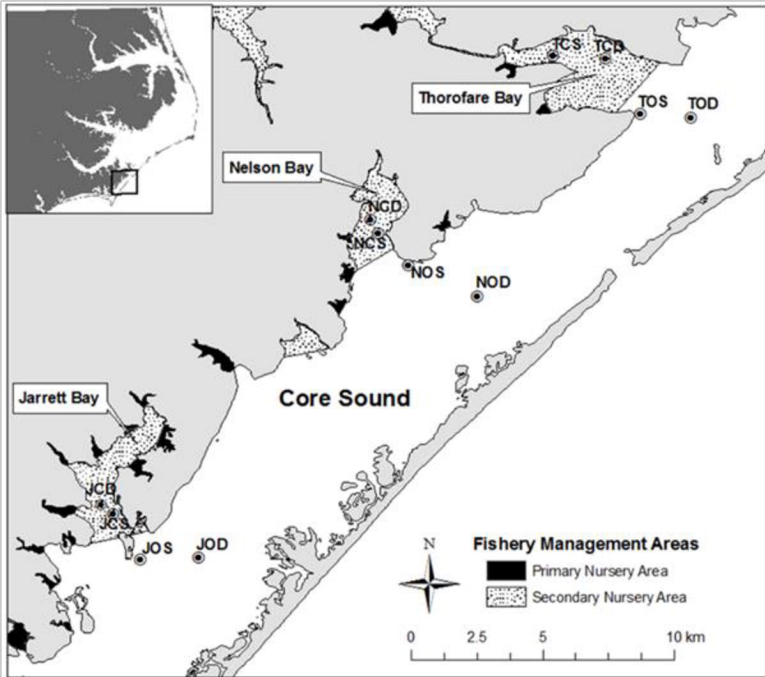


Figure 9



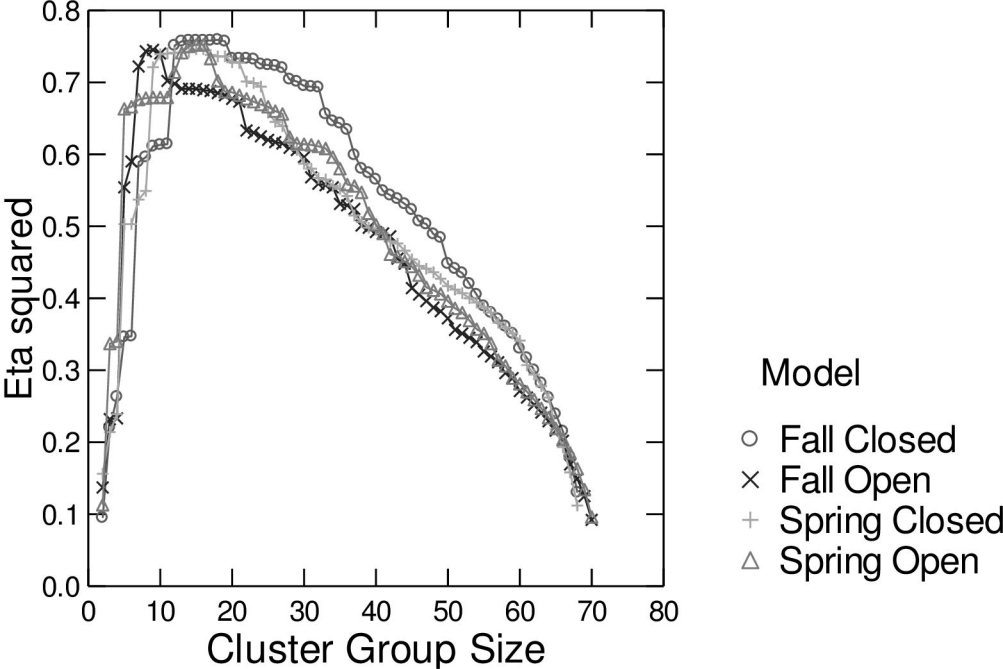
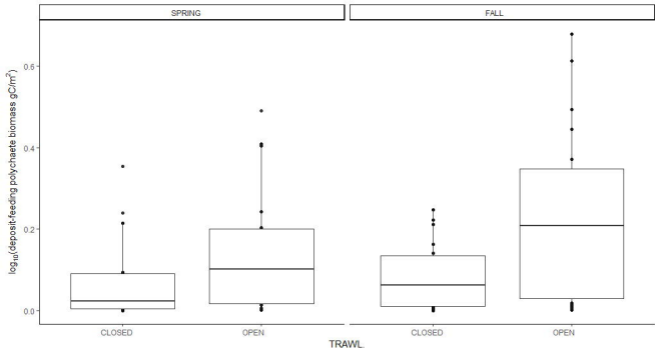


Figure 2



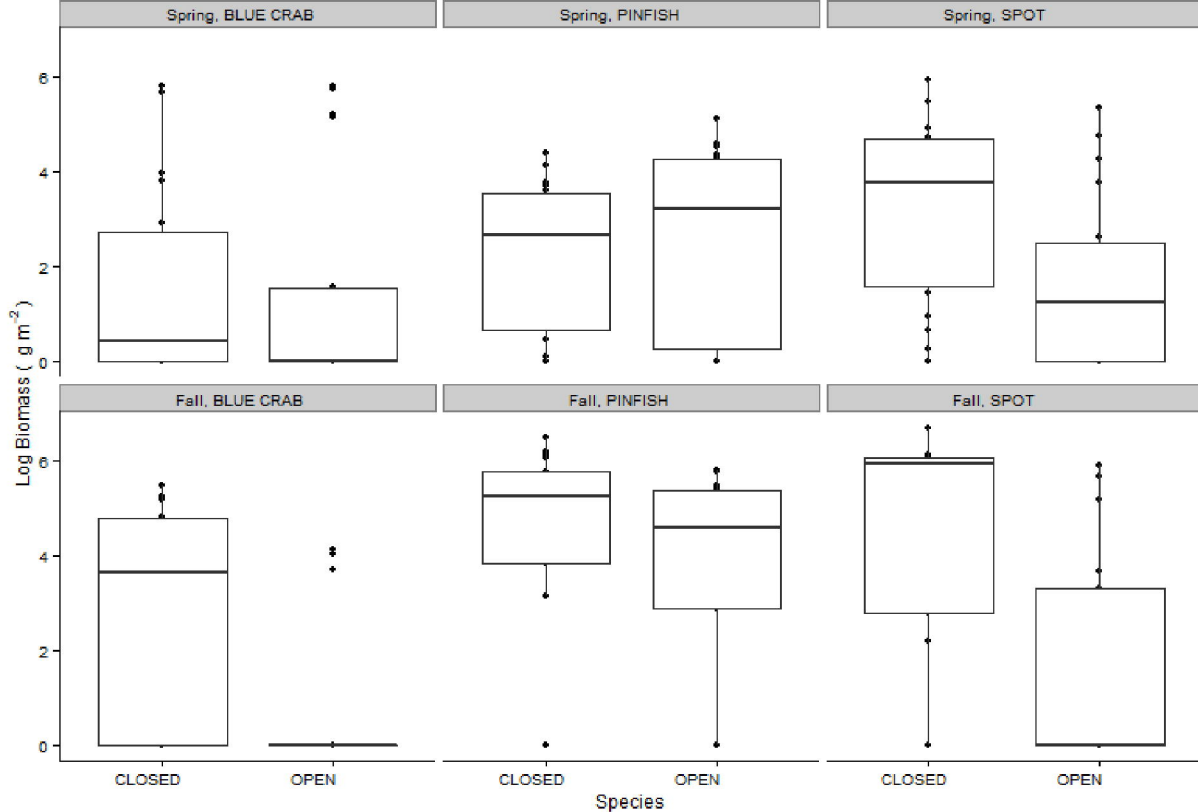
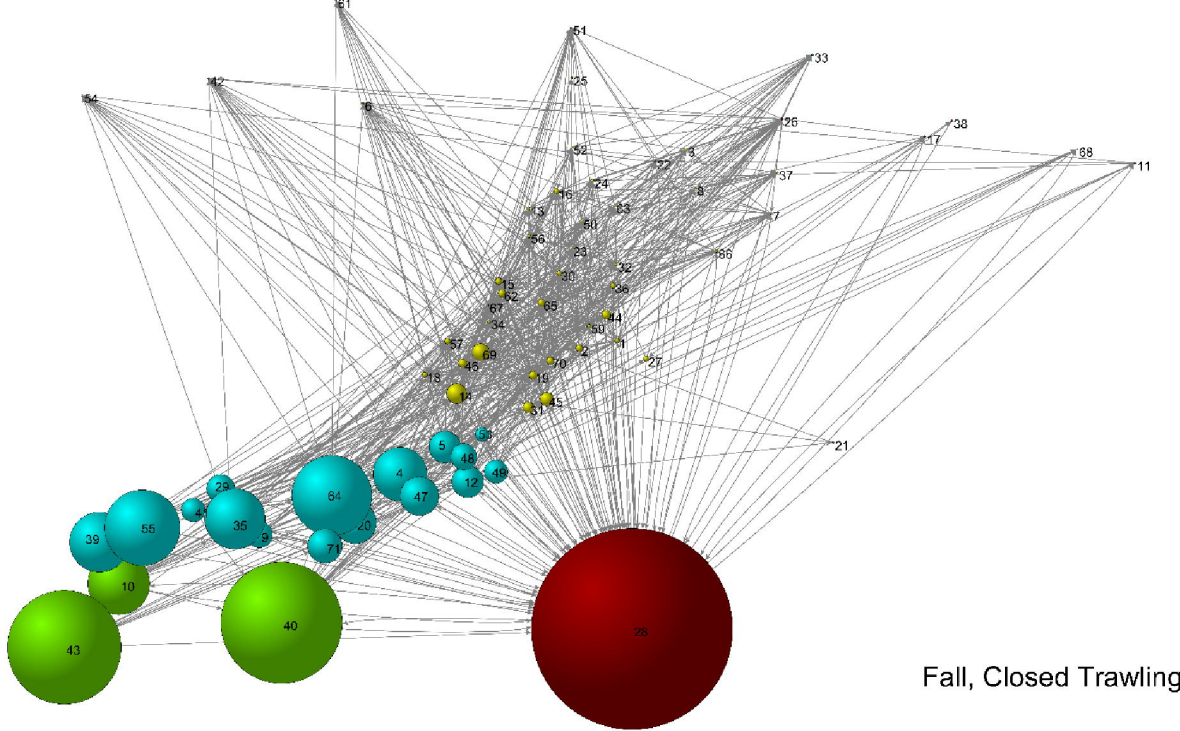
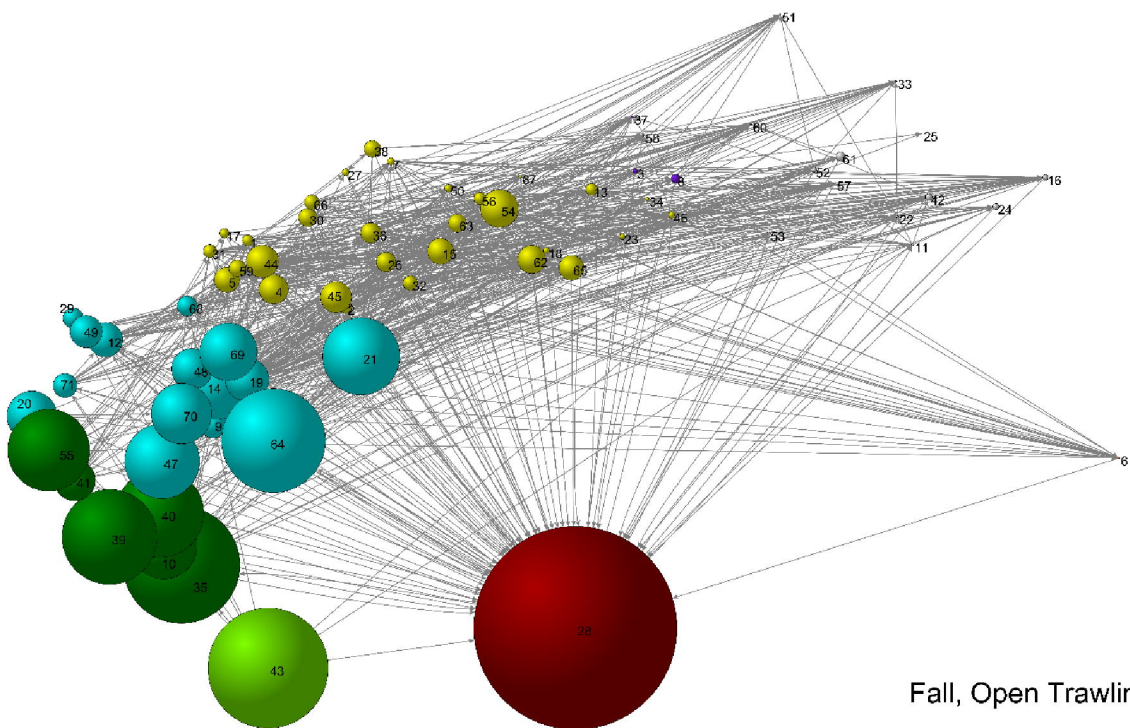


Figure 4



Fall, Closed Trawling



Fall, Open Trawling

Figure 5

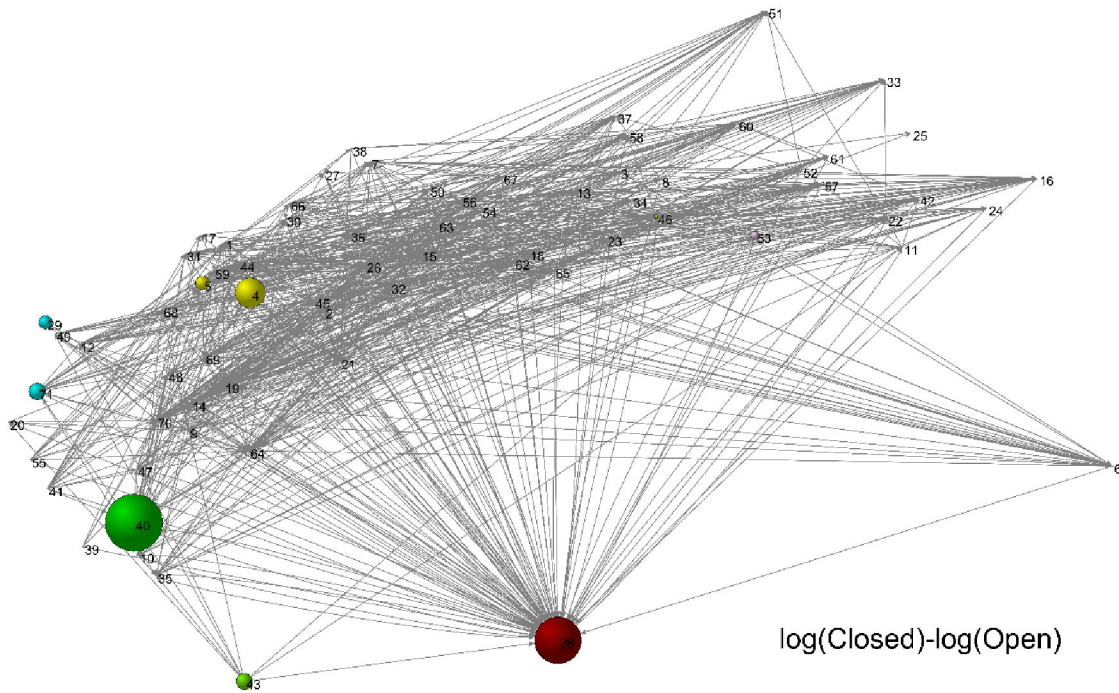
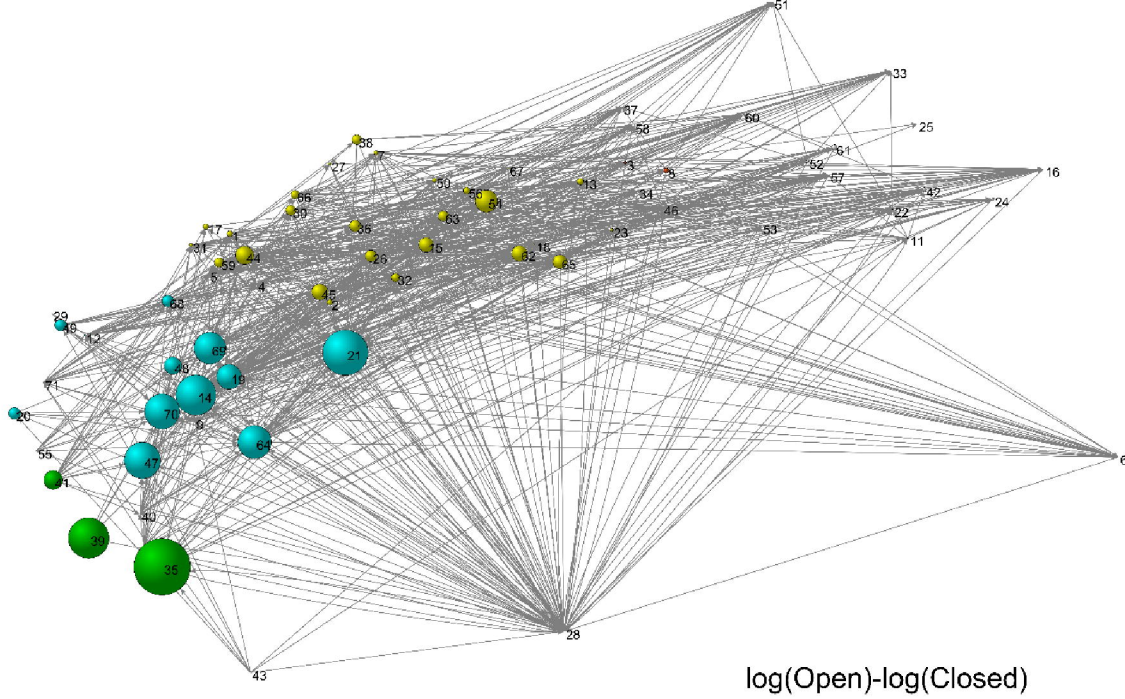


Figure 6

