

1 **Title: Biomass transfer subsidizes nitrogen to offshore food webs**

2 **Running Head:** *Biomass subsidies to offshore food webs*

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**Abstract**

We evaluated the potential contribution of allochthonous biomass subsidies to the upper trophic levels of offshore food webs in the northeastern Gulf of Mexico (GOM). We made this evaluation considering nitrogen, an essential and often limiting nutrient in coastal ecosystems, to estimate the potential production of within-ecosystem biomass relative to the known import of biomass from an adjacent seagrass dominated ecosystem. When adjusted for trophic transfer efficiency, we found the biomass subsidy from a single species (pinfish, *Lagodon rhomboides*) from neashore seagrass habitat to the offshore GOM to be greater than the amount of nitrogen exported by a two major rivers and local submarine ground water discharge. Our calculations show that seagrass-derived biomass accounts for ~25% of the total potential production in the northeastern GOM. This estimate is in agreement with a previous study that found 18.5-25% of the biomass in a predatory reef fish was derived from seagrass biomass inputs. These results indicate that all of the sources we consider account for the majority of the nitrogen available to the food web in the northeastern GOM. Our approach could be adapted to other coupled ecosystems to determine the relative importance of biomass subsidies to coastal ocean food webs.

**Key words:** ecosystem subsidies, allochthonous, biomass, seagrass, food web, secondary production

57 **Introduction**

58 The earliest ecological inquiries into the function of estuarine ecosystems found them to be  
59 intimately connected to the seas that they border (Nixon, 1980). An important connection,  
60 identified in early research, was the export of energy and materials from estuarine habitats to the  
61 coastal ocean (Odum, 1968; Haines and Montague, 1979). Research on estuarine exports or  
62 “outwelling” was initially focused on the export of detritus and dissolved nutrients acting to  
63 increase production at the base of food webs in the recipient ecosystem (Teal, 1962; Odum and  
64 de la Cruz, 1967; Odum, 1968; McCann et al., 1998). Increasingly however, researchers find  
65 this type of outwelling to be highly variable, exporting smaller amounts of material than  
66 previously thought, with relatively minor contributions to production outside of the estuary  
67 (Taylor and Allanson, 1995; Childers et al., 2002; Sutula et al., 2003).

68 A second form of estuarine export, particularly in temperate regions, is nekton biomass  
69 (Deegan, 1993; Kneib, 1997; Stevens et al., 2006; Nelson et al., 2012). The export of biomass  
70 from one system to another can act to “subsidize” production in the recipient ecosystem (Ben-  
71 David et al., 1997; Polis et al., 1997; Nelson et al., 2012). In the same way that organisms  
72 concentrate and transport organic contaminants, biomass subsidies concentrate nutrients and  
73 actively transport them across ecosystem boundaries (Blais et al., 2007). Unlike the flux of  
74 dissolved nutrients, organism transported biomass is readily incorporated directly into recipient  
75 food webs. These focused movements of nutrients are much more efficient than fluxes of  
76 dissolved nutrients that are more likely to be lost due to processes such as denitrification or  
77 sedimentation.

78 The roles of biomass subsidies in ecosystems have been well-studied. In lakes, mobile  
79 predators integrate production from the littoral zone coupling it with pelagic habitats (Dolson et

80 al., 2009). These littoral-pelagic subsidies have also been shown to stabilize the population  
81 dynamics of predators in lake communities (Schindler and Schuerell, 2002). Biomass subsidies  
82 via the movement of Pacific salmon (*Oncorhynchus* spp.) in lotic ecosystems are by far the most  
83 well-understood. The annual return of salmon from its oceanic feeding grounds provides energy  
84 and nutrients to stream food webs from primary producers to top carnivores (Hilderbrand et al.,  
85 1999; Holtgrieve and Schindler, 2010). Initially, subsidies of salmon biomass were thought to  
86 primarily increase productivity via bottom-up stimulation of the food web (Stockner, 2003;  
87 Claeson et al., 2006). However, more recent studies have shown net increases in total ecosystem  
88 respiration following the influx of salmon biomass indicating that the salmon are being  
89 incorporated directly into the food web at higher trophic levels (Holtgrieve and Schindler, 2010).  
90 Moreover, studies have demonstrated consumers shifted from their typical diets to salmon  
91 biomass (Ben-David et al., 2004; Hocking and Reimchen, 2006).

92         Although not as well known as salmonid migrations, those of estuarine fish to adjacent  
93 offshore ecosystems can also represent a large export of biomass. Coastal habitats such as  
94 estuaries, saltmarshes, and seagrass beds are among the most productive ecosystems (Fischlin et  
95 al., 2007; Waycott et al., 2009). Many of the coastal fishes accumulate their biomass during the  
96 growing season (typically spring through early fall), then migrate to the adjacent offshore waters  
97 in the winter, with few returning the following spring (Kneib, 1997; Stevens et al., 2006;  
98 Stallings et al., 2010; Nelson et al., 2012). The Florida Big Bend region of the northeastern GOM  
99 provides a prototypical example of this type of coastal ecosystem.

100         The Big Bend is a relatively pristine, warm-temperate, coastal ecosystem characterized by  
101 seagrass and salt marsh habitat that extends from the peninsular to panhandle regions of the state  
102 (Figure 1). Pinfish (*Lagodon rhomboides*, Family Sparidae) are the most abundant vertebrates in

103 seagrass habitats during the spring and summer months (Stallings and Koenig, 2011). Post-larval  
104 pinfish recruit to seagrass habitats from November to March (Nelson, 1998). After recruitment,  
105 young-of-year pinfish remain in the seagrass until the late fall when they migrate offshore to  
106 spawn (Muncy 1984). While offshore, pinfish are preyed upon heavily by offshore predators  
107 (Naughton and Saloman, 1985; Nelson et al., 2012). Although some pinfish return following their  
108 annual migration, size data suggest that >90 % of those that inhabit seagrass beds are less than 1  
109 year old, suggesting substantial over winter mortality (Nelson, 2002; Stallings and Koenig,  
110 2011).”

111 The adjacent offshore habitat of the Big Bend seagrass beds is characterized by a gently  
112 sloping continental shelf spotted with patchy “hard bottom” reef habitat. In terms of primary  
113 productivity, the northeastern GOM is oligotrophic and is nitrogen limited (Lohrenz et al., 1999;  
114 Mullholland, 2007; Vargo et al., 2008). Primary production is supported by nitrogen inputs from  
115 atmospheric deposition, groundwater discharge, and *in-situ* fixation (Lohrenz et al., 1999).  
116 Despite the low rate of primary productivity, the northeastern GOM sustains a fishery that lands  
117 ~ 3.6 million kilograms annually of red grouper (*Epinephelus morio*) and gag (*Mycteroperca*  
118 *microlepis*), two year-round resident upper trophic-level epinephelids (SEFSC, 2004, 2006).

119 Because biogenic flux of nutrients occurs between aquatic habitats and at large spatial  
120 scales, it can be difficult to determine the relative importance of biomass subsidies in coastal  
121 ecosystems. Here we use nitrogen, the limiting nutrient, as a “common unit” to compare the  
122 production exported from seagrass beds (Pinfish) to potential production from other major inputs  
123 of nitrogen in an offshore ecosystem. Fisheries production has been shown to be bottom-up  
124 controlled in several marine ecosystems (Iverson, 1990; Ware and Thomson, 2005). Therefore,  
125 external biomass subsidies can supplement offshore top level consumers resulting in greater

126 biomass than would be possible by *in situ* production alone. By coupling estimates of trophic  
127 transfer efficiency of nitrogen with estimates of trophic position we assess the relative  
128 importance of near-shore biomass to offshore within-ecosystem production available to  
129 predators. Our estimates are not proposed as a nitrogen budget and do not account for spatial or  
130 temporal variation, but they provide a basis for comparing the potential importance of biomass  
131 subsidies. All estimates are given as Total Nitrogen, which includes all organic and inorganic  
132 nitrogen sources. We hypothesize, that pinfish secondary production from seagrass habitats (in  
133 the form of fish prey) represents a significant source of energy available to offshore food webs  
134 when compared to offshore production sources.

## 135 **Methods and Results**

136 Our estimates are made by taking literature and database values and converting them to  
137 common units. To make these calculations easier to follow we have combined the methods and  
138 results sections. All values and error terms were converted from those given in the referenced  
139 studies to kg/km<sup>2</sup>/yr for comparison. For quick reference all initial values and conversions can be  
140 found in Table 1.

## 141 **Nitrogen Flux Calculations**

142 We compared nitrogen flux from seagrass habitats via pinfish migration to five previously  
143 identified N-sources in the northeastern GOM: 1) Apalachicola River, 2) Suwannee River 3)  
144 Atmospheric deposition, 4) Submarine groundwater discharge (SGD), and 5) Nitrogen fixation  
145 by a marine filamentous cyanobacteria diazotroph, *Trichodesmium*. Although not an exhaustive  
146 list of primary nitrogen sources to the northeastern GOM, these represent the major sources to  
147 the area (Lohrenz et al., 1999; Mullholland, 2007; Vargo et al., 2008) and the input of each has  
148 been quantified well enough for us to make reasonable estimates. Very little is known about

149 upwelling and nutrient recycling in the northeastern GOM. The available literature suggests the  
150 movement of water in this region of the GOM is out (down-welling) on an annual basis so we do  
151 not consider up-welling or recycled dissolved N as a source in our estimates (Harris et al., 2012).

152       Going forward we refer to these offshore nitrogen sources as “primary” sources because they  
153 are in the form of dissolved N and have not yet been incorporated into the food web. To make  
154 the primary nitrogen and pinfish estimates comparable, we first convert the nitrogen flux values  
155 to an annual nitrogen flux ( $\text{kg}/\text{km}^2/\text{yr}$ ). Then we multiply the annual primary nitrogen flux by the  
156 trophic transfer efficiency of nitrogen to bring the inputs of primary nitrogen to the trophic level  
157 of pinfish. We use trophic transfer efficiency of 28% (Iverson, 1990) and a trophic level of 3 for  
158 pinfish (Wilson, 2010). Equation 1 was used to calculate the primary nitrogen equivalence at  
159 trophic level 3:

172 GOM with a mean discharge of  $\sim 450 \text{ m}^3/\text{sec}$ . The Suwannee River is the second largest  
173 freshwater source to the northeastern GOM with a discharge approximately 45% that of the  
174 Apalachicola River. Mortazavi et al. (2000) estimated the annual nitrogen flux from  
175 Apalachicola Bay to the GOM was  $32,850 \pm 2,518 \text{ kg N km}^{-2} \text{ yr}^{-1}$ . The area refers to the areal  
176 extent of the Bay. Although some nitrogen transformations occur prior to the nitrogen escaping  
177 the Bay, with some uptake in the summer and more export in the winter net flux from the river is  
178 balanced on seasonal time scales. Here we use the estimate by Mortazavi et al. (2000) as the  
179 maximum potential contribution nitrogen to the GOM from the Apalachicola River on an annual  
180 basis.

181 The mean daily nitrogen flux was determined from June 1994-May 1996 when mean river  
182 flow was  $926 \text{ m}^3/\text{s}$ . This was higher than the long term flow average (Mortazavi et al., 2000),  
183 therefore our estimate of the amount of nitrogen delivered by the river is likely slightly higher  
184 than average. The area of Apalachicola Bay used for this study was  $260 \text{ km}^2$  (Mortazavi et al.,  
185 2000). Apalachicola River flux of nitrogen to the GOM was  $8.54 \times 10^6 \pm 6 \times 10^5 \text{ kg N yr}^{-1}$ ,  
186 which is equivalent to  $1.87 \times 10^5 \pm 6.97 \times 10^4 \text{ kg yr}^{-1}$  at trophic level three.

187 The Suwannee River has a mean discharge of  $208 \text{ m}^3/\text{sec}$ . The mean annual flux of nitrogen  
188 from the Suwannee is  $10 \times 10^6 \text{ kg N/year}$  (Bledsoe and Philips, 2000; Landing unpublished  
189 data). The Suwannee River empties directly into the northeastern GOM creating a plume  
190 approximately  $400 \text{ km}^2$  (Bledsoe and Philips, 2000). Although a portion of this flux passes over  
191 the Big Bend seagrass habitat little nitrogen is removed in the estuarine mixing zone (Bledsoe  
192 and Philips, 2000). This yields an annual flux of  $1.0 \times 10^7 \text{ kg N yr}^{-1} \pm 2 \times 10^6 \text{ kg N yr}^{-1}$ . At  
193 trophic level three the nitrogen available for secondary production would be  $2.2 \times 10^5 \text{ kg} \pm 2 \times$   
194  $10^4 \text{ kg N yr}^{-1}$ .

195 Wet and dry atmospheric deposition is a major source of nitrogen to the northeastern GOM  
196 contributing 10% to 40% to total annual loadings (Paerl et al., 2002). Mean annual atmospheric  
197 deposition of total nitrogen in the northeastern GOM was estimated using mean fluxes  
198 determined by the National Atmospheric Deposition Program (NADP) based on maps (generated  
199 at <http://nadp.sws.uiuc.edu>). The mean nitrogen flux used for our estimates was  $800 \pm 240 \text{ kg km}^{-2}$   
200  $\text{yr}^{-1}$ . This value is similar to those determined by previous studies of nutrient deposition in the  
201 northeastern GOM (Paerl et al., 2002; Vargo et al., 2008). The area of the northeastern GOM  
202 shelf used for our estimate was  $7 \times 10^4 \text{ km}^2$  (Paerl et al., 2002; Vargo et al., 2008). The total  
203 nitrogen flux from the atmosphere over the northern portion of the west Florida Shelf ( $7 \times 10^4$   
204  $\text{km}^2$ ) was estimated to be  $5.6 \times 10^7 \pm 1.22 \times 10^6 \text{ kg N yr}^{-1}$ . At trophic level 3, atmospheric  
205 deposition could potentially contribute  $1.23 \times 10^6 \pm 1.63 \times 10^5 \text{ kg N yr}^{-1}$ .

206 Water column nitrogen fixation is an important source in oligotrophic marine systems  
207 accounting for nearly half of new production (Mullholland, 2007). Nitrogen fixing cyanobacteria  
208 are abundant in the coastal waters of the northeastern GOM (Walsh and Steidinger, 2001).  
209 Estimates of nitrogen fixation in the surface waters of the northeastern GOM by *Trichodesmium*  
210 spp. are approximately  $1.07 \times 10^3 \text{ kg N km}^{-2}\text{yr}^{-1}$  (Holl, 2004; Mullholland et al., 2006;  
211 Mullholland, 2007). This production was multiplied by the area of the northern west Florida  
212 shelf to determine an annual nitrogen fixation rate (Figure 1). The nitrogen fixation by  
213 *Trichodesmium* was estimated to be  $7.47 \times 10^7 \pm 1.3 \times 10^6 \text{ kg N yr}^{-1}$ , which provides a potential  
214 contribution of  $1.64 \times 10^6 \pm 4.87 \times 10^5 \text{ kg N yr}^{-1}$  to trophic level 3.

215 The Floridan Aquifer covers an area of  $260,000 \text{ km}^2$  and is one of the largest sources of  
216 submarine ground water discharge in the world (Santos et al., 2008). Submarine groundwater  
217 discharge (SGD) is a significant source of nitrogen to the coastal zone (Burnett et al., 2006). The

218 flux of nitrogen via SGD in the northeastern GOM has been reported as  $4.55 \times 10^{14} \text{ kg}^{-1} \text{ m}^{-2}$   
219 (Santos et al., 2008). The vast majority (95%) of this nitrogen is recycled from the overlying  
220 water with 5% new nitrogen coming from the aquifer. This discharge occurs over the entire  
221 northern Gulf coast of Florida (i.e., 800km) along a 200m seepage face extending from shore;  
222 thus the areal extent to which we applied seepage was 200m by 800km of coastline, yielding 160  
223  $\text{km}^2$ . This provides an initial new nitrogen flux of  $2.40 \times 10^5 \pm 1.92 \times 10^4 \text{ kg N yr}^{-1}$ . If fixed into  
224 prey items available to upper level predators the flux would be equivalent to  $5.27 \times 10^3 \pm 1.78 \times$   
225  $10^2 \text{ kg N yr}^{-1}$ .

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### 227 **Pinfish Collection and Biomass Estimates**

228 Pinfish were captured using 1.9 m beam trawls (19 mm mesh with 3 mm mesh liner) towed  
229 on both sides of a 6.1 m research vessel. Sampling was conducted during June and July each  
230 year in 2009 and 2010 at 170 sites throughout the seagrass meadows of the Florida Big Bend.  
231 The trawls were towed for 2.5 minutes at a standard rate of 1.8 - 2.0 km/h (approximately 75 m)  
232 within the seagrass meadows. Sampling locations were selected using a random, spatially-  
233 balanced approach where every replicate of the sample exhibited a spatial density pattern that  
234 closely mimicked that of the seagrass (Stevens and Olsen, 2004; Stallings and Koenig, 2011).

235 All captured pinfish were counted and assigned to one of five length bins (26-50 mm, 51-75  
236 mm, 76-100 mm, 101-150 mm, and 151-200 mm) and most pinfish were then released unharmed  
237 back into the water. All fish less than A sub-sample of pinfish was placed in plastic bags on ice,  
238 taken back to the laboratory and frozen at  $-20^\circ\text{C}$  until they could be processed for nitrogen  
239 content analysis. All work involving animals was conducted under the auspices of (and approved  
240 by) the Florida State University Animal Care and Use Committee (Protocol #9408).

241 The mean number of pinfish caught per size bin per site was divided by the total area sampled  
242 during the study to estimate the per hectare (ha) density estimate of pinfish. This value was then  
243 multiplied by the area of seagrass habitat in the Big Bend (2688km<sup>2</sup>) (Stallings and Koenig,  
244 2011) to estimate the abundance of each size class pinfish in the Big Bend.

245 The abundance of pinfish in each size bin was then used to estimate the biomass contained in  
246 each size class. A hypothetical population was created using the *R* statistical package to generate  
247 a continuous uniform distribution (Fox, 2005). In this method there was an equal probability of  
248 any length within the size class being generated. These sizes were applied to a length-weight  
249 curve for pinfish to estimate the total amount of biomass within each size class. The length-  
250 weight relationship was determined by Nelson (2002) and is:

264  $\times 10^6$  kg). The increase in biomass is primarily due to the greater abundance of the two largest  
265 size classes in 2010. With a mean N content of 13%, pinfish transported  $6.08 \times 10^5 \pm 1.99 \times 10^5$   
266 kg N and  $1.1 \times 10^6 \pm 3.44 \times 10^5$  kg N offshore in 2009 and 2010, respectively. There is an  
267 additional 553 km<sup>2</sup> of seagrass in the rest of the Florida Panhandle (17% the size of the Big  
268 Bend), so we multiplied the average pinfish N flux estimate from 2009 and 2010 ( $8.6 \times 10^5 \pm$   
269  $3.55 \times 10^5$ ) by 1.17 to yield a mean export of  $1.01 \times 10^6$  kg N per year for the entire seagrass  
270 habitat. All biomass estimates are compared in figure 2.

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## 272 **Discussion**

273 Our study has demonstrated that fish migration can be a potential conduit for the transfer of  
274 production from shallow nearshore habitats to the coastal ocean (Figure 2). Other studies have  
275 quantified the amount of production contained in abundant estuarine consumers (e.g. Deegan,  
276 1993, Steven et al. 2006), but in our work we tried to directly quantify estuarine subsidies  
277 relative to production sources in offshore habitats.

278 In the northeastern GOM seagrass habitats act to “package” large quantities of nitrogen into  
279 prey items in a relatively small area (i.e., Big Bend region), that is then transported to adjacent  
280 offshore habitats of low *in-situ* primary productivity. From a bottom-up perspective, the amount  
281 of nitrogen contained in pinfish is approximately an order of magnitude smaller than inputs from  
282 other sources and although the GOM is oligotrophic the impact on primary production is likely  
283 small. However, because the export is incorporated directly into the offshore food web via  
284 consumption the effects on community structure and upper trophic level production are  
285 potentially quite large. Unlike fluxes of primary nutrients that are dispersed widely and may or  
286 may not be easily incorporated into the offshore food web, biomass fluxes are delivered directly

287 to suitable fish habitats. When pinfish egress from the seagrass beds in the fall move offshore to  
288 small reefs occupied by upper-level consumers (Muncy, 1984; Nelson et al., 2012). Furthermore,  
289 the timing of the pinfish flux in the northeastern GOM occurs prior to the spawning season of  
290 several groupers that prey on them, contributing directly to the production of eggs (Coleman et  
291 al., 1996; Nelson et al., 2012).

292 Our estimates of absolute flux by pinfish are likely conservative because of continued pre-  
293 migratory growth beyond the date of sampling. The pinfish would remain in the seagrass habitat  
294 and continue to grow through the month of October, when the annual migration to offshore  
295 habitats occurs. The most abundant size classes observed in the study were 26-50 mm and 51-75  
296 mm bins, which are still in the exponential portion of the growth curve (Nelson, 2002). Pinfish  
297 have a low rate of mortality while in the seagrass habitat (Nelson 2002), and therefore the  
298 nitrogen fluxed via pinfish at the end of the growing season would likely be greater than the  
299 estimates made from fish captured in June and July (i.e., two to three months prior to egress).

### 300 **Conclusion**

301 Although it is widely accepted that ecosystems send and receive material across their  
302 boundaries, the occurrence and effect of biomass subsidies in coastal ecosystems is poorly  
303 understood. Our estimated pinfish biomass flux of nitrogen to the offshore grouper habitat is  
304 greater than the amount of nitrogen (when transferred to the 3<sup>rd</sup> trophic level) delivered from the  
305 Apalachicola River, the Suwannee River, and from SGD, and is on the same order as  
306 atmospheric deposition and Trichodesmium N fixation in the northeastern GOM. Furthermore,  
307 isotopic evidence suggests that because the flux is in the form of prey, it is has a disproportional  
308 effect on offshore food webs (Deegan, 1993; Nelson et al., 2012). By our estimates pinfish are  
309 23% of the total nitrogen available to upper trophic levels. This is in good agreement with a

310 previous study that found 18.5-25 % seagrass-derived biomass in grouper muscle tissue in the  
311 northeastern GOM (Nelson et al. 2012). Therefore, we conclude that our estimates are  
312 reasonable and include all the major nitrogen potentially entering offshore food webs. Although  
313 this method has short comings (e.g., assuming 100% of nitrogen is directed toward the food  
314 web), our results demonstrate the power of this method for quantifying biomass subsidies in  
315 marine habitats. Given the limited information available on the occurrence, size, and impacts of  
316 the export of secondary production in coastal ecosystems, we suggest that our method for  
317 estimating the impacts of various nitrogen sources on piscivore productivity in offshore habitats  
318 can be applied to other coastal marine ecosystems.

319 It is likely there is a high degree of trophic connectivity among coastal ecosystems.  
320 Incorporating biomass subsidies into our understanding of ecosystem function will require us to  
321 rethink the limits on productivity in marine ecosystems. Worldwide, productive near-shore  
322 habitats such as coral reefs, salt marshes, and seagrass beds have all shown significant declines  
323 in recent years (Day et al., 2000; Pandolfi et al., 2003; Silliman and Bertness, 2004; Waycott et  
324 al., 2009). Reduction in the output of biomass from these habitats has the potential to effect  
325 secondary production in the ecosystems that receive biomass subsidies from these habitats. In  
326 our system loss of seagrass habitat could result in an indirect loss of grouper fishery production  
327 with no observed change in overall offshore productivity.

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**Acknowledgements**

We thank the anonymous reviewers for their constructive input. We acknowledge Rachel Wilson and Behzad Mortazavi for their input during manuscript preparation. The field work required an enormous effort from many students, technicians and volunteers, especially A. Mickle, J. Brower, A. Cruz Benitez, E. Field, B. Hall, E. Simmons, and M. Sosa, plus excellent logistical support from the Florida State Coastal and Marine Laboratory staff, especially by B. Henderson for his efforts to design and construct the trawls and boom system. Funding for the field surveys was provided by the US Fish and Wildlife Service / State Wildlife federal grant number T-15, Florida Fish and Wildlife Conservation Commission agreement number 08007. Additional funding support was provided by the Florida Institute of Oceanography and the U.S. National Oceanic and Atmospheric Administration (Northern Gulf of Mexico Cooperative Institute 191001-363558-01).

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**Tables**

Table 1 The raw input and conversion factors used to make the potential production estimates for the Atmospheric deposition, fixation of nitrogen by Trichodesmium, nitrogen contained in submarine groundwater discharge (SGD), and the flux of nitrogen from the Apalachicola and Suwannee Rivers. The pinfish (*Lagodon rhomboids*) flux of nitrogen is listed for comparison.

Source	N Input (kg/km <sup>2</sup> /yr)	Area (km <sup>2</sup> )	Flux Total (kg/yr)	Trophic Steps	Production (kg/yr)
Atmosphere	800	70000	5.60 x 10 <sup>7</sup>	0.022	1.23 x 10 <sup>6</sup>
Trichodesmium	1068	70000	7.47 x 10 <sup>7</sup>	0.022	1.64 x 10 <sup>6</sup>
SGD	1500	160	2.40 x 10 <sup>5</sup>	0.022	5.27 x 10 <sup>3</sup>
Apalachicola River	32850	260	8.54 x 10 <sup>6</sup>	0.022	1.87 x 10 <sup>5</sup>
Suwannee River	25000	400	1.00 x 10 <sup>7</sup>	0.022	2.20 x 10 <sup>5</sup>
Pinfish ( <i>Lagodon</i> )	NA	3241	1.01 x 10 <sup>6</sup>	0	1.01 x 10 <sup>6</sup>

539 **Figure Legends**

540 Figure 1 The areas used to calculate the nitrogen fluxes. The area of the seagrass habitat is  
541 3,241km<sup>2</sup>. The area of Apalachicola Bay used was 260km<sup>2</sup>, but the Apalachicola-Flint-  
542 Chattahoochee (ACF) watershed covers an area of 50,505 km<sup>2</sup>. The Suwannee River plume is  
543 400 km<sup>2</sup> with a 25,406 km<sup>2</sup> drainage basin. The offshore area, indicated by the black line, used to  
544 calculate the amount of nitrogen input from atmospheric deposition and nitrogen fixation was  
545 70,000 km<sup>2</sup> The groundwater seepage area is was calculated to be 160 km<sup>2</sup>.

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547 Figure 2 Amount of potential production supplied to the offshore environment from the  
548 Apalachicola River, Suwannee River, Atmosphere, submarine groundwater discharge (SGD),  
549 and *Trichodesmium* fixation (Equation 2). The pinfish estimate is the amount of nitrogen  
550 contained in the biomass of pinfish in the Big Bend plus 17% to account for all Florida  
551 panhandle seagrass beds. The error bars indicate Standard Error.

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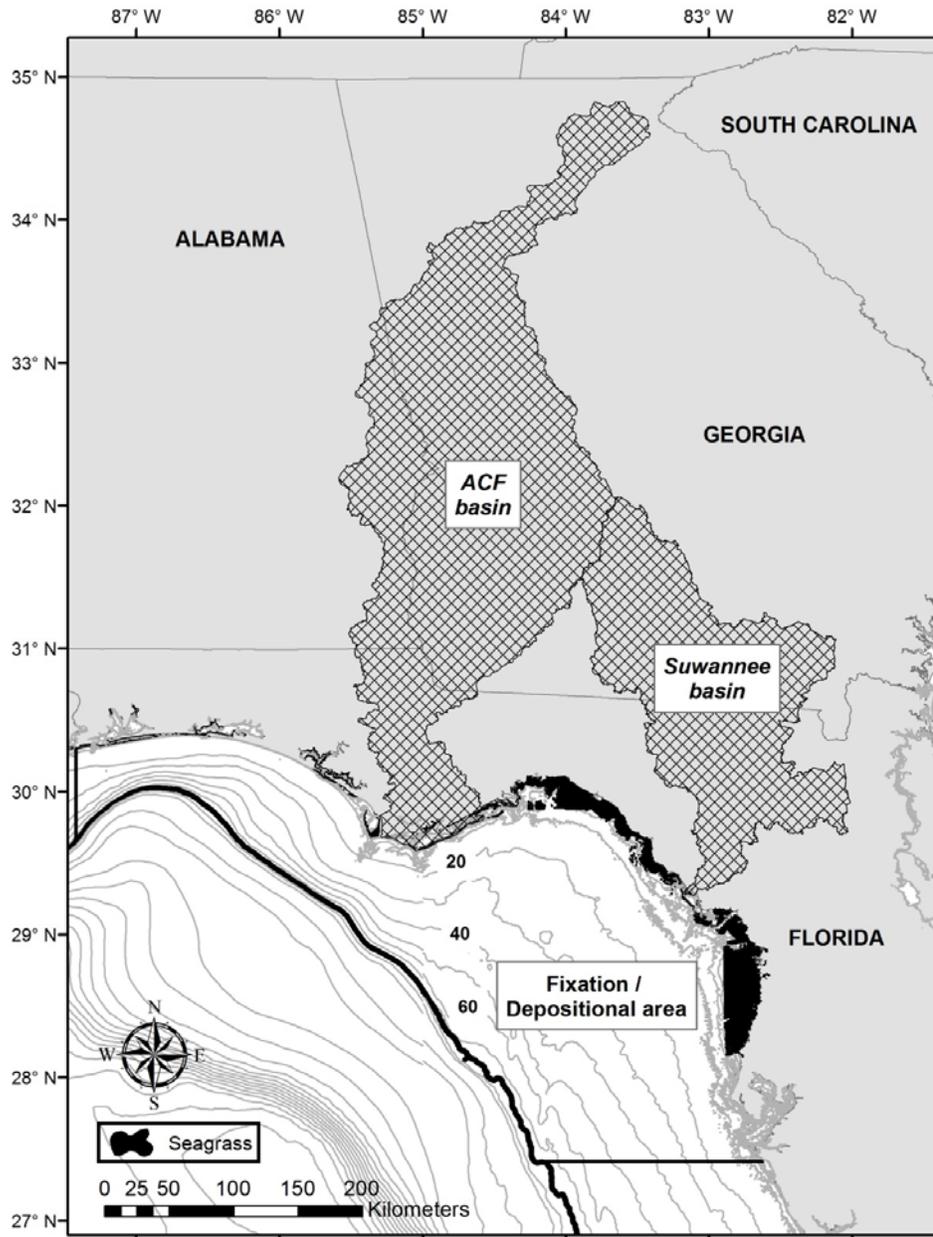
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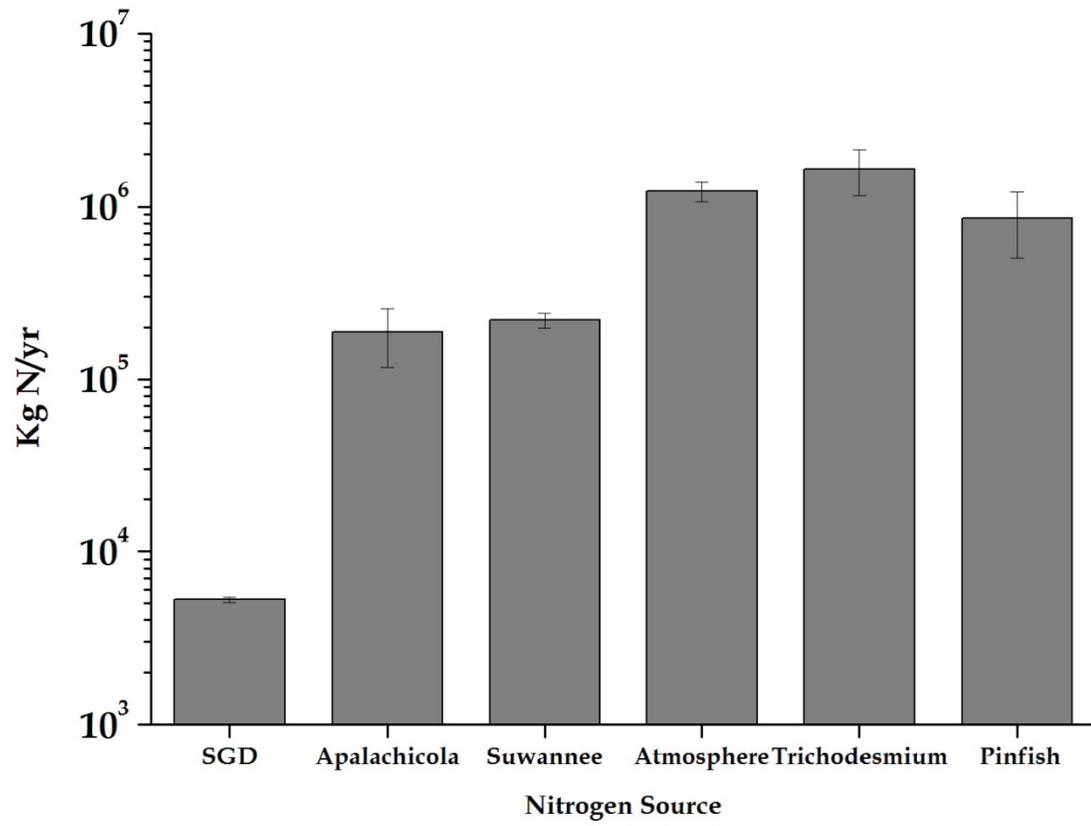
562 **Figures**



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564 **Figure 1**

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567 Figure 2

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