

# Biomass Transfer Subsidizes Nitrogen 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 nearshore seagrass habitat to the offshore GOM to be greater than the amount of nitrogen exported by two major rivers and local submarine ground water discharge. Our

calculations show that seagrass-derived biomass accounts for approximately 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.

## INTRODUCTION

The earliest ecological inquiries into the function of estuarine ecosystems found them to be intimately connected to the seas that they border (Nixon 1980). An important connection, identified in early

research, was the export of energy and materials from estuarine habitats to the coastal ocean (Odum 1968; Haines and Montague 1979). Research on estuarine exports or “outwelling” was initially focused on the export of detritus and dissolved nutrients acting to increase production at the base of food webs in the recipient ecosystem (Teal 1962; Odum and de la Cruz 1967; Odum 1968; McCann and others 1998). Increasingly, however, researchers find this type of outwelling to be highly variable, exporting smaller amounts of material than previously thought, with relatively minor contributions to production outside of the estuary (Taylor and Allanson 1995; Childers and others 2002; Sutula and others 2003).

Received 18 January 2013; accepted 22 March 2013

**Author Contributions:** James A. Nelson conceived and designed the study, performed the research, analyzed data, and wrote the article. Christopher D. Stallings designed the study, performed research, analyzed data, and assisted in writing. William Landing analyzed data, performed research, and assisted in writing. Jeffery Chanton designed the study, performed research, and assisted in writing.

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

The roles of biomass subsidies in ecosystems have been well studied. In lakes, mobile predators integrate production from the littoral zone coupling it with pelagic habitats (Dolson and others 2009). These littoral–pelagic subsidies have also been shown to stabilize the population dynamics of predators in lake communities (Schindler and Schuerell 2002). Biomass subsidies via the movement of Pacific salmon (*Oncorhynchus* spp.) in lotic ecosystems are by far the most well understood. The annual return of salmon from its oceanic feeding grounds provides energy and nutrients to stream food webs from primary producers to top carnivores (Hilderbrand and others 1999; Holtgrieve and Schindler 2010). Initially, subsidies of salmon biomass were thought to primarily increase productivity via bottom-up stimulation of the food web (Stockner 2003; Claeson and others 2006).

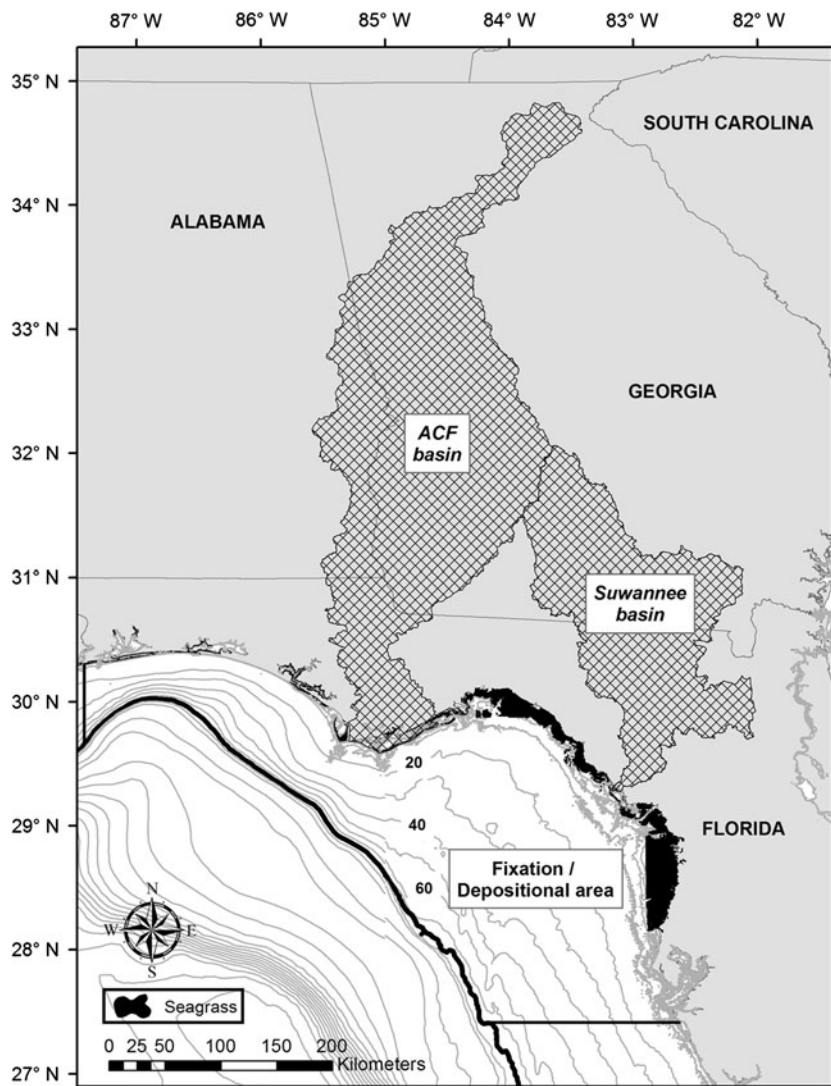


Figure 1. The areas used to calculate the nitrogen fluxes. The area of the seagrass habitat is 3,241 km<sup>2</sup>. The area of Apalachicola Bay used was 260 km<sup>2</sup>, but the Apalachicola-Flint-Chattahoochee (ACF) watershed covers an area of 50,505 km<sup>2</sup>. The Suwannee River plume is 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 calculate the amount of nitrogen input from atmospheric deposition and nitrogen fixation was 70,000 km<sup>2</sup>. The groundwater seepage area was calculated to be 160 km<sup>2</sup>.

However, more recent studies have shown net increases in total ecosystem respiration following the influx of salmon biomass indicating that the salmon are being incorporated directly into the food web at higher trophic levels (Holtgrieve and Schindler 2010). Moreover, studies have demonstrated consumers shifted from their typical diets to salmon biomass (Ben-David and others 2004; Hocking and Reimchen 2006).

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

The Big Bend is a relatively pristine, warm-temperate, coastal ecosystem characterized by seagrass and salt marsh habitat that extends from the peninsular to panhandle regions of the state (Figure 1). Pinfish (*Lagodon rhomboides*, Family Sparidae) are the most abundant vertebrates in seagrass habitats during the spring and summer months (Stallings and Koenig 2011). Post-larval pinfish recruit to seagrass habitats from November to March (Nelson 1998). After recruitment, young-of-year pinfish remain in the seagrass until the late fall when they migrate offshore to spawn (Muncy 1984). While offshore, pinfish are preyed upon heavily by offshore predators (Naughton and Saloman 1985; Nelson and others 2012). Although some pinfish return following their annual migration, size data suggest that greater than 90% of those that inhabit seagrass beds are less than 1 year old, suggesting substantial over winter mortality (Nelson 2002; Stallings and Koenig 2011).

The adjacent offshore habitat of the Big Bend seagrass beds is characterized by a gently sloping continental shelf spotted with patchy “hard bottom” reef habitat. In terms of primary productivity, the northeastern GOM is oligotrophic and is nitrogen limited (Lohrenz and others 1999; Mullholland 2007; Vargo and others 2008). Primary production is supported by nitrogen inputs from atmospheric deposition, groundwater discharge, and in situ fixation (Lohrenz and others 1999).

Despite the low rate of primary productivity, the northeastern GOM sustains a fishery that lands approximately 3.6 million kilograms annually of red grouper (*Epinephelus morio*) and gag (*Mycteroperca microlepis*), 2-year round resident upper trophic-level epinephelids (SEFSC 2004, 2006).

Because biogenic flux of nutrients occurs between aquatic habitats and at large spatial scales, it can be difficult to determine the relative importance of biomass subsidies in coastal ecosystems. Here, we use nitrogen, the limiting nutrient, as a “common unit” to compare the production exported from seagrass beds (Pinfish) to potential production from other major inputs of nitrogen in an offshore ecosystem. Fisheries production has been shown to be bottom-up controlled in several marine ecosystems (Iverson 1990; Ware and Thomson 2005). Therefore, external biomass subsidies can supplement offshore top level consumers resulting in greater biomass than would be possible by in situ production alone. By coupling estimates of trophic transfer efficiency of nitrogen with estimates of trophic position we assess the relative importance of nearshore biomass to offshore within-ecosystem production available to predators. Our estimates are not proposed as a nitrogen budget and do not account for spatial or temporal variation, but they provide a basis for comparing the potential importance of biomass subsidies. All estimates are given as total nitrogen, which includes all organic and inorganic nitrogen sources. We hypothesize that pinfish secondary production from seagrass habitats (in the form of fish prey) represents a significant source of energy available to offshore food webs when compared to offshore production sources.

## METHODS AND RESULTS

Our estimates are made by taking literature and database values and converting them to common units. To make these calculations easier to follow we have combined the methods and results sections. All values and error terms were converted from those given in the referenced studies to  $\text{kg}/\text{km}^2 \text{y}^{-1}$  for comparison. For quick reference all initial values and conversions can be found in Table 1.

### Nitrogen Flux Calculations

We compared nitrogen flux from seagrass habitats via pinfish migration to five previously identified N sources in the northeastern GOM: (1) Apalachicola River, (2) Suwannee River, (3) atmospheric deposition,

**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

Source	N input (kg/km <sup>2</sup> y)	Area (km <sup>2</sup> )	Flux total (kg y <sup>-1</sup> )	Trophic steps	Production (kg y <sup>-1</sup> )
Atmosphere	800	70,000	$5.60 \times 10^7$	0.022	$1.23 \times 10^6$
Trichodesmium	1,068	70,000	$7.47 \times 10^7$	0.022	$1.64 \times 10^6$
SGD	1,500	160	$2.40 \times 10^5$	0.022	$5.27 \times 10^3$
Apalachicola River	32,850	260	$8.54 \times 10^6$	0.022	$1.87 \times 10^5$
Suwannee River	25,000	400	$1.00 \times 10^7$	0.022	$2.20 \times 10^5$
Pinfish (Lagodon)	NA	3,241	$1.01 \times 10^6$	0	$1.01 \times 10^6$

The pinfish (*Lagodon rhomboids*) flux of nitrogen is listed for comparison.

(4) submarine groundwater discharge (SGD), and (5) nitrogen fixation by a marine filamentous cyanobacteria diazotroph, *Trichodesmium*. Although not an exhaustive list of primary nitrogen sources to the northeastern GOM, these represent the major sources to the area (Lohrenz and others 1999; Mullholland 2007; Vargo and others 2008) and the input of each has been quantified well enough for us to make reasonable estimates. Very little is known about upwelling and nutrient recycling in the northeastern GOM. The available literature suggests the movement of water in this region of the GOM is out (down-welling) on an annual basis so we do not consider upwelling or recycled dissolved N as a source in our estimates (Harris and others 2012).

Going forward we refer to these offshore nitrogen sources as “primary” sources because they are in the form of dissolved N and have not yet been incorporated into the food web. To make the primary nitrogen and pinfish estimates comparable, we first convert the nitrogen flux values to an annual nitrogen flux (kg/km<sup>2</sup> y<sup>-1</sup>). Then, we multiply the annual primary nitrogen flux by the trophic transfer efficiency of nitrogen to bring the inputs of primary nitrogen to the trophic level of pinfish. We use trophic transfer efficiency of 28% (Iverson 1990) and a trophic level of 3 for pinfish (Wilson 2010). Equation 1 was used to calculate the primary nitrogen equivalence at trophic level 3:

$$N = B \times 0.28^T \quad (1)$$

where  $B$  is the quantity of observed nitrogen,  $T$  is mean trophic level the biomass occupies and is the primary nitrogen equivalent production required to produce that quantity of biomass. After transferring the nitrogen to the third trophic level, we assume that 100% of the primary nitrogen that had been fixed into the food web and available for consumption by upper level carnivores. Of course in

nature not all of the nitrogen is fixed into the food web so we will overestimate the amount of production from the primary nitrogen sources, thus providing a conservative estimate of the biomass subsidy to the upper trophic levels of the offshore food web.

### Primary Nitrogen Sources

The largest riverine sources of nitrogen in the northeastern GOM are the Apalachicola and Suwannee Rivers. The Apalachicola River is the largest river that drains into the northeastern GOM with a mean discharge of approximately 450 m<sup>3</sup>/s. The Suwannee River is the second largest freshwater source to the northeastern GOM with a discharge approximately 45% that of the Apalachicola River. Mortazavi and others (2000) estimated the annual nitrogen flux from Apalachicola Bay to the GOM was  $32,850 \pm 2,518$  kg N km<sup>-2</sup> y<sup>-1</sup>. The area refers to the areal extent of the Bay. Although some nitrogen transformations occur prior to the nitrogen escaping the Bay, with some uptake in the summer and more export in the winter net flux from the river is balanced on seasonal time scales. Here, we use the estimate by Mortazavi and others (2000) as the maximum potential contribution nitrogen to the GOM from the Apalachicola River on an annual basis.

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

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

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

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

The Floridan Aquifer covers an area of  $260,000 \text{ km}^2$  and is one of the largest sources of

submarine ground water discharge in the world (Santos and others 2008). SGD is a significant source of nitrogen to the coastal zone (Burnett and others 2006). The flux of nitrogen via SGD in the northeastern GOM has been reported as  $4.55 \times 10^{14} \text{ kg}^{-1} \text{ m}^{-2}$  (Santos and others 2008). The vast majority (95%) of this nitrogen is recycled from the overlying water with 5% new nitrogen coming from the aquifer. This discharge occurs over the entire northern Gulf coast of Florida (that is,  $800 \text{ km}$ ) along a  $200 \text{ m}$  seepage face extending from shore; thus the areal extent to which we applied seepage was  $200 \text{ m}$  by  $800 \text{ km}$  of coastline, yielding  $160 \text{ km}^2$ . This provides an initial new nitrogen flux of  $2.40 \times 10^5 \pm 1.92 \times 10^4 \text{ kg N y}^{-1}$ . If fixed into prey items available to upper level predators the flux would be equivalent to  $5.27 \times 10^3 \pm 1.78 \times 10^2 \text{ kg N y}^{-1}$ .

## Pinfish Collection and Biomass Estimates

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

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

The mean number of pinfish caught per size bin per site was divided by the total area sampled during the study to estimate the per hectare (ha) density estimate of pinfish. This value was then multiplied by the area of seagrass habitat in the Big Bend ( $2,688 \text{ km}^2$ ) (Stallings and Koenig 2011) to estimate the abundance of each size class pinfish in the Big Bend.

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

$$TW = 0.0269 * SL^{3.11}, \quad (2)$$

where TW is the total weight in grams and SL is the standard length of the pinfish in millimeters. The nitrogen content was determined by multiplying the biomass by the mean fraction of nitrogen in pinfish (13%) as determined by CHN analysis (Wilson and others 2009). These values were used to calculate the per km<sup>2</sup> estimate for nitrogen fluxed from the Big Bend via pinfish migration.

The 2,688 km<sup>2</sup> of seagrass habitat in the Florida Big Bend contained  $1.46 \times 10^9 \pm 2.39 \times 10^8$  individual pinfish in 2009 and  $1.39 \times 10^9 \pm 2.38 \times 10^8$  in 2010. The most abundant size class of pinfish in both years was 26–50 mm comprising  $8.13 \times 10^8 \pm 1.53 \times 10^8$  and  $6.67 \times 10^8 \pm 1.21 \times 10^8$  individuals in 2009 and 2010, respectively. In 2009, the 51– to 75-mm size class contained the greatest amount of biomass  $2.17 \times 10^6 \pm 6.99 \times 10^5$  kg. In 2010, the largest size class (151–200 mm) contained the most biomass  $2.44 \times 10^6 \pm 5.89 \times 10^5$  kg. The total amount of biomass produced in 2010 was slightly higher ( $7.42 \times 10^6 \pm 2.30 \times 10^6$  kg) than in 2009 ( $4.68 \times 10^6 \pm 1.53 \times 10^6$  kg). The increase in biomass is primarily due to the greater abundance of the two largest size classes in 2010. With a mean N content of 13%, pinfish transported  $6.08 \times 10^5 \pm 1.99 \times 10^5$  and  $1.1 \times 10^6 \pm 3.44 \times 10^5$  kg N offshore in 2009 and 2010, respectively. There is an additional 553 km<sup>2</sup> of seagrass in the rest of the Florida Panhandle (17% the size of the Big Bend), so we multiplied the average pinfish N flux estimate from 2009 and 2010 ( $8.6 \times 10^5 \pm 3.55 \times 10^5$ ) by 1.17 to yield a mean export of  $1.01 \times 10^6$  kg N y<sup>-1</sup> for the entire seagrass habitat. All biomass estimates are compared in Figure 2.

## DISCUSSION

Our study has demonstrated that fish migration can be a potential conduit for the transfer of production from shallow nearshore habitats to the

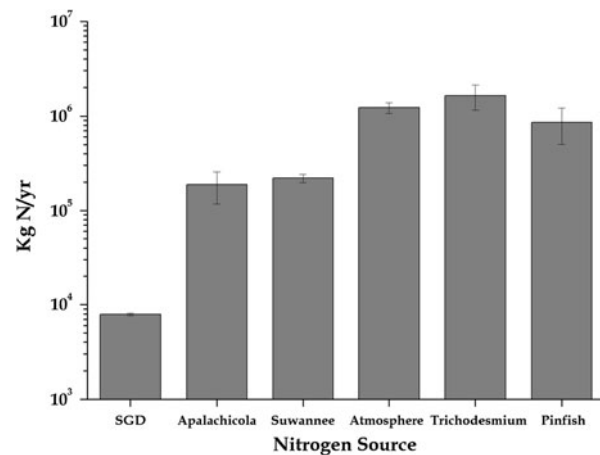


Figure 2. Amount of potential production supplied to the offshore environment from the Apalachicola River, Suwannee River, Atmosphere, submarine groundwater discharge (SGD), and *Trichodesmium* fixation (Eq. 2). The pinfish estimate is the amount of nitrogen contained in the biomass of pinfish in the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

coastal ocean (Figure 2). Other studies have quantified the amount of production contained in abundant estuarine consumers (for example, Deegan 1993; Stevens and others 2006), but in our study we tried to directly quantify estuarine subsidies relative to production sources in offshore habitats.

In the northeastern GOM, seagrass habitats act to “package” large quantities of nitrogen into prey items in a relatively small area (that is, Big Bend region), that is then transported to adjacent offshore habitats of low in situ primary productivity. From a bottom-up perspective, the amount of nitrogen contained in pinfish is approximately an order of magnitude smaller than inputs from other sources and although the GOM is oligotrophic the impact on primary production is likely small. However, because the export is incorporated directly into the offshore food web via consumption the effects on community structure and upper trophic level production are potentially quite large. Unlike fluxes of primary nutrients that are dispersed widely and may or may not be easily incorporated into the offshore food web, biomass fluxes are delivered directly to suitable fish habitats. When pinfish egress from the seagrass beds in the fall they move offshore to small reefs occupied by upper level consumers (Muncy 1984; Nelson and others 2012). Furthermore, the timing of the pinfish flux in the northeastern GOM occurs prior to the spawning season of several groupers that

prey on them, contributing directly to the production of eggs (Coleman and others 1996; Nelson and others 2012).

Our estimates of absolute flux by pinfish are likely conservative because of continued pre-migratory growth beyond the date of sampling. The pinfish would remain in the seagrass habitat and continue to grow through the month of October, when the annual migration to offshore habitats occurs. The most abundant size classes observed in the study were 26- to 50- and 51- to 75-mm bins, which are still in the exponential portion of the growth curve (Nelson 2002). Pinfish have a low rate of mortality while in the seagrass habitat (Nelson 2002), and therefore the nitrogen fluxed via pinfish at the end of the growing season would likely be greater than the estimates made from fish captured in June and July (that is, 2–3 months prior to egress).

## CONCLUSION

Although it is widely accepted that ecosystems send and receive material across their boundaries, the occurrence and effect of biomass subsidies in coastal ecosystems is poorly understood. Our estimated pinfish biomass flux of nitrogen to the offshore grouper habitat is greater than the amount of nitrogen (when transferred to the 3rd trophic level) delivered from the Apalachicola River, the Suwannee River, and from SGD, and is on the same order as atmospheric deposition and *Trichodesmium* N fixation in the northeastern GOM. Furthermore, isotopic evidence suggests that because the flux is in the form of prey, it has a disproportional effect on offshore food webs (Deegan 1993; Nelson and others 2012). By our estimates pinfish are 23% of the total nitrogen available to upper trophic levels. This is in good agreement with a previous study that found 18.5–25% seagrass-derived biomass in grouper muscle tissue in the northeastern GOM (Nelson and others 2012). Therefore, we conclude that our estimates are reasonable and include all the major nitrogen potentially entering offshore food webs. Although this method has shortcomings (for example, assuming 100% of nitrogen is directed toward the food web), our results demonstrate the power of this method for quantifying biomass subsidies in marine habitats. Given the limited information available on the occurrence, size, and impacts of the export of secondary production in coastal ecosystems, we suggest that our method for estimating the impacts of various nitrogen sources on piscivore productivity

in offshore habitats can be applied to other coastal marine ecosystems.

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

## ACKNOWLEDGMENTS

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 US National Oceanic and Atmospheric Administration (Northern Gulf of Mexico Cooperative Institute 191001-363558-01).

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