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Commercial trawling in seagrass beds: bycatch and long-term trends in effort of a major shrimp fishery

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ABSTRACT: Fisheries for penaeid shrimp have historically represented one of the largest in the Gulf of Mexico (GOM). Fishing grounds include both deeper, offshore areas, which have received considerable attention from scientists and managers, as well as shallow, nearshore areas. In the eastern GOM, the nearshore fishing grounds are in highly productive seagrass beds, which serve as nursery, temporary and permanent habitats to a multitude of fishes and invertebrates, including many of economic importance. Despite concerns regarding high levels of bycatch often observed in penaeid shrimp fisheries that use trawling gears, studies of potential gear impacts to seagrass ecosystems are surprisingly limited. We combined fishery-independent and -dependent methods to examine the temporal trends in bycatch rates and catch composition for the trawling gears used by the inshore fishery as well as the intra- and inter-annual patterns in fishing effort. The proportion of bycatch was consistently high (0.74 to 0.93) across the late spring through fall months, corresponding to the period of highest primary and secondary productivity in eastern GOM seagrass beds. Fifty species were captured by the rollerframe trawls, including several species of economic concern as well as abundant fishes that serve as linkages between primary and secondary production in seagrass ecosystems. Using 24 yr of fishery data, we found long-term evidence of an intra-annual shift from offshore grounds to seagrass beds during the spring through fall period of high productivity. Moreover, the proportion of total effort in seagrass beds during this period has increased in recent years, largely due to unprecedented declines in offshore effort. Extraction of both bycatch and targeted fauna from this highly productive ecosystem represents an impact that has largely been ignored. Understanding the effects of this extraction on seagrass-associated populations and communities should be considered in future ecosystem-based management and conservation efforts.

KEY WORDS: Essential fish habitat · Field study · Fishery dynamics · Indirect effects · Latent effects · Spatial fisheries management · Submerged aquatic vegetation · Time-series

INTRODUCTION

The Gulf of Mexico (GOM) supports extensive fisheries, with annual landings often exceeding 1 million tonnes (Vidal & Pauly 2004). Fisheries for penaeid shrimp are the second most important in terms of total landings (behind clupeid fishes), comprising approximately one-third of the total non-clupeid catch. The fishing grounds for penaeid shrimp are separated into offshore (federal waters) and inshore areas (state waters), and the fleet is composed of 'large' (i.e. ≥18 m length) and 'small' (i.e. <18 m length) vessels (GMFMC 2005). The large vessels have a greater and more consistent dependency on the offshore grounds (87 to 98% of landings) than the small vessels (61 to 94%; Funk 1998, GMFMC 2005), suggesting the latter may shift their efforts between the 2 areas, but a careful examination of the relative

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trends in effort between fishing grounds is required to better understand these dynamics.

Over the past 50 yr, fishing effort for penaeid shrimp in the eastern GOM (west Florida shelf) has typically ranged from 15 000 to 30 000 days (24 h) fished per year, resulting in annual landings of 4536 to 9072 metric tonnes (t) of shrimp tails (Hart et al. 2012). However, recent effort (2001 to present) has been reduced by ~90%, largely due to economic drivers, especially the rising costs of fuel and increased competition with farm-raised imports that have driven down market prices (Ward et al. 1995, Haby et al. 2003). These same economic drivers may also push efforts from offshore to inshore areas to help reduce fuel and other operating costs, especially among the small vessels in the fleet, which have the capacity to operate in state waters and require less investment capital relative to large vessels (e.g. smaller and non-permanent crews). Indeed, the GOM Shrimp Fisheries Management Plan (GMFMC 2005) suggested this shift toward inshore areas was a likely scenario that would change the spatial distribution of landings and revenue toward inshore habitats with varying effects on local fishing communities. Because the inshore fisheries for shrimp in the eastern GOM occur predominantly in seagrass beds, and because of the high levels of bycatch commonly associated with trawling gears (Hall et al. 2000, Diamond 2004), there is also concern about how a shift or increase in effort to inshore waters may affect these highly productive systems that serve as nursery habitats for a multitude of fishes and invertebrates.

Seagrass habitats in the eastern GOM are inhabited by hundreds of species of fauna (Dawes et al. 2004, Stallings & Koenig 2011), including 186 identified as 'species of greatest conservation need' (FWC 2005). The role of seagrass beds as nursery habitat has been discussed extensively in previous papers and reviews (e.g. Heck et al. 2003, Dawes et al. 2004, Gillanders 2006). Both primary (Dawes et al. 1987, Duarte 1989, Tomasko & Hall 1999, Fourqurean et al. 2001) and secondary productivity (Reid 1954, Livingston 1976, Tuckey & Dehaven 2006) are highest during the late spring through fall months in eastern GOM seagrass beds. A common annual trend in these and other shallow subtropical marine habitats in the region is for high levels of larval settlement coupled with increased immigration from adjacent habitats in the spring and summer months, giving rise to high faunal abundance and richness (Livingston 1976, Tuckey & Dehaven 2006). As primary productivity peaks during summer months, it supports a rich food web and high secondary productivity. Many species then undergo a fall egress from seagrass to adjacent habitats as productivity and the structural support of the habitat decreases (Stallings et al. 2010, Switzer et al. 2012, Nelson et al. 2013). Although seagrass habitats provide year-round food and shelter to some species, their ecological role in supporting a highly abundant and diverse fauna, including the juvenile stages of many species, is greatest during this spring through fall period. Given the potential of shifting or increased efforts of inshore trawling, it is important to consider the levels of bycatch and the seasonal trends of the fishery during this critical period.

In the present study, we combined fishery-independent and -dependent data to address several aspects of the inshore shrimp fishery in the eastern GOM. Focusing specifically on the late-spring through early-fall period comprising peak productivity in seagrass beds, we used fishery-independent methods to estimate the trends in (1) total bycatch rates and (2) catch composition by the rollerframe trawling methods employed by the inshore fishery. We then analyzed 24 years of fishery-dependent data to examine the intra-annual trends in effort and efficiency in the inshore fishery, again focusing on the period of peak productivity in seagrass beds. Last, we used 24 years of fishery-dependent data from both the inshore and offshore fishing grounds to determine whether there was evidence of either inter- or intra-annual switching between the two.

MATERIALS AND METHODS

Catch composition from rollerframe trawls

To characterize the catch composition from the inshore trawling gear and methods, we conducted fishery-independent surveys in seagrass beds across 3 regions (St. Joe Bay, St George Sound and Apalachee Bay) on the west Florida coast in the northeastern GOM (Fig. 1). Fishery-independent methods are preferred for describing bycatch characteristics of trawl gears as they allow the researchers more control in the study design and circumvent the problem of under-reported and non-representative bycatch common in commercial log books, even when observers are placed onboard fishing vessels (GMFMC 2005). The 3 regions differed slightly in sediment type (from soft to packed sand) and seagrass composition (mainly dominated by *Thalassia testudinum* with *Syringodium filiforme* and *Halodule beaudettei*), representing the typical range of seagrass habitats across the region (Stallings & Koenig

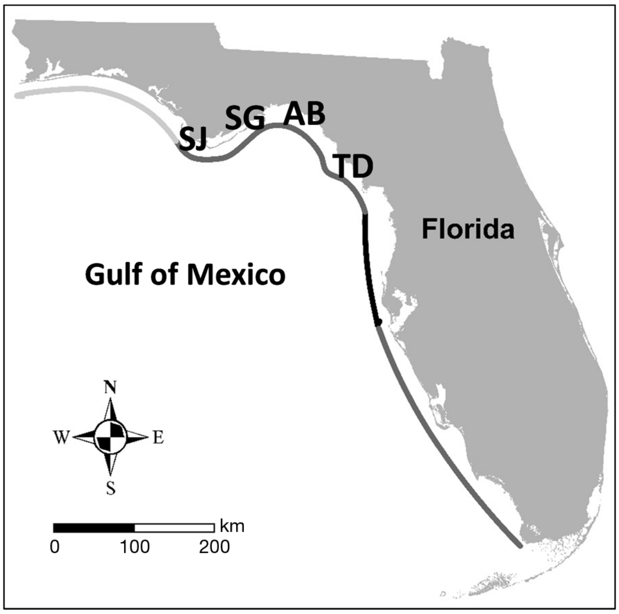

Fig. 1. Locations of the fishery-independent sampling in St. Joe Bay (SJ), St. George Sound (SG) and Apalachee Bay (AB); and the sampling location used by Tuckey & Dehaven (2006) (TD). The relative intensity of inshore fishing effort, based on landings in each coastal county in Florida, is shown with a grayscale gradient: high (black), moderate (dark gray) and low (light gray)

2011). Despite these minor differences in habitat, which can influence the abundance, richness and composition of associated fauna, Stallings et al. (2014) demonstrated such variation did not affect the catch characteristics of rollerframe trawls.

We used the same rollerframe trawls employed by the inshore fishery in the eastern GOM. Previous work demonstrated that rollerframe trawls do not damage seagrass habitats (Meyer et al. 1999), so we focused on their catch characteristics. Our trawls were constructed for a previous study (Coleman & Koenig 1998) by a company that provides most of the commercial nets in the Big Bend-Panhandle area of Florida. All aspects of the trawls were consistent with those used in the commercial fishery: frame width = 1.8 m wide (the recommended size for vessels between 6 and 7 m in length; vessels over 13 m in length can tow wider trawls, often with widths ≥ 3.6 m; Tabb & Kenny 1969), frame depth = 0.67 m, distance between frame vertical bars = 4 to 5 cm, roller diameter = 10 cm, stretch net mesh = 1.9 cm. Importantly, Coleman & Koenig (1998) determined that the frames and nets used here did not differ in capture efficiency or characteristics from those used in the inshore commercial fishery. One net was pulled on each side of a 6.1 m research vessel from booms mounted on the port and starboard gunnels at about amidships. Concurrently during each sampling event, we also towed a 5 m otter trawl (net body = 1.9 cm stretch mesh, bag = 3 mm mesh) in parallel, non-overlapping lanes as the rollerframe trawls. Otter trawls have been used extensively in fishery-independent studies and were used here for comparison of catch with the rollerframe trawls.

Sampling was conducted monthly in 2008 from May through September, encompassing the period when seagrass beds reach their highest levels of primary and secondary productivity (Duarte 1989, Fourqurean et al. 2001) and when their role as nursery grounds for fishes and invertebrates is most important (Reid 1954, Tuckey & Dehaven 2006, Nakamura et al. 2012). In a 3 yr study performed in seagrass beds on the west coast of Florida, this 5 mo period accounted for 76% of the total observed density of fishes (based on density data corrected for effort in number of hauls from Table 1 from Tuckey & Dehaven 2006). This period also represents approximately the entire seagrass phase for many species, which settle in the spring and egress in the late summer or early fall (Stallings et al. 2010, Switzer et al. 2012, Nelson et al. 2013). We sampled at night to mimic the shrimp fishery, which operates then because pink shrimp *Farfantepenaeus duorarum* are nocturnal (Reynolds & Casterlin 1979). During each monthly sampling event across the 3 study regions, we made 12 tows with each trawl gear (rollerframe N = 52 tows; otter N = 51 tows) of 150 m in length at speeds of 1.8 to 2.0 km h^{-1}. Monthly sampling took place on 3 consecutive nights, with 1 region sampled each night. Weather-related logistical problems prevented sampling at 2 of the 3 regions in August; all regions were otherwise equally sampled during the other 4 mo.

All captured animals were identified to the lowest possible taxon, counted and measured. Due to the large quantity of animals that had to be measured, we used size classes to expedite the process. Based on previous research using trawl gears in seagrass beds (e.g. Stallings et al. 2010), we used 6 size classes for the current study: (1) 1–25 mm, (2) 26–50 mm, (3) 51–75 mm, (4) 76–100 mm, (5) 101–150 mm, (6) >150 mm. We measured the total length for teleosts, carapace width for crabs, post-orbital head length for shrimp and longest plane for molluscs. Once animals were identified, measured and counted, they were then released back into the water. Care was taken to minimize harm to the animals. Some animals were retained to allow for identification in the laboratory, where microscopes and detailed taxonomic keys were present. The proportion of captured animals that was bycatch was calculated for each rollerframe tow as follows:

$$P_{By} = \frac{NT}{T} \qquad (1)$$

where P_{By} is proportion that is bycatch, NT is number of non-target animals captured, and T is total number of animals captured (target + non-target). We used numerical responses to stay consistent with how the inshore fishery is inventoried by management, instead of weight responses more typical of the offshore fishery. We also calculated the mean (±1 SE) density (number captured per 100 m^2) of each size class (1 to 6) for each taxa, captured by the rollerframe versus otter trawls. The relative densities of all taxa captured by the 2 gears are presented in tabular form. We also present 1:1 plots of the capture densities for each size class-by-gear combination for the 3 most abundant fishes of economic importance (spotted seatrout *Cynoscion nebulosus*, gulf flounder *Paralichthys albigutta* and lane snapper *Lutjanus synagris*) and the 3 most abundant overall (pinfish *Lagodon rhomboides*, pigfish *Orthopristis chrysoptera* and silver perch *Bairdiella chrysoura*).

Long-term inter- and intra-annual trends in the inshore fishery

Trawling effort data for the U.S. penaeid fisheries in GOM waters have been collected by a port sampler interview program operated by the U.S. National Oceanic and Atmospheric Administration National Marine Fisheries Service since the 1960s. Although the data generated from this program are considered to be fairly reliable for estimating effort on offshore fishing grounds (i.e. federal waters — seaward of COLREGS), they have been criticized for being biased with extremely poor coverage of the effort on inshore grounds as well as for the vessels and gears used by fishermen in state waters (Griffin et al. 1997). Griffin (2004) further illustrated that the percent of interviewed trips fell sharply in the mid-1980s, which coincided with a disproportionately high representation of larger, offshore vessels (i.e. fewer small, inshore vessels), resulting in a near non-existent sampler program for inshore effort since 1990. Similar concerns about spatial accuracy and non-representative offshore-inshore effort data have also come from others (e.g. Travis 2000, Haby et al. 2002, Gallaway et al. 2003). Thus, quantifying effort and trends in the inshore shrimp fisheries has proven to be difficult and a topic of contention across the region.

Trip ticket programs may circumvent the problems inherent to the port sampler data and have been implemented in all 5 U.S. states bordering the GOM. Florida's trip ticket program was the first in the region[1] and began collecting data on the shrimp fishery in 1986, thus allowing for a multi-decadal analysis of the trends in effort for the penaeid fisheries operating in the eastern GOM. Moreover, the trip ticket program in Florida began just prior to when the federal program may have begun to miss the majority of inshore trips (Griffin 2004).

We compared the trends in effort and CPUE from the inshore fishery with estimates of secondary productivity from eastern GOM seagrass beds. As a proxy of intra-annual trends in secondary productivity, we extracted data on fish abundance and richness from Tuckey & Dehaven (2006). Their 3 yr study was the only one we found in our search of the peer-reviewed literature that collected data each month, for a minimum of 12 continuous months, on faunal abundance in seagrass beds located in the eastern GOM. We standardized fish abundances to densities, accounting for variation in the monthly sampling effort reported by Tuckey & Dehaven (2006). Because our goal was to examine qualitative relationships between biological productivity and the metrics from the inshore fishery, and since the patterns reported by Tuckey & Dehaven (2006) were similar to those from other studies that did not fully meet our search criteria (e.g. Reid 1954, Livingston 1976, Stallings & Koenig 2011), we assumed this single study was satisfactory for our purposes.

Using data from the Florida trip ticket program for the inshore fishery and the NOAA port interview program from statistical zones 1 to 9 for the offshore fishery, we analyzed the trends in effort between the 2 areas for the years 1986 to 2009 (24 yr). To allow comparison between the fisheries, we measured effort as 24 h days fished. We used the Pearson correlation coefficient to investigate how long-term trends in effort between the 2 fisheries tracked each other across the entire 24 yr period as well as during multiple-year intervals within the dataset. We also pooled the 24 yr data to determine the mean monthly trends in effort and catch-per-unit-effort (CPUE; defined as kilograms per 24 h day fished with a conversion of 220 shrimp = 1 kg for the relatively small, young shrimp landed inshore).

[1]Trip ticket programs for inshore shrimp fisheries began in the years 2000 for Alabama, 2007 for Texas and 2012 for Mississippi. Louisiana authorized a trip ticket program in 1991, but data collection did not begin until 1999 due to a lack of funding

RESULTS

Bycatch from the inshore gears and methods

The mean (±1 SE) proportion of bycatch for the rollerframe trawls, pooled across all tows, was 0.82 (±0.02). Fishes comprised 56% of the non-target catch, 43% were arthropods, and 1% was the recreationally important bay scallop *Argopecten irradians* (Table S1 in the supplement at www.int-res.com/articles/suppl/m513p143_supp.pdf). Bycatch remained high across the duration of the study, ranging from a low of 0.74 (±0.06) in August to a high of 0.93 (±0.01) in May (Fig. 2A). In contrast, the proportion of target shrimp caught by rollerframe trawls was between 0.06 (±0.01) and 0.26 (±0.06).

We observed a total of 50 species captured by the rollerframe gear, and the number landed per tow remained consistent throughout the 5 mo study (Fig. 2B). Among the animals captured, 97% of the individuals were composed of 4 species: the target pink shrimp (17%) and non-target arrow shrimp (58%), pinfish (18%) and pigfish (4%). Several species of economic importance were captured with the rollerframe trawls, including (listed in decreasing proportion of catch) bay scallop, spotted seatrout, gulf flounder, lane snapper, blue crab *Callinectes sapidus*, gag *Mycteroperca microlepis*, black seabass *Centropristis striata* and red grouper *Epinephelus morio*.

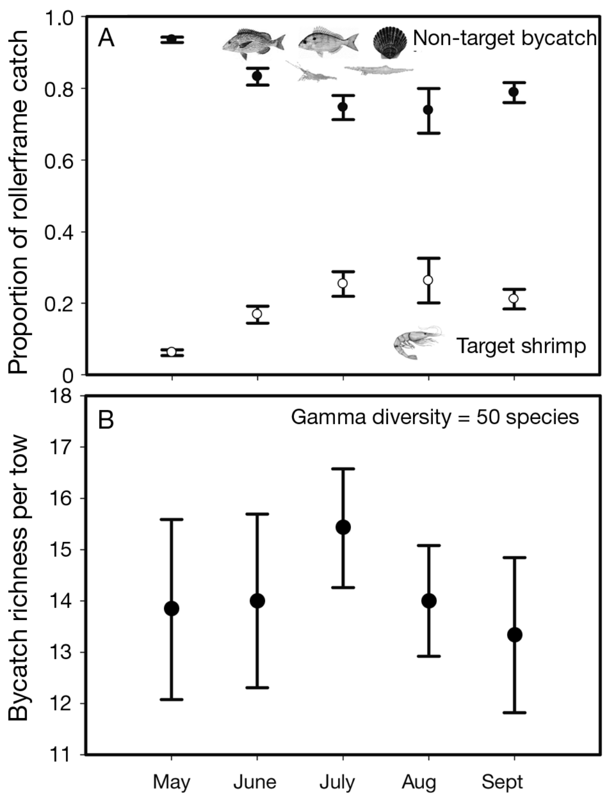

Fig. 2. Catch from fishery-independent sampling conducted monthly using rollerframe trawls (n = 52 tows) across 3 seagrass systems in the Gulf of Mexico (GOM). Mean (±1 SE) values are reported for the (A) proportion of non-target bycatch and target penaeid shrimp and (B) richness of bycatch. Fish drawings courtesy of D. R. Peebles

For most taxa, rollerframe trawls tended to catch higher densities than the otter trawls (Table S1 in the Supplement). In general, higher densities caught by the rollerframe trawls were more pronounced for the small size classes than the larger ones (Table S1); however, note that for fishes in Size Class 1 (1 to 25 mm), some species were either captured at extremely low densities or not captured at all in both gears. Across taxa, the rollerframe trawls captured more arthropods from Size Class 1 and more fishes from Size Classes 1 to 4 (1 to 100 mm), compared to that captured by otter trawls. No difference in capture between gears was observed for the other size classes when taxa were pooled. The 3 most abundant fishes of economic importance (Fig. 3A–C) and 2 of the 3 most abundant overall (Fig. 3D–F) displayed this basic pattern of higher densities captured by the rollerframe trawls.

Fauna captured by the rollerframe trawls displayed varying physical and physiological responses. Most taxa appeared to be in fairly good condition when released, but a few species consistently did not fare as well. For example, sciaenid fishes, including juveniles of both the numerically abundant silver perch and the recreationally important spotted seatrout, were often dead when brought aboard the research vessel or died shortly thereafter.

Long-term inter- and intra-annual trends in the inshore fishery

Across the 24 yr of fishery data, the trends in annual inshore effort generally tracked those offshore (r = 0.53, p = 0.004; Fig. 4). On average (±1 SE), there were 434.89 (±23.28) 24 h days fished inshore per year, with a 24 yr minimum of 283 d and a maximum of 678 d. Inshore effort was more stable (CV = 0.26) than the offshore counterpart (CV = 0.47). Annual effort on both fishing grounds declined in the last 5 yr of the 24 yr dataset (2005 to 2009), but declined more sharply offshore (−92%) than inshore (−15%). Moreover, the 2005 to 2009 decrease in inshore effort was approximately equal to previous

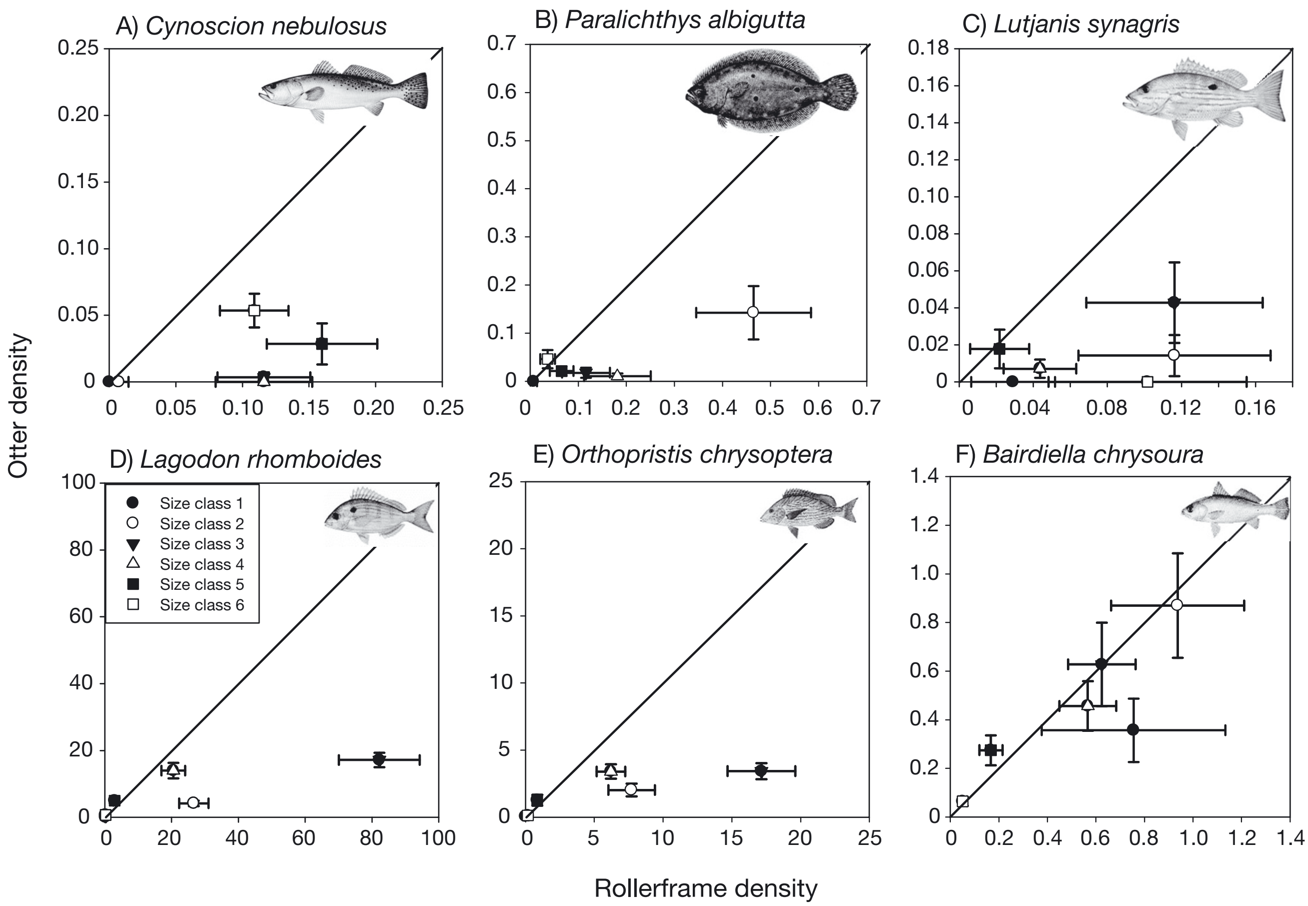

Fig. 3. Catch comparisons from fishery-independent sampling using rollerframe trawls (n = 52 tows) and otter trawls (n = 51 tows in the GOM). Mean (±1 SE) densities (number caught per 100 m^2) are reported for the 3 most abundant fishes of economic importance: (A) spotted seatrout *Cynoscion nebulosus*, (B) gulf flounder *Paralichthys albigutta*, (C) lane snapper *Lutjanus synagris*; and the 3 most abundant overall: (D) pinfish *Lagodon rhomboides*, (E) pigfish *Orthopristis chrysoptera*, and (F) silver perch *Bairdiella chrysoura*. Size classes below the 1:1 line were captured at higher densities in the rollerframe trawls, and those crossing the line were not different between gears. A single size class of silver perch was captured at higher densities in the otter trawl (above and not crossing the 1:1 line). Drawings courtesy of D. R. Peebles

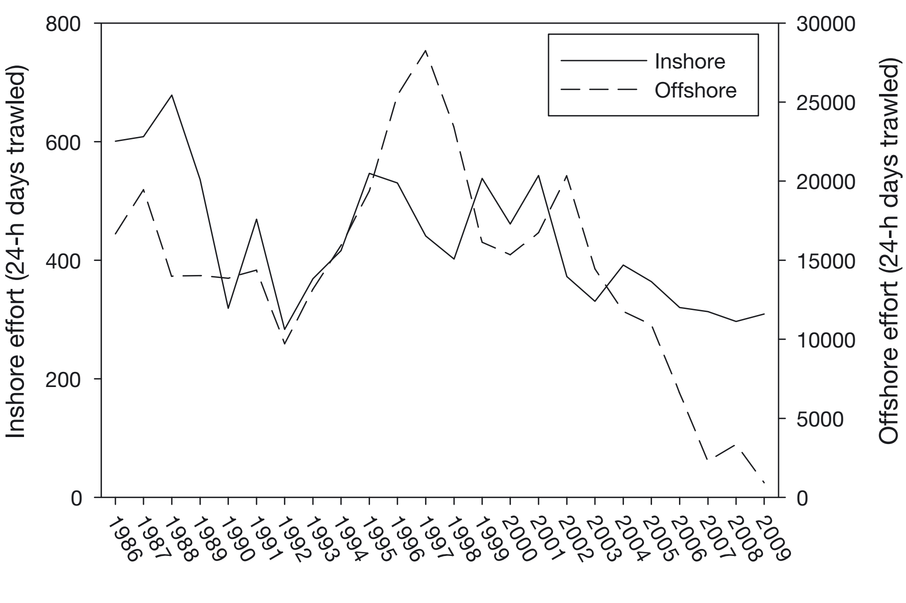

Fig. 4. Annual trawling effort between the inshore and offshore fishing grounds in the eastern GOM from 1986 to 2009

lowest levels that were observed in the late 1980s to early 1990s, while that decrease offshore hit a 24 yr low at ~25% the effort expended during the next lowest levels observed during the early 1990s.

The trends in monthly effort were also more stable inshore (CV = 0.11) compared to offshore (CV = 0.56). Offshore effort was highest from January through April, decreased by 62% in May through September and increased by 30% in October through December (Fig. 5A). Monthly inshore effort was bimodal, with the first peak in the spring, dropping temporarily during early summer, then increasing sharply to a second peak in the late summer through fall months (Fig. 5A). On average (±1 SE), there were 36.46 (±2.37) 24 h days fished inshore per month. With the exception of July, monthly effort during the focal period of May through September was greater than the long-term monthly average. The proportion of annual effort inshore was typically below 5% of the total effort (inshore + offshore) throughout most of the 24 yr dataset (Fig. 5B). However, the mean monthly proportion effort inshore was generally 2- to 4-fold higher during the months of May through September (24 yr mean = 11.6%) compared to the other 7 months (24 yr mean = 4.5%; Fig. 5B and inset). Across all years, the proportion inshore effort began to gradually increase in May and June, with peak proportions in August and September exceeding 20% of the total effort, before dropping back to values ≤10% total effort in October through winter and early spring months (Fig. 5B inset).

The relationship between inshore effort and CPUE from the shrimp fishery was dynamic and complex. These values generally tracked each other during the late winter through early summer, followed by a sharp increase in effort despite continued low and slowly rising CPUE in the late summer through fall months (Fig. 6). The first peak in inshore effort during the spring occurred during the period of high larval settlement to seagrass habitats, resulting in an overlapping peak in faunal (fish) abundance based on the data from Tuckey & Dehaven (2006). Faunal abundance reached a second peak in the late summer through early fall months due to continued larval settlement as well as seasonal immigration from adjacent habitats, resulting in the period of highest intra-annual faunal richness and abundance. This late summer to early fall peak in secondary productivity, as reported by Tuckey & Dehaven (2006), occurred when inshore trawling efforts hit its second peak despite low CPUE and before the fall egress for many species (Fig. 6).

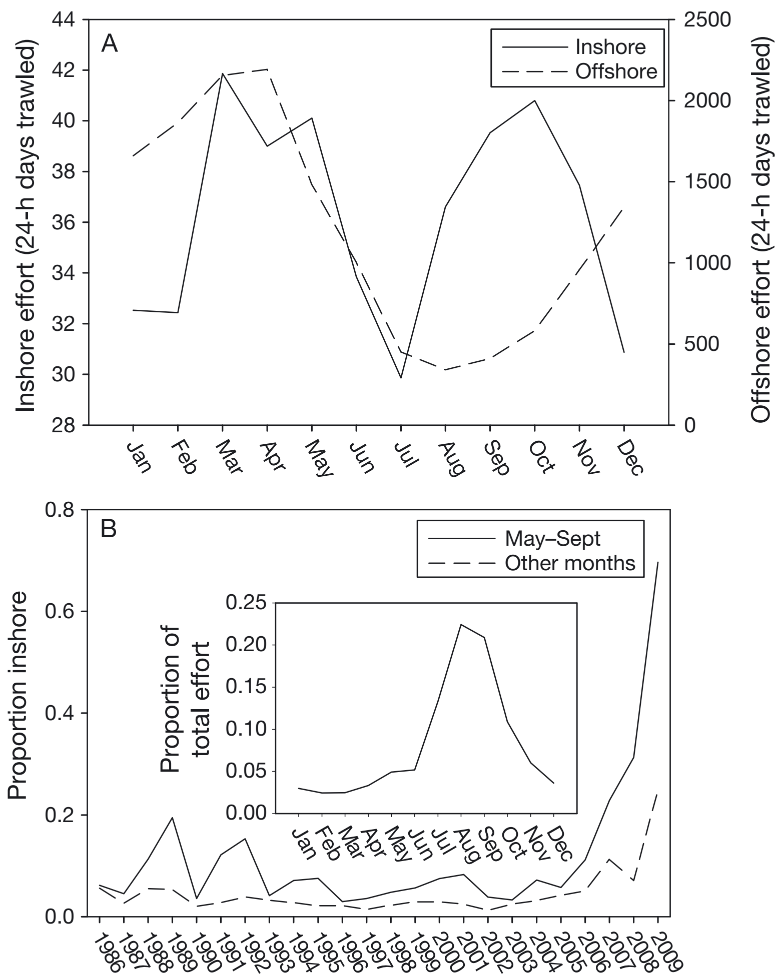

Fig. 5. (A) Monthly trawling effort between inshore and offshore fishing grounds in the eastern GOM from 1986 to 2009. (B) Proportion of total effort allocated to inshore fishing grounds, averaged annually across May–September months (solid line) versus the other 7 months (dashed line). Inset shows mean monthly proportion effort inshore across the 24 yr data set

DISCUSSION

Bycatch from the inshore trawling fishery for penaeid shrimp in the eastern GOM can be incredibly high, ranging from bycatch:target ratios (proportion bycatch) of approximately 4:1 (0.75) to over 9:1 (0.90). Such high bycatch is similar to the highest levels reported from other penaeid shrimp fisheries (e.g. Andrew & Pepperell [1992]: 0.85; Helies & Jamison

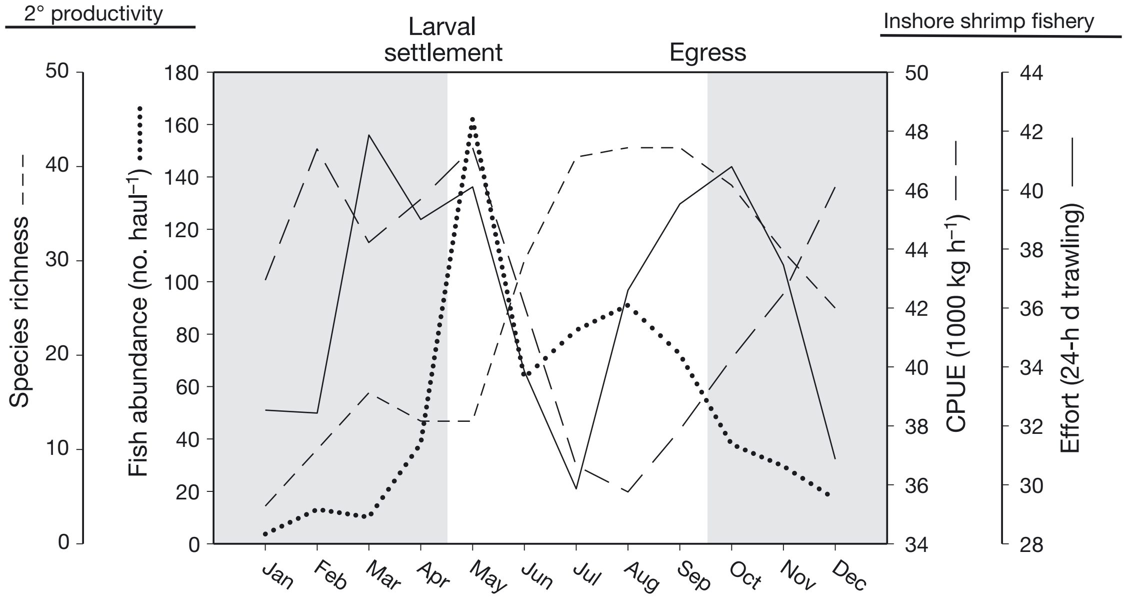

Fig. 6. Trends in effort (solid line) and CPUE (long-dashed line) from the inshore fishery relative to secondary productivity in eastern GOM seagrass beds. Secondary productivity estimates were derived from Table 1 of Tuckey & Dehaven (2006) and include the richness (short-dashed line) and density (dotted line) of fishes. The focal 5 mo period of May to September is high-lighted (white background)

[2009]: 0.75; NMFS [2011]: 0.76) and is well above the average (0.56) calculated from 52 records by Kelleher (2005). Bycatch was high across the duration of the study, which focused on the spring through fall period of high secondary productivity and associated nursery functions of seagrass habitats. We augmented our fishery-independent efforts by combining fishery data from 2 management agencies, NOAA's federal port interview and Florida's trip ticket programs, to produce the first long-term analysis of annual and monthly trends in the inshore shrimp fishery that operates in the eastern GOM. Commercial trawling effort in the inshore habitats peaked during both the early and late stages of this critical period in eastern GOM seagrass ecosystems. Although trawling effort in seagrass beds has declined in recent years, the proportion of inshore effort has increased substantially, and there is long-term evidence of an intra-annual shift from offshore to inshore grounds during this period of high secondary productivity.

Our analysis shows the inshore fishery was relatively stable in annual effort from 1986 to 2009. During this same period, offshore effort was less stable and ultimately decreased to its lowest levels in 50 yr (Hart et al. 2012). The offshore fishery experienced several sharp declines in effort during the 24 yr study period, most notably post-2001. The recent decline in offshore effort was due to large vessels exiting the fishery due to the combined economic drivers of high and unstable fuel costs and increased competition with farm-raised imported shrimp driving down post-vessel prices, resulting in net losses for fishermen (Haby et al. 2003, Travis & Griffin 2004, GMFMC 2005). Large vessels, which would have difficulties operating in shallow waters, rely on offshore grounds more consistently and at higher levels (87%) than small vessels in the fleet (61%; GMFMC 2005). Moreover, Funk (1998) showed that profitability tended to be greater on average for smaller vessels relative to large ones and that the former participated in the shrimp fishery on a flexible basis when revenues were high. Such observations support the potential for small vessels to shift effort between offshore to inshore grounds, according to profit potential. Inter-annual switching between offshore and inshore grounds was not evident from our analysis. Although there were periods when inshore and offshore effort trended in opposite directions, the overall pattern was a positive correlation, suggesting the 2 sectors respond in similar ways to various biological, socio-economic or management drivers. The post-2001 decline in offshore effort was also the main reason for an increased annual proportion in inshore effort during those years, but this trend is more complex when considering long-term monthly patterns.

The observed monthly trends of inshore effort may suggest that switching between fishing grounds occurred on an intra-annual basis, especially during the summer through fall months when inshore effort increased sharply while that offshore remained low. The increase in inshore effort occurred despite relatively low CPUE persisting through the fall months, suggesting demand was higher for shrimp landed inshore (especially live shrimp for bait; Gandy 2007) or that conditions benefited fishermen to work inshore despite low efficiencies (e.g. offshore efficiencies were even lower, or economic drivers favored inshore fishing). The trend of increased inshore effort during the focal months of May through September was consistent across the 24 yr period, again providing further support that switching behaviors occurred within most years and that the trend was not driven by recent and unprecedented changes to the fishery.

Increased inshore effort bracketed the May through September period, when larval settlement peaks (Sheridan & Livingston 1983, Switzer et al. 2012), seagrass habitat supports the greatest abundance and diversity of organisms (Reid 1954, Tuckey & Dehaven 2006, Stallings & Koenig 2011), and many species will soon migrate from the system (e.g. Stallings et al. 2010, Nelson et al. 2013). Using the same gears and methodologies employed by the inshore fishery, we found high levels of bycatch consistent with previous work (e.g. Meyer et al. 1999, Baum et al. 2003, Crawford et al. 2011, Stallings et al. 2014). Additionally, high overall bycatch was consistent across all 5 mo of the field study and included a wide range of taxa. Both arthropods (including the target pink shrimp) and the bay scallop smaller than 75 mm were captured at high densities, as were most fishes with TL < 100 mm. Larger fishes (i.e. > 100 mm TL) tended to be captured at lower densities, possibly due to the combined effects of lower existing population densities in the seagrass beds and lower capture efficiency by the rollerframe trawls. Lower capture efficiency may be the result of exclusion of larger animals by the vertical bars that span the mouth of the rollerframe trawl (described in 'Materials and Methods') in addition to increased evasion abilities. Indeed, this basic pattern was observed across most fishes, including those of economic importance and of high overall abundance.

Many species captured by the rollerframe trawls appeared to be in good condition when released, while others were typically dead when brought aboard the research vessel (e.g. spotted seatrout). However, our study did not account for latent mortality, which can be high due to physiological stress for certain taxa (sciaenid and gerreid fishes), for smaller animals and during warmer months (i.e. when the inshore fishery in the eastern GOM is most active; Coleman & Koenig 1998, Meyer et al. 1999). Additionally, numerous opportunistic avian (e.g. gulls), piscean (e.g. ladyfish *Elops saurus* and ariid sea catfishes) and mammalian predators (e.g. delphinid dolphins) follow commercial bait-shrimp boats (see Fig. S1 in the Supplement) and gorge upon discarded bycatch (Baum et al. 2003; C. Koenig pers. comm. [observation as an onboard scientist]; J. Locascio pers. comm. [observation as a commercial fisherman]). Even animals not injured by the rollerframe trawls themselves may be disoriented and displaced by being captured, thus potentially increasing their vulnerability to predators upon release. Estimating the magnitude of mortality from these sources was beyond the scope of our study, but this mortality requires further attention to understand the effects on populations of economically important species. Future work should also address the potential food web disruptions or alterations by this high-bycatch fishery both to seagrass ecosystems and to adjacent habitats which receive energy and nutrients derived from the seagrass systems (Stallings 2010, Nelson et al. 2013).

Worldwide, seagrass ecosystems have and continue to experience multiple stressors from human activities, resulting in habitat loss and compromised ecosystem function (Orth et al. 2006, Waycott et al. 2009). Much of the attention regarding these deleterious effects has focused on activities that directly affect the seagrass (e.g. excess nutrient input, pollution, sedimentation, physical damage) with ensuing, and often assumed, indirect effects on the fauna they support. Here, we have made the first effort of which we are aware to quantify the activity levels of a trawl fishery that operates in these seagrass systems of the eastern GOM. Although the inshore fishery has been largely overshadowed by the incredibly high historical efforts on the offshore grounds, we argue that the amount of effort in seagrass is not trivial (i.e. >20% of total effort during months of peak productivity) and appears to increase when many species are using this nursery habitat as juveniles. Moreover, the proportion of total effort in seagrass beds has increased sharply in recent years. Extraction of fauna — both targeted and bycatch — from this ecosystem represents an additional impact that may directly affect the populations and communities it supports and therefore should be considered in future ecosystem-based management and conservation efforts (Francis et al. 2007, McLeod & Leslie 2009).

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The following supplement accompanies the article

Commercial trawling in seagrass beds: bycatch and long-term trends in effort of a major shrimp fishery

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Supplement. Catch comparison between rollerframe and otter trawls (Table S1), and photographs of potential predators on post-release by-catch from a commercial bait-shrimp trawler (Fig. S1)

Table S1. Catch composition from fishery-independent sampling with paired rollerframe (n = 52 tows) and otter trawls (n = 51 tows). Taxa are listed from the most to least abundant captured by rollerframe trawls. The mean (± SE) densities (number catch per 100 m^2) of captured animals are provided for Size Classes 1 to 6

Species	Common Name	Gear	No. caught	L_1 (1–25 mm)	L_2 (26–50 mm)	L_3 (51–75 mm)	L_4 (76–100 mm)	L_5 (101–150 mm)	L_6 (>150 mm)
Arthropoda									
Tozeuma carolinense	Arrow Shrimp	rollerframe	90,146	327.30 (73.22)	0.03 (0.03)	–	–	–	–
		otter	38,510	137.29 (44.29)	–	–	–	–	–
Farfantepenaeus duorarum	Pink Shrimp	rollerframe	27,124	96.10 (10.71)	2.38 (0.42)	0.02 (0.02)	–	–	–
		otter	3,474	11.76 (2.16)	0.62 (0.11)	–	–	–	–

Periclimenes longicaudatus	Longtail Grass Shrimp	rollerframe	394	1.43 (0.60)	–	–	–	–	–
		otter	768	2.75 (1.27)	–	–	–	–	–
Libinia dubia	Longnose Spider Crab	rollerframe	258	0.04 (0.02)	0.80 (0.21)	0.09 (0.03)	–	–	–
		otter	386	0.04 (0.02)	1.08 (0.24)	0.25 (0.08)	–	–	–
Metoporhaphis calcarata	Arrow Crab	rollerframe	110	0.40 (0.09)	–	–	–	–	–
		otter	27	0.09 (0.03)	–	–	–	–	–
Callinectes sapidus	Blue Crab	rollerframe	76	–	0.06 (0.03)	0.05 (0.03)	0.07 (0.02)	0.07 (0.03)	0.02 (0.01)
		otter	66	0.01 (0.01)	0.11 (0.05)	0.02 (0.01)	0.03 (0.01)	0.06 (0.02)	0.01 (0.01)
Hippolyte zostericola	Zostera Shrimp	rollerframe	4	0.01 (0.01)	–	–	–	–	–
		otter	0	–	–	–	–	–	–
Chordata									
Lagodon rhomboides	Pinfish	rollerframe	36,554	0.20 (0.10)	26.64 (4.39)	82.24 (12.09)	20.52 (3.53)	2.93 (0.36)	0.20 (0.04)
		otter	11,511	0.02 (0.01)	4.20 (0.81)	17.15 (2.17)	14.00 (2.32)	4.98 (0.77)	0.69 (0.09)
Orthopristis chrysoptera	Pigfish	rollerframe	8,868	0.10 (0.05)	7.71 (1.69)	17.15 (2.467)	6.21 (1.03)	0.86 (0.25)	0.17 (0.06)
		otter	2,886	0.06 (0.03)	2.02 (0.48)	3.43 (0.61)	3.39 (0.549)	1.27 (0.40)	0.13 (0.02)
Bairdiella chrysoura	Silver Perch	rollerframe	854	0.76 (0.38)	0.94 (0.27)	0.62 (0.14)	0.57 (0.12)	0.17 (0.05)	0.05 (0.02)
		otter	743	0.36 (0.13)	0.87 (0.21)	0.63 (0.17)	0.46 (0.10)	0.27 (0.06)	0.06 (0.02)
Opsanus beta	Gulf Toadfish	rollerframe	634	0.01 (0.01)	0.12 (0.07)	0.16 (0.06)	0.49 (0.08)	1.17 (0.13)	0.34 (0.04)
		otter	196	0.01 (0.01)	0.01 (0.01)	0.01 (0.01)	0.05 (0.03)	0.37 (0.06)	0.25 (0.04)
Monacanthus hispidus	Planehead Filefish	rollerframe	422	0.17 (0.06)	0.49 (0.09)	0.51 (0.12)	0.28 (0.07)	0.05 (0.02)	0.03 (0.02)
		otter	360	0.19 (0.15)	0.22 (0.06)	0.43 (0.15)	0.32 (0.08)	0.11 (0.03)	0.02 (0.01)

Syngnathus floridae	Florida Pipefish	rollerframe	528	–	–	0.04 (0.04)	0.14 (0.06)	0.53 (0.10)	1.21 (0.24)
		otter	186	–	–	–	0.01 (0.01)	0.19 (0.06)	0.47 (0.14)
Syngnathus scovelli	Gulf Pipefish	rollerframe	346	–	–	0.04 (0.02)	0.33 (0.10)	0.88 (0.19)	0.01 (0.01)
		otter	36	–	–	0.01 (0.01)	0.01 (0.01)	0.11 (0.03)	–
Hyporhamphus unifasciatus	Atlantic Silverstripe Halfbeak	rollerframe	280	–	0.01 (0.01)	0.01 (0.01)	0.01 (0.01)	0.11 (0.04)	0.87 (0.12)
		otter	0	–	–	–	–	–	–
Hippocampus erectus	Lined Seahorse	rollerframe	270	0.36 (0.33)	0.01 (0.01)	0.20 (0.06)	0.34 (0.12)	0.07 (0.03)	0.01 (0.01)
		otter	170	0.01 (0.01)	0.03 (0.02)	0.20 (0.07)	0.29 (0.13)	0.07 (0.05)	0.01 (0.01)
Cynoscion nebulosus	Spotted Seatrout	rollerframe	240	0.01 (0.01)	0.46 (0.12)	0.12 (0.05)	0.18 (0.07)	0.07 (0.02)	0.04 (0.02)
		otter	67	–	0.14 (0.06)	0.02 (0.01)	0.01 (0.01)	0.02 (0.01)	0.05 (0.02)
Chilomycterus schoepfi	Striped Burfish	rollerframe	232	0.04 (0.03)	0.05 (0.02)	0.17 (0.05)	0.15 (0.04)	0.17 (0.04)	0.27 (0.05)
		otter	148	0.04 (0.02)	0.01 (0.01)	0.06 (0.02)	0.05 (0.01)	0.13 (0.03)	0.23 (0.05)
Paralichthys albigutta	Gulf Flounder	rollerframe	140	–	0.01 (0.01)	0.12 (0.03)	0.12 (0.04)	0.16 (0.04)	0.11 (0.03)
		otter	24	–	–	0.01 (0.01)	–	0.03 (0.02)	0.05 (0.01)
Lactophrys quadricornis	Scrawled Cowfish	rollerframe	92	0.07 (0.03)	0.17 (0.09)	0.01 (0.01)	–	0.04 (0.02)	0.04 (0.02)
		otter	44	0.03 (0.02)	0.10 (0.05)	–	0.01 (0.01)	0.01 (0.01)	0.02 (0.01)
Lutjanus synagris	Lane Snapper	rollerframe	90	0.03 (0.02)	0.12 (0.05)	0.12 (0.05)	0.04 (0.02)	0.02 (0.02)	–
		otter	23	–	0.01 (0.01)	0.04 (0.02)	0.01 (0.01)	0.02 (0.01)	–
Anchoa mitchilli	Bay Anchovy	rollerframe	86	–	0.19 (0.08)	0.09 (0.05)	0.03 (0.03)	–	–
		otter	97	0.01 (0.01)	0.32 (0.10)	0.018 (0.01)	–	–	–

Diplodus holbrooki	Spottail Pinfish	rollerframe	72	–	0.06 (0.03)	0.06 (0.04)	0.03 (0.02)	0.12 (0.04)	–
		otter	39	–	0.02 (0.01)	0.01 (0.01)	0.02 (0.02)	0.08 (0.03)	0.01 (0.01)
Eucinostomus argenteus	Spotfin Mojarra	rollerframe	68	0.06 (0.05)	0.17 (0.10)	0.01 (0.01)	–	–	–
		otter	3	–	–	0.01 (0.01)	–	–	–
Trinectes maculatus	Hogchoker	rollerframe	62	–	0.10 (0.05)	0.12 (0.05)	–	–	–
		otter	0	–	–	–	–	–	–
Eucinostomus gula	Silver Jenny	rollerframe	48	0.04 (0.04)	0.14 (0.08)	–	–	–	–
		otter	2	–	0.01 (0.01)	–	–	–	–
Sphoeroides nephelus	Southern Puffer	rollerframe	44	0.03 (0.03)	–	0.02 (0.02)	0.03 (0.02)	0.05 (0.02)	0.03 (0.02)
		otter	51	–	0.01 (0.01)	0.01 (0.01)	0.04 (0.01)	0.10 (0.03)	0.03 (0.01)
Aluterus scriptus	Scrawed Filefish	rollerframe	42	0.01 (0.01)	0.04 (0.03)	0.09 (0.04)	0.01 (0.01)	–	0.01 (0.01)
		otter	24	–	0.01 (0.01)	0.02 (0.01)	0.05 (0.02)	0.01 (0.01)	0.01 (0.01)
Gobiosoma robustum	Code Goby	rollerframe	24	–	0.06 (0.05)	0.03 (0.03)	–	–	–
		otter	4	0.01 (0.01)	0.01 (0.01)	–	–	–	–
Synodus foetens	Inshore Lizardfish	rollerframe	22	–	–	–	0.04 (0.04)	0.02 (0.01)	0.02 (0.01)
		otter	3	–	–	–	–	–	0.01 (0.01)
Hippocampus reidi	Slender Seahorse	rollerframe	20	–	–	–	0.07 (0.06)	0.01 (0.01)	–
		otter	12	–	–	0.02 (0.02)	0.02 (0.02)	–	–
Symphurus plagiusa	Blackcheek Tonguefish	rollerframe	18	–	–	0.03 (0.02)	0.04 (0.03)	–	–
		otter	1	–	–	–	0.01 (0.01)	–	–
Diplectrum bivittatum	Dwarf Seabass	rollerframe	18	–	–	0.07 (0.05)	–	–	–
		otter	0	–	–	–	–	–	–

Ariopsis felis	Hardhead Catfish	rollerframe	14	–	–	0.02 (0.02)	–	–	0.03 (0.01)
		otter	6	–	–	–	–	–	0.02 (0.01)
Mycteroperca microlepis	Gag	rollerframe	14	–	–	–	0.01 (0.01)	0.01 (0.01)	0.04 (0.02)
		otter	29	–	–	–	–	–	0.10 (0.03)
Diplectrum formosum	Sand Perch	rollerframe	12	–	–	0.02 (0.02)	0.01 (0.01)	0.01 (0.01)	–
		otter	2	–	–	–	–	0.01 (0.01)	0.01 (0.01)
Strongylura marina	Atlantic Needlefish	rollerframe	12	–	–	–	–	0.02 (0.01)	0.02 (0.019)
		otter	0	–	–	–	–	–	–
Chloroscombrus chrysurus	Atlantic Bumper	rollerframe	8	–	0.03 (0.03)	–	–	–	–
		otter	6	–	0.04 (0.04)	–	–	–	–
Centropristis striata	Black Seabass	rollerframe	6	–	–	–	–	0.01 (0.01)	0.01 (0.01)
		otter	30	–	0.01 (0.01)	–	–	0.02 (0.01)	0.07 (0.02)
Brevoortia patronus	Gulf Menhaden	rollerframe	6	–	–	–	–	0.02 (0.02)	–
		otter	0	–	–	–	–	–	–
Achirus lineatus	Lined Sole	rollerframe	4	–	–	0.01 (0.01)	–	–	–
		otter	0	–	–	–	–	–	–
Microgobius gulosus	Clown Goby	rollerframe	4	–	–	0.01 (0.01)	–	–	–
		otter	0	–	–	–	–	–	–
Monacanthus ciliatus	Fringed Filefish	rollerframe	4	–	–	0.01 (0.01)	–	–	–
		otter	0	–	–	–	–	–	–

Lactophrys trigonus	Trunkfish	rollerframe	4	0.01 (0.01)	0.01 (0.01)	–	–	–	–
		otter	1	0.01 (0.01)	–	–	–	–	–
Selene vomer	Lookdown	rollerframe	4	–	–	0.01 (0.01)	–	–	–
		otter	5	–	0.02 (0.02)	–	–	–	–
Halichoeres bivittatus	Slippery Dick	rollerframe	2	–	0.01 (0.01)	–	–	–	–
		otter	0	–	–	–	–	–	–
Ophidion holbrookii	Bank Cusk-eel	rollerframe	2	–	–	–	–	–	0.01 (0.01)
		otter	0	–	–	–	–	–	–
Epinephelus morio	Red Grouper	rollerframe	2	–	–	–	–	–	0.01 (0.01)
		otter	2	–	–	–	–	–	0.01 (0.01)
Lophogobius cyprinoides	Crested Goby	rollerframe	0	–	–	–	–	–	–
		otter	1	–	–	0.01 (0.01)	–	–	–
Myrophis punctatus	Speckled Worm Eel	rollerframe	0	–	–	–	–	–	–
		otter	1	–	–	–	–	–	0.01 (0.01)
Scorpaena brasiliensis	Barbfish	rollerframe	0	–	–	–	–	–	–
		otter	1	–	–	–	–	–	0.01 (0.01)
Engraulis eurystole	Silver Anchovy	rollerframe	0	–	–	–	–	–	–
		otter	22	–	0.07 (0.04)	0.01 (0.01)	–	–	–
Mollusca									
Argopecten irradians	Bay Scallop	rollerframe	276	0.11 (0.05)	0.49 (0.11)	0.41 (0.07)	–	–	–
		otter	151	0.01 (0.01)	0.23 (0.06)	0.30 (0.06)	–	–	–

Fig. S1. Post-release mortality of fishes and invertebrates may occur via predation by (A) large flocks of birds (e.g. gulls) and (B) predatory fishes (e.g. Ladyfish and Gafftopsail Catfish—note the reflection of eyes in photo) that follow commercial bait-shrimp trawlers. Photos taken at night aboard a commercial bait-shrimp trawler in the Big Bend, FL, courtesy of C. C. Koenig

(**A)**

(B)