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Research Article

Invasion of Asian tiger shrimp, *Penaeus monodon* Fabricius, 1798, in the western north Atlantic and Gulf of Mexico

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Abstract

After going unreported in the northwestern Atlantic Ocean for 18 years (1988 to 2006), the Asian tiger shrimp, *Penaeus monodon*, has recently reappeared in the South Atlantic Bight and, for the first time ever, in the Gulf of Mexico. Potential vectors and sources of this recent invader include: 1) discharged ballast water from its native range in Asia or other areas where it has become established; 2) transport of larvae from established non-native populations in the Caribbean or South America via ocean currents; or 3) escape and subsequent migration from active aquaculture facilities in the western Atlantic. This paper documents recent collections of *P. monodon* from the South Atlantic Bight and the Gulf of Mexico, reporting demographic and preliminary phylogenetic information for specimens collected between North Carolina and Texas from 2006 through 2012. The increased number of reports in 2011 and 2012, ranging from 102 mm to 298 mm total length, indicates that an adult population is present in densities sufficient for breeding, which is indicative of incipient establishment. Based on these reports of *P. monodon*, its successful invasion elsewhere, and its life history, we believe that this species will become common in the South Atlantic Bight and Gulf of Mexico in less than 10 years. *Penaeus monodon* is an aggressive predator in its native range and, if established, may prey on native shrimps, crabs, and bivalves. The impacts of an established *P. monodon* population are potentially widespread (e.g., alterations in local commercial fisheries, direct and indirect pressures on native shrimp, crab and bivalve populations, and subsequent impacts on the populations of other predators of those organisms) and should be considered by resource managers. The impacts of *P. monodon* on native fauna and the source(s) or vector(s) of the invasion, however, remain unknown at this time.

Key words: Asian tiger shrimp, *Penaeus monodon*, western Atlantic, Gulf of Mexico, invasion, population status, phylogenetics

Introduction

The Asian tiger shrimp, *Penaeus monodon*, is a widespread penaeid shrimp species that is native to the Indo-West Pacific (Figure 1), with a range comprising southern Japan, Korea, China, Taiwan, the Philippines, Vietnam, Cambodia, Malaysia, Singapore, Indonesia, Papua New Guinea, Australia, Thailand, Myanmar, Bangladesh, Sri Lanka, India, Pakistan, Tanzania, Madagascar, and South Africa (Motoh 1981; FAO 2012), and the Red Sea off Yemen (US National Museum of Natural History Cat. No. 171584). *Penaeus monodon* has been widely farmed outside of its native range, including West Africa and various locations in the western Atlantic. This species is now established in many areas due to escapes from aquaculture including West Africa (Sahel and West Africa Club 2006; Ayinla et al. 2009; Anyanwu et al. 2011; Global Biodiversity Information Facility 2013), the Caribbean (Gómez-Lemos and Campos 2008), and along the northern and northeastern coasts of South America from Venezuela to eastern Brazil (e.g., Coelho et al. 2001; Silva et al. 2002; Aguado and Sayegh 2007; Cintra et al. 2011). *Penaeus monodon* has also been introduced to Hawaii, Tahiti, and England (Rodríguez and Suárez 2001), but is not established in these locations. There

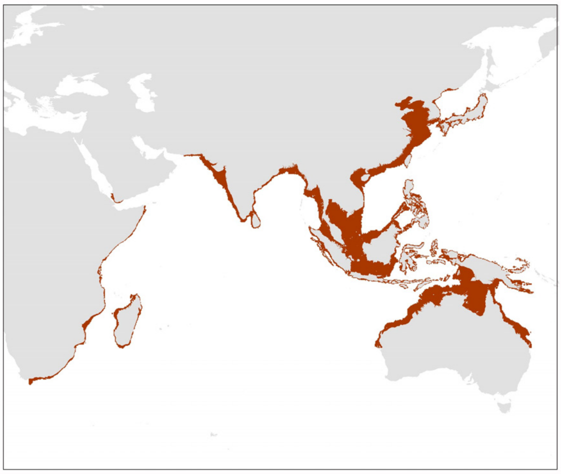

Figure 1. Native distribution of *Penaeus monodon* (adapted from FAO 2012).

are recent unconfirmed reports of shrimpers catching *P. monodon* in Haiti and a single confirmed report from the Dominican Republic in 2006 (A. Stokes, South Carolina Department of Natural Resources, Waddell Mariculture Center, Bluffton, SC, pers. comm.). The first occurrence in Puerto Rico was reported in June 2012 (USGS 2013), and an August 2012 report from Jamaica was also verified (D. Buddo, University of West Indies, Discovery Bay Marine Laboratory, Kingston, Jamaica, pers. comm.). There was an attempt to culture *P. monodon* in Florida in 2004 (P. Zajicek, Florida Department of Agriculture and Consumer Services, Tallahassee, FL, pers. comm.) but it was unsuccessful and the facility subsequently closed.

In the summer of 1988, an unknown number of *P. monodon* were accidentally released from a culture pond in South Carolina (A. Stokes, pers. comm.; D. Whitaker, South Carolina Department of Natural Resources, Marine Resources Division, Charleston, SC, pers. comm.). Nearly 300 of these shrimp were subsequently collected in trawl nets off the coasts of South Carolina, Georgia, and northeastern Florida in the following two months (D. Knott, pers. comm.) with no additional reports during the following 18 years. In September 2006, a single adult male was captured in the Mississippi Sound near Dauphin Island, Alabama (L. Hartman, pers. comm.). One month later, five specimens were collected in Pamlico Sound, North Carolina (T. Moore, North Carolina Department of Environment and Natural Resources, Mooresville, NC, pers. comm.). In late summer 2007, a single specimen was caught in Vermilion Bay, Louisiana (H. Blanchet, Louisiana Department of Wildlife and Fisheries, Baton, Rouge, LA, pers. comm.), and several more were reported from North Carolina, South Carolina, and Florida. The first verified collections of *P. monodon* in Georgia, Mississippi, and Texas occurred in 2008, 2009, and 2011, respectively. To date, *Penaeus monodon* has been documented in the U.S. from North Carolina to Texas (Figure 2), with many locations reporting multiple collections per year. In all cases, only a few specimens of *P. monodon* were caught. In October 2013, however, two commercial shrimpers reported catches of 11 and 18 kg of *P. monodon* in single trips off Flagler Beach, Florida. Clearly at least one breeding population of *P. monodon* now exists in eastern waters of the USA.

Following the 2006 reappearance of *P. monodon* in the waters of the South Atlantic Bight and the Gulf of Mexico, researchers from state and federal agencies and independent scientists came together, under the auspices of the Gulf and South Atlantic Regional Panel (GSARP) of the Aquatic Nuisance Species Task Force to: 1) review information on the biology of *P. monodon*, in order to make informed predictions of economic and ecological impacts; and 2) coordinate information on reports of recreational and commercial catches of *P. monodon* within the waters covered by the GSARP, namely the U.S. coastline from North Carolina to Texas. In this paper, we present demographic data (distribution, size, weight, and sex ratio) of the animals collected between 2006 and 2012, highlight the pertinent aspects of the biology of *P. monodon* related to this invasion, and discuss preliminary phylogenetic information on the animals collected between 2006 and 2012.

Methods

Species biology and life history

Estuaries serve as nursery grounds for *P. monodon* (Mohamed 1967; Chaudhari and Jalihal 1993), with larvae, juveniles, and young sub-adults occupying shallow coastal estuaries, lagoons, and mangrove areas. Sub-adults subsequently move offshore, where they are typically found in depths up to 70 m, although they are known to occur in water as deep as 162 m (Motoh 1981). *P. monodon* matures and breeds predominantly on sand or muddy-sand bottom in these nearshore marine habitats.

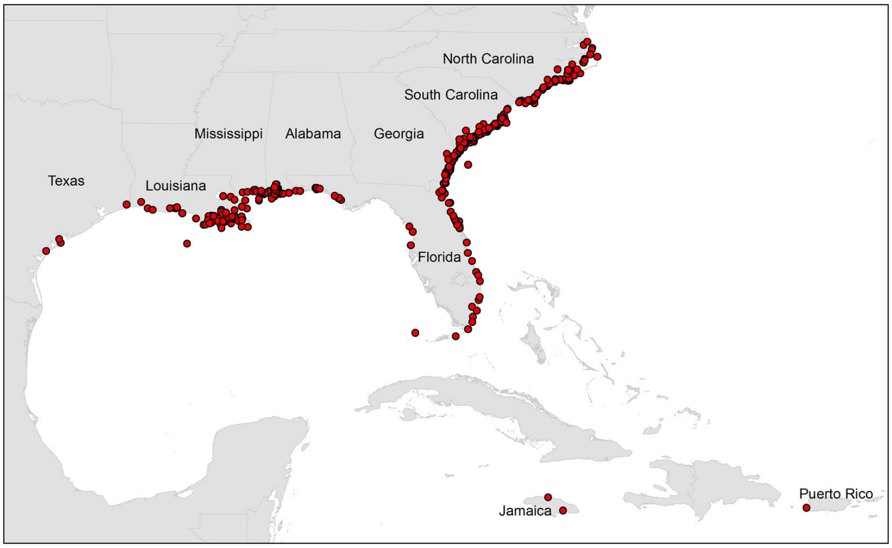

Figure 2. Map showing reported *Penaeus monodon* collections in the U.S. from 2006–2012 (USGS 2013).

Females grow larger than males (Primavera et al. 1998) and can reach 330 mm total length (hereafter TL, measured from tip of rostrum to tip of telson) (FAO 2013), with the largest specimen recorded being 337 mm TL (Crosnier 1965 in Mohamed 1967). The maximum size of males reported by Motoh (1985) is 71 mm carapace length (hereafter CL), which is equivalent to ~240 mm TL (Primavera et al. 1998). In wild populations, males become sexually mature at an age of ~5 months and a body weight of ~35 g (~32 mm CL ≈150 mm TL). Females are capable of breeding at ~6 months and a body weight of ~70 g (~45–50 mm CL ≈175 mm TL) (Primavera et al. 1998; FAO 2013). In one particular pond culture setting, *P. monodon* size and age were related as follows: 4 months (120 mm TL, 14 g), 6 months (142 mm TL, 22 g), 10 months (211 mm TL, 63 g), 12 months (229 mm TL, 95 g) (Delmendo and Rabanal 1956 in Mohamed 1967). The difference between body size and age for wild versus cultured shrimp implies that, at least in this culture situation (Delmendo and Rabanal 1956), wild animals grow faster than cultured ones.

Male and female *P. monodon* live 1.5 and 2 years, respectively, based on pond rearing experiments in the Philippines (Motoh 1981). A shorter life span of 12–14 months was determined for wild penaeids (including *P. monodon*), in western India (Srivatsa 1953 in Mohamed 1967).

The timing of spawning activity has been studied in Singapore and the Philippines. Hall (1962) suggested that in the waters off Singapore, *P. monodon* breeds between February and April. In the Philippines, there is limited spawning year round, but there are peaks in March, and October or November depending on the location (Motoh 1981). Female *P. monodon* are highly fecund, producing between 200,000 and 1 million eggs in a complete spawn with an average of ~500,000 (Primavera 1982). Following spawning, both pond-reared and wild-caught females may re-mature and repeat spawning, with large individuals doing so more frequently and producing more eggs than small ones (Menasveta et al. 1994). Pond-reared females of 50–63 mm CL, with one eyestalk removed, spawned viable eggs repeatedly within inter-molt periods of 20–30 days, indicating that one impregnation was sufficient to fertilize several batches of eggs spawned within one inter-molt period (Beard and Wickins 1980).

Penaeus monodon tolerate salinities from 0 to as high as 38 psu (Motoh 1981; Chaudhari and Jalihal 1993). Lethal thermal extremes are not definitively known, although mortality has been reported at water temperatures below 13 °C and above 33 °C (Jintoni 2003) and below 10 °C or above 39 °C for postlarvae and juveniles (Motoh 1981). Survival and growth, however, are severely limited below 20 °C (Lumare et al. 1993).

A primary concern regarding the impacts of the introduction of *P. monodon* outside of its native range is the potential to compete with, or

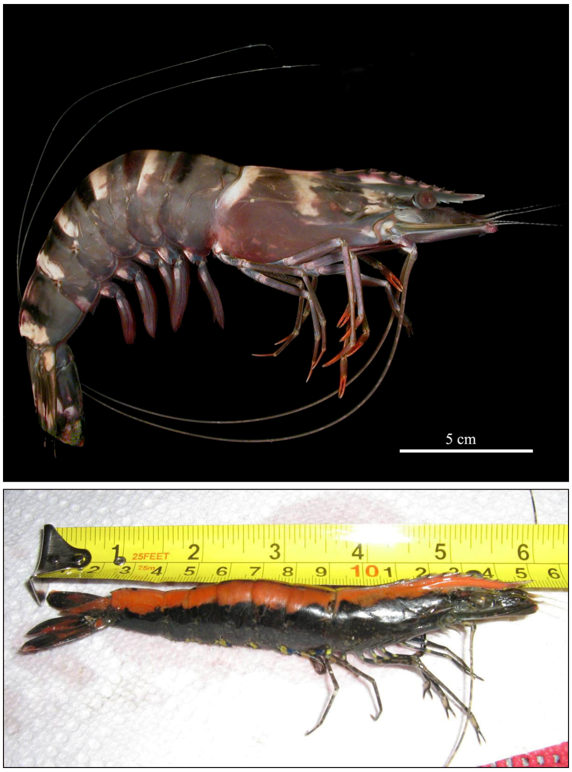

Figure 3. *Top*: Lateral view of a mature female *Penaeus monodon* (279 mm TL) caught in 2008 off Charleston Harbor, SC (photo courtesy of the SCDNR Southeastern Regional Taxonomic Center, SERTC). *Bottom*: An immature "red-striped" specimen (152 mm TL) caught by cast net in April 2012 in the Intracoastal Waterway near Vero Beach, FL (photo courtesy of Tom Stokes).

prey directly upon, native species. *Penaeus monodon* preys upon young penaeid prawns (Thomas 1972); a wide variety of macro-invertebrates (e.g., gastropods, bivalves, crustaceans, and polychaetes), fish, as well some plant material, and small amounts of echinoderms, hydroids, debris, silt, and sand (Marte 1980; Luna-Marte 1982; Dall 1992; Smith et al. 1992). At least one study suggests that they do not feed upon carrion (Hill and Wassenberg 1987).

Identification

Mature *Penaeus monodon* can be distinguished from native penaeid shrimp of the southeastern U.S. by their large size (up to 330 mm TL and 330 g in total wet weight, hereafter WT), their overall rusty brown to black color, and/or by the distinctive dark and light alternating banding across the back of the thorax and abdomen (Figure 3, top panel) (Mohamed 1967). Although the lighter bands are sometimes indistinct on juvenile shrimp (e.g., ~100–150 mm TL), yellow patches near the bases of the pereopods and pleopods and yellow banding on the antennules and antennae can be useful in distinguishing *P. monodon* from penaeids native to the U.S. (Knott, pers. obs.). Aside from their characteristic coloration, juveniles and sub-adults of *P. monodon* can be differentiated from native species by the posterior extent of the adrostral sulci and the morphology of the external genitalia (Motoh and Buri 1980; Pérez Farfante and Kensley 1997).

There is also a color variant of *P. monodon* that has a conspicuous, wide, reddish-orange stripe along the dorsum that extends from the rostrum to the telson (Figure 3, bottom panel). This "red-striped" morph expresses an allele that is present in < 1% of wild populations in Australia; however, lineages expressing the trait in ~60% of individuals in some families have been derived through selective breeding of animals taken from Australian populations (J. Wyban, High Health Aquaculture Inc., Kurtistown, HI, pers. comm.). A low proportion (6.6%) of the *P. monodon* reported in the U.S. in 2012 showed this trait; however, a much greater proportion (52.9%) of individuals ≤ 152 mm TL exhibited this trait, suggesting that it may be an age- or size-related characteristic.

Gathering information on reports of Penaeus monodon *in the U.S.*

Regional coordinators from North Carolina to Texas distributed information and coordinated *P. monodon* reports from recreational and commercial fishermen. Most state agencies between North Carolina and Texas conducted publicity campaigns in the form of press releases and the distribution of flyers and posters that informed the public that collection information and specimens were being sought to investigate the *P. monodon* invasion. Outreach information was dispersed freely with some coordination on the content and presentation. In cases where the specimens were given to biologists, TL, WT, and gender were recorded for each specimen collected, along with precise information on collection location (e.g., latitude and longitude, if available). Females were determined by the presence of a thelycum, an external reproductive opening; males by the presence of a petasma (Mohamed 1967; Motoh 1981). None of the females were examined for eggs. Persons collecting *P. monodon* were also encouraged to submit photographs of specimens as part of their reports

Table 1. Number of individuals of *Penaeus monodon* collected by state and year from 2005–2012.

Year	NC	SC	GA	FL	AL	MS	LA	TX	Total
2005	0	0	0	0	0	0	0	0	0
2006	5	0	0	0	1	0	0	0	6
2007	1	1	0	1	0	0	1	0	4
2008	8	6	4	2	1	0	0	0	21
2009	14	15	3	1	5	3	4	0	45
2010	2	20	1	2	0	0	7	0	32
2011	329	144	3	25	28	16	128	5	678
2012	21	64	43	41	3	13	9	1	195
Total	380	250	54	72	38	32	149	6	981

in order to confirm species identification. In some cases, objects in these photographs (e.g., coins, rulers, newspaper headlines, etc.) were used to determine specimen size when measurements were not provided directly or their accuracy was questionable.

Statistical analyses

In order to examine the effects of sex and length on weight and the interaction between sex and length, an ANCOVA was performed on $\log_{10}$-$\log_{10}$ transformed TL and WT using both the entire data set and also separately on the subset of data for *P. monodon* from 150–250 mm TL. Any eggs that may have been present in females were not removed. All statistical analyses were performed using Minitab version 16.2.2.

Results

As of December 31, 2012, the distribution of *P. monodon* in coastal and estuarine waters of the southeastern U.S. extended from Albemarle Sound, North Carolina on the Atlantic U.S. coast to Aransas Bay, Texas in the western Gulf of Mexico, as well as a few locations in the eastern Caribbean (Figure 2). A detailed account of reports that define this distribution can be found in the validated collections of specimens in the USGS Nonindigenous Aquatic Species database (USGS 2013).

Following initial reports of small numbers of *P. monodon* in 2006 and 2007, the number of reported specimens increased slightly between 2008 and 2010 (Table 1, Figure 4) and was followed by a 20-fold increase in reports in 2011. Some of this increase may be attributable to increased levels of public outreach and widespread media coverage; however, numerous shrimp fishermen described catching *P. monodon* with increased frequency and in greater numbers, suggesting that their actual abundance increased substantially in 2011. The primary source of *P. monodon* reports was direct communication with commercial shrimpers who were actively fishing in the Gulf of Mexico and the South Atlantic Bight. In 2012, a number of commercial fishermen informed dock personnel that *P. monodon* had become more abundant than in the previous year, but in some cases specimens were eaten or sold without being reported. Fisheries-independent and catch-per-unit-effort data are not available to examine how well the reported occurrences reflect changes in the actual abundance of this invasive species since its arrival in coastal U.S. waters.

By region, the number of *P. monodon* reported from the Gulf of Mexico is lower than that in the South Atlantic Bight. From 2006–2012, 737 *P. monodon* were captured along the Atlantic coast, from Albemarle Sound, North Carolina through the Florida Keys. The greatest number (~85%) was caught by commercial shrimp fishermen trawling in North and South Carolina (Table 1). During that same period in the Gulf of Mexico, 244 specimens were captured, with all but one individual (from the Dry Tortugas National Park off southwest Florida Keys) being captured between Clearwater, Florida and Aransas Bay, Texas (Figure 2). More than 60% of these *P. monodon* from the Gulf of Mexico were captured in the waters of Louisiana (Table 1).

Among those specimens for which a definitive month of capture was recorded, by far the greatest number (>90%) of *P. monodon* was captured during the months of August through November (Figure 5). This peak coincided with the latter half of the most intense commercial shrimp fishing effort (NOAA 2013). The 3–6 month lag

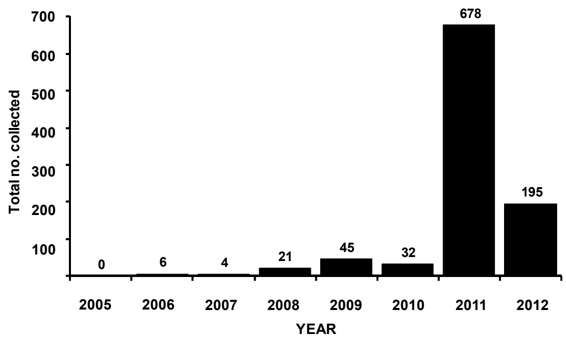

Figure 4. Number of *Penaeus monodon* collected by year from 2005–2012.

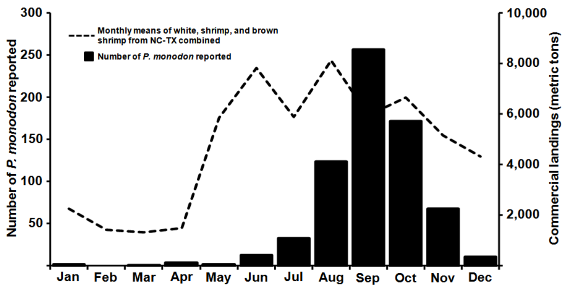

Figure 5. Number of *Penaeus monodon* collected by month from 2006–2012 and monthly average (in metric tons) of south Atlantic and Gulf coast state's total commercial landings of native white, pink and brown shrimp from 2006–2011 (latest available data from query of NOAA's NMFS Monthly Commercial Landings Statistics database).

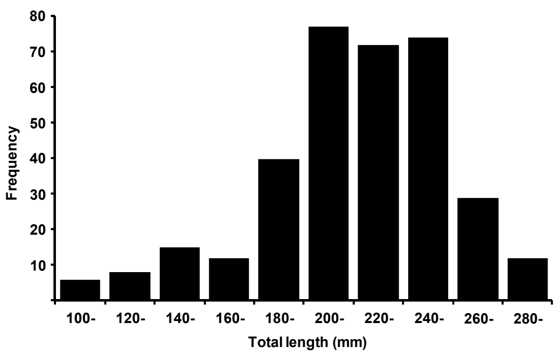

Figure 6. Length-frequency distribution of *Penaeus monodon* collected in U.S. waters from 2006–2012 (total n = 345).

time between the seasonal increase in shrimp landings and the peak period of *P. monodon* collection suggests that the peak is not merely a reflection of commercial shrimp fishing effort (Figure 5) and may be a result of reduced *P. monodon* detection at smaller sizes.

Individuals ranged in size from 102 mm to 298 mm TL, with the majority being adults between 200 mm and 259 mm TL (Figure 6). The occurrence of smaller individuals (juveniles) strongly suggests that *P. monodon* may be reproducing within or close to waters of the South Atlantic Bight and/or the Gulf of Mexico. Among the shrimp caught between April and August, the number of juveniles (< 160 mm TL) increased more than two-fold between 2011 and 2012 (Figure 7). Despite the fact that overall fewer *P. monodon* were collected in 2012 (Figure 4), the greatest abundance of small *P. monodon* was observed during that year (Figure 7d). Among *P. monodon* specimens for which both the date of collection and size were available, those captured in the late spring and early summer (April-August) were smaller, on average, than those caught later in the year (September-January) during the period of peak shrimp trawling (195.6 mm TL, n = 72 vs. 226.7 mm TL, n = 273, respectively; $t = -5.45$, $P < 0.001$).

Although the vast majority of *P. monodon* (89%) were captured by commercial fishermen, a seasonal difference was observed in the type of gear used by reporters. Approximately 20% of the reports from April through August (n = 142) were made by individuals using gear other than commercial trawl nets, principally cast nets and crab pots. For the following months (September through January), the percentage of reports where non-commercial gear was used decreased to 6% (n = 281). This decline likely reflects the appreciable elevation in commercial fishing pressure during the fall and early winter months. It is possible, however, that some of the difference could also be attributed to *P. monodon* occurring at greater depths during this period, making them less likely to be captured by non-trawling methods.

The greatest increase in *P. monodon* size (TL) occurred between May and August, followed by relatively little change through the fall and early winter (Figure 8). As a proxy for growth, this amounts to an average increase of 9–10 mm TL per month for combined males and females collected between May and January of the following year.

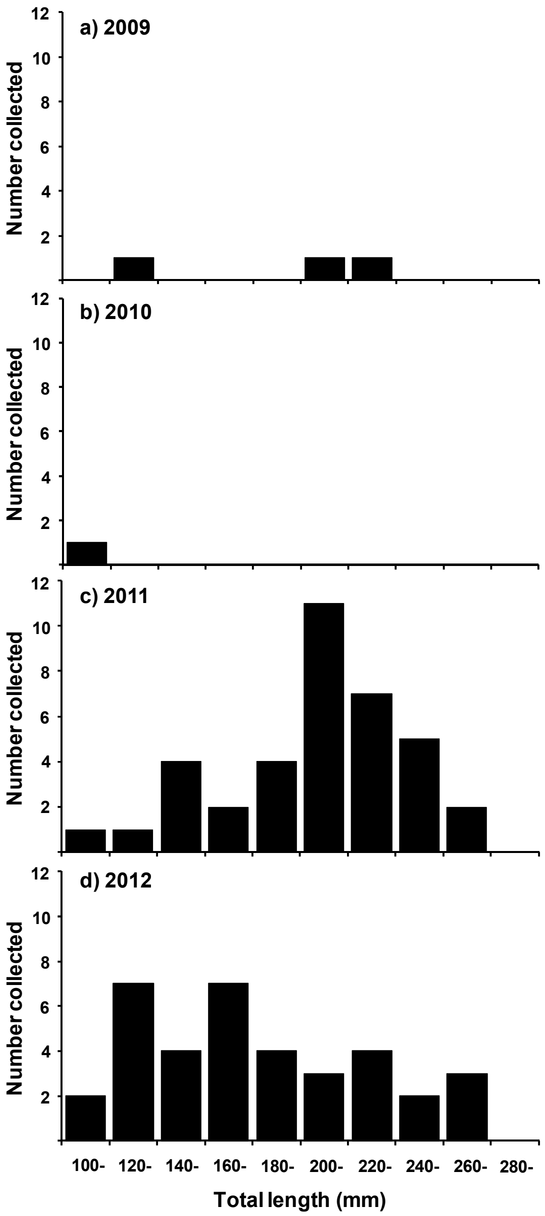

Figure 7. Length frequency of *Penaeus monodon* captured in the late spring and early summer (April – August) from 2009–2012.

For the full dataset, the total length*sex interaction on WT was significant ($P = 0.002$), precluding us from examining TL ($P < 0.001$) and sex ($P = 0.002$) by themselves. For individuals between 150 and 250 mm TL, neither the effects of sex nor the total length*sex interaction were significant ($P = 0.081$ and $P = 0.072$, respectively). This indicates that the relationship between WT and TL did not differ significantly between males and females, although larger animals (TL > 250 mm) in our study tended to be female (Figure 9). Power curves resulted in a better fit than plotting quadratic equations to these data. Separate equations were determined for the sexes separately (Figure 9); however, given that statistical analysis did not find a difference in length-weight relationships between sexes for individuals between 150 and 250 mm, the equation for these pooled data was determined as:

$$WT = 7E^{-06}\ TL^{3.0401};\ r^2 = 0.918$$

In our study, the largest female specimens were approximately 285 mm TL and 200 g, while the largest males were ~250 mm TL and ~140 g. Among the 191 *P. monodon* for which gender was definitively determined, the male to female ratio was 1.36:1.

Discussion

Reports of *Penaeus monodon* in the South Atlantic Bight and Gulf of Mexico have increased from 2008 levels. Some of the increase in the numbers reported in 2011 compared to earlier years may be attributable to greater efforts to document their occurrence; however, the magnitude of the increase suggests it is more than an artifact of this expanded reporting effort. Based on information from fisherman, the reduction in reports from 2011 to 2012, was probably due to “reporting apathy”, as the novelty of reporting this species diminished. A similar phenomenon was observed for Indo-Pacific lionfish, *Pterois volitans/miles* (Linnaeus, 1758/Bennett, 1828) (Ruttenberg et al. 2012). Considering the increase, it is probable that a breeding population(s) is present, either in the South Atlantic Bight, the Gulf of Mexico, or both. In addition, the size range of individuals collected (102 mm to 298 mm TL) documents the presence of both juveniles and adults in the coastal waters of the U.S.

The geographic patterns in the number of *P. monodon* captured may be influenced by differences in commercial fishing effort among those areas and not entirely reflective of the abundance or distribution of the species. For example, *P. monodon* postlarvae typically recruit into estuaries from offshore breeding grounds in spring/summer, followed by their growth through early sub-adult stages in these shallow nursery grounds and subsequent offshore egress as observed within its native range (Motoh 1981).

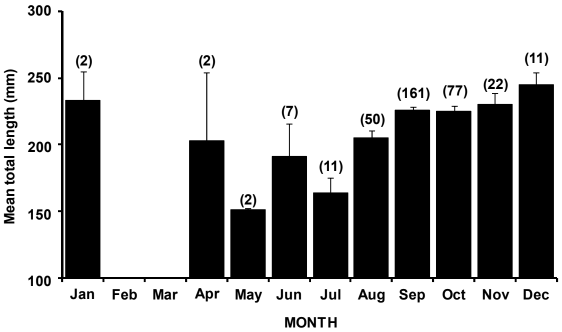

Figure 8. Monthly mean length of *Penaeus monodon* collected from 2009–2012. Numbers shown in parentheses are sample sizes; error bars represent 1 S.E. of the mean.

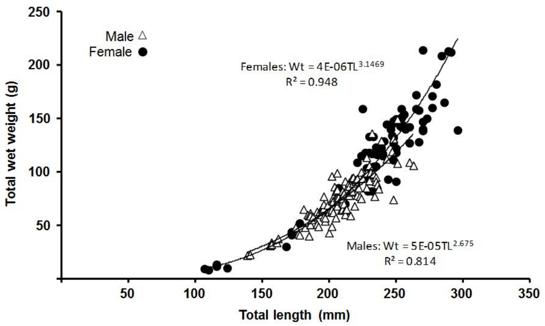

Figure 9. Length-weight scatter plot of female and male *Penaeus monodon* captured from 2009–2012 (open triangles: males, n = 117; closed circle: females, n = 80).

This pattern of migration would provide inland access to *P. monodon* with a wider variety of fishing gear earlier in the year than can be successfully employed to capture adult *P. monodon* once they have moved offshore.

Introductions of *P. monodon* into the southeastern U.S. have three potential sources: 1) the release of larvae in ballast water taken onboard within their native range; 2) migration from areas in the Atlantic or Caribbean Sea where wild populations have become established (most likely as a result of prior aquaculture escape); and 3) escape from active and ongoing aquaculture facilities in the western Atlantic. Individuals found in U.S. waters may have arrived as a result of a continuous supply of *P. monodon* transported by currents from aquaculture facilities or wild populations in the Caribbean Sea or coastal South America.

Among the many vectors that can facilitate the introduction of nonindigenous marine and estuarine invertebrate species, ballast water release, along with hitchhikers in hull-fouling communities, are the most prominent (Carlton 2011). Chu et al. (1997) and G. Ruiz (Smithsonian Environmental Research Center, Edgewater, MD, pers. comm.) report having recovered viable larval decapod crustaceans from ballast water, and numerous crab species are believed to have been transferred between geographic regions via ballast water. This may have been the vector for the introduction from Asia to the eastern U.S. of the Oriental shrimp, *Palaemon macrodactylus*, and the Asian shore crab, *Hemigrapsus sanguineus* (De Haan, 1853) (G. Ruiz, pers. comm.). Although they recognized the uncertainty involved in determining the source of *P. monodon* introduced to Brazil, Severino-Rodrigues et al. (2000) hypothesized that ballast water discharge may have played a role in its introduction there.

Lessepsian transport of penaeid shrimps (i.e., from their native range into the Mediterranean via the Suez Canal; Rodriguez and Suárez 2001) and migration from areas where they have been introduced (e.g., along the South American coastline; Pérez Farfante and Kensley 1997; Cintra et al. 2011; Leão et al. 2011) are also significant means of their dispersal. Altuve et al. (2008) suggested that the natural migration of *P. monodon*, assisted by the Guiana Current, spread the species from northern Brazil into the Caribbean, a distance of nearly 1600 km, in about four years.

Hurricanes and tropical storms frequently take a path through the Caribbean northward into the South Atlantic Bight or more westerly into the Gulf of Mexico. Tropical Storm Noel dropped 38-51 cm of rain along the southern coast of the Dominican Republic in 2007, where floodwaters came within 0.3 meters of pond berms at a facility where *Litopenaeus vannamei* was being cultured, and a massive escape was narrowly avoided (D. Drennan, Industria Nacional Agropesquera, Dominican Republic, pers. comm.). Those same ponds had previously been breached by flooding during periods when *P. monodon* was being cultured. In subsequent years, when *L. vannamei* was again being farmed, *P. monodon* larvae or postlarvae occasionally made their way into the ponds during post-harvest re-filling, indicating that a breeding population existed in nearby waters (D. Drennan, pers. comm.). Hurricanes Earl (2010) and Irene (2011) took similar tracks, providing more recent opportunities for storm-related transport to carry *P. monodon* into U.S. waters from the Caribbean. There is additional anecdotal information that suggests that shrimp farms in the Caribbean often lose portions of their crop during storm flooding, pond maintenance, or harvest operations (D. Knott, pers. comm.). Similar routine escape associated with shrimp pond harvest has been documented elsewhere (Wenner and Knott 1992).

An accidental release of *P. monodon* into the South Atlantic Bight, where they remained undetected for 18 years following their 1988 escape, is an unlikely explanation for their recent appearance in the U.S. Although commercial shrimpers caught them in the two months following their release (August-September 1988; D. Knott, pers. comm.), there were no subsequent reports until 2006. Considering the intense fishing efforts of the shrimp trawling industry along the entire southeastern U.S. coastline, along with the estuarine nursery habitat of *P. monodon*, it is improbable that a population became established there following the 1988 release and avoided detection until 2006.

Carlton (2011) disputed the notion that introduced species seldom have a notable impact in the newly colonized communities (e.g., see Vander Zanden 2005), declaring that for up to 95% of the known marine crustacean invasions there is a dearth of qualitative, quantitative, or experimental studies of ecological or other impacts. In light of this information gap, Ruiz et al. (2011) assembled a summary of historical records of marine crustacean invasions in North America and concluded that the negative ecological or economic impacts have only been reported for 28% of the 108 nonindigenous crustaceans found in marine, estuarine, and freshwater habitats of that continent. Furthermore, even for that 28%, the impacts were poorly documented. Not surprisingly then, the impacts of *P. monodon* on native fauna in areas where it has been introduced are currently poorly documented. Because *P. monodon* feeds on benthic organisms, primarily small crabs, shrimp, bivalves, and gastropods (Marte 1980), direct predation on local fauna is a concern. In addition to the potential effects of predation, the larger size of *P. monodon* may also confer greater nutritional requirements and a competitive advantage over native species in obtaining food.

The continual emergence, discovery, and global spread of novel shrimp pathogens (Flegel 2012; Lightner et al. 2012) pose the potential for unpredictable impacts on native crustacean fauna. Although the mortality caused by many of these pathogens is generally greater in culture facilities than in the wild, the impact of infected seed and broodstock transfers on wild shrimp populations is poorly known. In 2003, the Pacific whiteleg shrimp, *Litopenaeus vannamei* (Boone, 1931) eclipsed *P. monodon* in terms of global culture production, largely due to the susceptibility of *P. monodon* to a variety of viral diseases (Spaargaren 1996; Flegel 1997; Primavera and Quinitio 2000; Flegel 2012), with white spot syndrome virus (WSSV) considered the most deleterious (Flegel and Alday-Sanz 1998; Global Aquaculture Alliance 1999; Soowannayan and Phanthura 2011). *Penaeus monodon* is capable of transmitting viral diseases such as WSSV to native shrimp species and other crustaceans (Chou et al. 1998; Kanchanaphum et al. 1998; Soowannayan and Phanthura 2011). The most recent threat to cultured *P. monodon* and *L. vannamei* in Asia, acute hepatopancreatic necrosis syndrome (AHPNS), was discovered in China in 2009 and has since caused widespread shrimp mortality on farms throughout southeast Asia, including Vietnam, Malaysia, and Thailand (Flegel 2012; Leaño and Mohan 2012). This disease is an emerging idiopathic disease whose potential for transmission to wild populations of penaeid shrimp is virtually unknown.

We are currently working to identify the source(s) of Asian tiger shrimp along the Gulf and Atlantic coasts of the U.S., with the hope of answering some of the questions regarding their establishment, the number of introductions, and their population structure. Preliminary phylogenetic analyses have indicated little genetic diversity in samples collected along the coast from North Carolina through the Gulf of Mexico. This lack of genetic differentiation indicates that founding individuals are highly related or inbred as a result of related stocks or genetic bottlenecks in the aquaculture industry. Further studies using additional markers and Hardy-Weinberg linkage equilibrium assessments could assist in determining whether *P. monodon* populations are established and reproducing in the region. With adequate samples and genetic markers, information can be gleaned on the populations of origin, number of founding populations, and dispersal pathways in the U.S. Samples examined to date are dissimilar to published mitochondrial genome and voucher specimen sequences of animals collected in their native range.

We propose that *P. monodon* is established in the southeastern U.S. along the Atlantic coast and in the Gulf of Mexico. This is suggested by the overall increase in specimen collections, as well as the occurrence of individuals that span a range of sizes (juvenile to adult) and the increasing number of reports from inshore areas that are typically considered to be nursery grounds for many penaeid species. Ongoing genetic studies are being conducted to verify this establishment, including the development of a genetic probe to conduct environmental-DNA (eDNA) analyses for the detection of *P. monodon* at sizes that are not typically captured by trawl, seine, or cast nets. Such analyses could be applied to plankton samples to see whether or not they contain *P. monodon* larval stages. Specific nursery areas have yet to be identified, and these genetic approaches are likely to assist in this regard. Once these are located, a comparison of the temperature regime of the South Atlantic Bight with that required to support reproduction by this species is needed, as is a determination of the seasonality of reproduction in its newly introduced range. Neither the impacts on native fauna of this recently arrived shrimp species nor the source(s) or vector(s) of the invasion are known at this time. Further research on the sources of this introduction, the locations of breeding populations, and the ecological consequences of this invasion are warranted.

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