Estimating the dispersal capacity of the introduced green mussel, *Perna viridis* (Linnaeus, 1758), from field collections and oceanographic modeling

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**Abstract**

Introduced species can often cause negative environmental and economic effects, but also offer opportunities to study the rate of range expansion from localized population centers. The green mussel, *Perna viridis*, was introduced to the waters of the Caribbean and Florida from the Indo-Pacific and remains relatively isolated in portions of northeastern Florida. The present study aimed at identifying the factors that influence the spatial and temporal patterns of green mussel larval settlement throughout the Intracoastal Waterway (ICW) of northeastern Florida, and to estimate dispersal distance using both field observations and a hydrographic model. Green mussel spat were collected from sites within the ICW on a monthly basis for much of 2007, 2008 and 2010 and a particle tracking model was used to predict larval movement during observed settlement periods from 2007. Settlement typically occurred during the summer months and was correlated to water temperature but not salinity or chlorophyll a concentration. Habitat also significantly influenced settlement patterns since most of the settlement occurred within the main channel of the ICW and not in adjacent feeder creeks. Observed settlement patterns suggested that most green mussel larvae likely dispersed 10 km or less but some were collected a minimum of 18 km from a potential source population. Model projections suggested that dispersal distance could often exceed 100 km but most of the particles dispersed along the coast as opposed to remaining within the ICW making comparisons between the model results and the observed settlement patterns difficult.

**Keywords:**
Introduced species  
Larval dispersal  
*Perna viridis*  
Range expansion

**1. Introduction**

Due to the well documented negative effects of many non-native species on the economies and ecology of the areas to which they have been introduced (Pimentel et al., 2000), there is considerable interest in predicting the potential for range expansion and the speed at which expansion is likely to occur. The potential and realized range expansion of introduced species is often determined by first, the ability of the species to move outside its current range, and second, its ability to survive in the areas to which it disperses (Andow et al., 1990; Grosholz, 1996). The ability of a particular species to do either of these things is going to be determined by a variety of abiotic and biotic factors. For example, in marine invertebrates that have a pelagic larval stage, their ability to expand their range will be determined by their own behavior (or lack thereof) in the larval stage, the prevailing directions of currents (tidal, wind, etc.), the presence or absence of predators, appropriate habitat in which to settle, and the physical environmental conditions of the area in which they settle among other considerations.

Considerable effort has been put into understanding the movement of invertebrates with pelagic larvae using a variety of different tools (reviewed in Levin, 2006). Many studies have utilized spatial population genetic structure to estimate historical dispersal patterns within regions (Hutchinson and Templeton, 1999; Neigel, 2002; Palumbi, 2003; Weersing and Toonen, 2009). Some of the best work has utilized some kind of natural marker, such as polymorphic genetic loci or chemical signatures that can be used to identify the origin of larvae that are settling at a given location (DiBacco and Levin, 2000; Hellberg et al., 2002; Sortka et al., 2004; Gilg et al., 2007). In several cases, these estimates or observations of larval dispersal have been combined with dispersal simulation models in an effort to describe the observed patterns from the prevailing oceanic currents and wind vectors (Gilg and Hilbish, 2003a, 2003b; Galindo et al., 2010; Selkoe et al., 2010).

One of the unique aspects of introduced species is that their relatively localized range during the initial stages of introduction can...
also be utilized to estimate larval dispersal. Since the population is typically introduced to a very narrow range, that area can be assumed to be the source for any larvae settling outside that range. For example, McQuaid and Phillips (2000) estimated the effective dispersal range of the introduced blue mussel *Mytilus galloprovincialis* by observing settlement of *M. galloprovincialis* larvae outside of the known adult range. The distance between the source population and the newly settled larvae could be considered the effective dispersal distance in that situation.

The green mussel, *Perna viridis*, is native to the waters of the Indo-Pacific and has been subsequently introduced to a number of locations in the Caribbean and the Southeastern United States (Agard et al., 1992; Rylander et al., 1996; Benson et al., 2001; Ingrao et al., 2001; Buddo et al., 2003; Gilg et al., 2013). It was first discovered in the United States in Tampa Bay on the Gulf coast of Florida in 1999 (Benson et al., 2001). In 2002 and 2003 isolated populations of *P. viridis* had been observed on the Atlantic coast of Florida near St. Augustine and on off-shore reefs near the coast of Georgia (Power et al., 2004; Baker et al., 2007). *P. viridis* populations showed a rapid initial expansion in Tampa Bay and the surrounding area but have since declined substantially in numbers throughout that region, with population declines sometimes associated with low temperatures (Firth et al., 2011; Urian et al., 2011) or susceptibility to red tides (Leverone et al., 2007; May et al., 2010). Along the Atlantic coast, intertidal populations of *P. viridis* have been identified from approximately the Georgia/Florida border south to the Indian River Lagoon (Spinuzzi et al., 2013). Within that area, however, populations tend to be very isolated due to a number of factors, including lack of hard substrates for settlement, reduced reproductive success due to low population density (allelo effects), and mortality events associated with cold winter temperatures. Therefore, nearly all of the mussels are found near inlets where jetties and bridges provide more hard substrates.

Within the Intracoastal Waterway (ICW) of northeastern Florida, for instance, several hundred green mussels could be found in the intertidal zone on rock structures in three specific locations at the St. Augustine inlet. Another population of several hundred individuals could be found on floating docks and a rock jetty at the Matanzas inlet. Surveys of the ICW between these sites and further north of St. Augustine by the authors and the staff of the Guana Tolomato Matanzas National Estuarine Research Reserve (GTM NERR) between 2005 and 2009 found very few specimens at locations outside the two specified inlets (unpublished data). So even though the mussels have been present in the area since 2002, little expansion has occurred away from the inlets in that time. While a few mussels can be found at locations away from inlets, they rarely exist in groups that are close enough in space to successfully reproduce, and they are often ephemeral (most likely due to significant winter mortality events every 2–3 years). Outside the ICW, the closest population of mussels is in the waters at the mouth of the St. Johns River approximately 60 km to the North of St. Augustine Inlet with a second population on the Florida/Georgia border on Amelia Island.

Therefore, the purpose of the present study was to determine the factors that influence dispersal and settlement of introduced *P. viridis* populations in the ICW of northeastern Florida, and to utilize their isolated range to estimate the dispersal potential of *P. viridis* larvae. This estimation included both the approximate distance of dispersal as well as the amount of settlement within different habitats, and the influence of various environmental factors on the timing of observed settlement. Furthermore, we attempted to determine whether the observed settlement patterns corresponded to predictions based on a model of the local physical oceanography (CH3D — Sheng, 1986). By understanding the factors that govern spawning and the movement and subsequent settlement of *P. viridis* larvae we can better predict locations that are susceptible to future range expansion.

### 2. Methods

#### 2.1. Spat collections

Recently settled green mussel larvae, or spat, were collected from several locations in the waters of the Northeast Florida ICW and adjacent feeder creeks in 2007, 2008 and 2010. At each location, a spat collector consisting of a frame made of PVC that held four 12 cm × 12 cm quarry tiles were deployed for one month, after which the quarry tiles would be collected and replaced with clean tiles. These frames were either strapped onto channel markers or other large posts within the ICW, or in cases where such structures could not be found, were suspended underneath buoys that had been anchored to the bottom. In all cases, the tiles were placed such that they were 1–3 m below the low tide mark. After collection, fouled tiles were allowed to dry in the sun for at least two weeks before being analyzed. The surface of tiles was observed under a dissecting microscope at 20× magnification to look for the presence of *P. viridis* spat. Any spat found were measured using an optical micrometer and the total number and sizes found on each tile were recorded.

In the first year of the study, spat collectors were deployed at seven sites within the main channel of the ICW at varying distances from known source populations of *P. viridis* near St. Augustine and Matanzas inlets. These sites included channel markers 25, 51, 1, 46, and 77, as well as the Conch House Marina (CH), and a dock at the Whitney Laboratory (WL) (Fig. 1). An additional collector was placed in each of four feeder creeks of the ICW including Casacola Creek (CC), Oyster Creek (OC), Moses Creek (MC), and Pellicer Creek (PC). The collectors in each of the feeder creeks were essentially paired with a collector in the main channel of the ICW that was at a similar distance from either of the two inlets. This allowed us to compare settlement density in the two different habitats (feeder creek vs. main channel) while controlling for distance from source. Monthly collections were made from July through December in year one.

In years two and three of the study, collectors were only deployed within the main channel of the ICW at the same sites as in year one, except for the addition of channel marker 55 near the mouth of St. Augustine inlet, and a sign post near Fort Matanzas (FM) near the Matanzas inlet. Collections were made from January through November in 2008, but only from April through October in 2010 since no settlement had been observed in previous years outside of that time period (see below).

Sites 25, 1, FM and PC all have permanent data sondes maintained by the GTM NERR and, therefore, allow us to obtain environmental data including temperature and salinity which are collected at 15 minute intervals, and chlorophyll a which is sampled twice on the same day (diel sampling) on one day each month.

Settlement density in each month at each location was recorded as the number of *P. viridis* spat per plate. Since settlement density consistently had unequal variances and did not conform to a normal distribution, all comparisons among means utilized non-parametric tests. A Mann–Whitney U test was used to compare settlement density between feeder creeks and the main channel sites located at similar distances from the inlets to determine if habitat differences were associated with differences in settlement density. The mean number of spat per plate collected over all sampling events in 2007 were included in the analysis. Since settlement was extremely limited within feeder creeks (see below), all other analyses of spatial and temporal settlement patterns were confined to sites within the main channel of the ICW. Kruskal–Wallis tests were used to test for temporal and spatial variation in settlement density within the same habitat. We used Pearson Correlations to determine if settlement density was correlated with distance from the nearest inlet, with mean monthly temperature, salinity or chlorophyll a concentration. All statistical tests were performed using SPSS software and distances between locations were estimated using GoogleEarth.
2.2. Coupled current-wave model — CH3D-SWAN

The transport of mussel larvae was estimated by a hydrodynamic model CH3D, which is a three dimensional circulation model originally developed by Sheng (1986) and has been successfully applied to simulate the circulation driven by tide, wind, density gradients and waves in various water bodies (e.g., Sheng et al., 2008, 2010a, 2010b; Sheng and Kim, 2009; Sheng and Liu, 2011). CH3D uses a boundary fitted non-orthogonal curvilinear grid in the horizontal directions to resolve complex shoreline and geometry, and a terrain-following σ-grid in the vertical direction. The model uses a Smagorinsky type horizontal turbulent eddy coefficient (Smagorinsky, 1964) and a robust turbulent closure model (Sheng and Villaret, 1989) for vertical mixing.

Sheng et al. (2010a and 2010b) and Sheng and Liu (2011) dynamically coupled the hydrodynamic model CH3D with a wave model SWAN (Simulating WAves Nearshore) (Booij et al., 1999) to study the wave induced circulation. At each grid cell, SWAN simulated wave field (e.g., wave height, period and direction) is used to estimate the radiation stress or vortex force, as well as the wave enhanced bottom friction and vertical turbulent eddy coefficient, in the momentum equations of CH3D. Wave setup and wave induced currents are computed by CH3D, while water elevation which includes wave setup may change the total water depth and alter the wave propagation process. The CH3D simulated currents may affect the wave propagation by inducing wave refraction. Therefore, the coupled CH3D-SWAN allows the wave and current to interact with each other. In the present study, a depth independent radiation stress by Longuet-Higgins and Stewart (1964, hereafter referred to as LHS), a depth dependent radiation stress by Mellor (2008, hereafter referred to as M08) and a vortex force formulation by McWilliams et al. (2004, hereafter referred to as MRL04) are used to represent wave effects on circulation. The formulations of LHS, M08 and MRL04, together with the equations and boundary conditions of CH3D, are shown in Sheng et al. (2010a), Sheng and Liu (2011), and Liu and Sheng (2014).

In the simulation, a parcel of larvae is tracked individually by a Lagrangian Parcel (particle tracking) model, which consists of two

Fig. 1. A coastline map of the intracoastal waterway and the Atlantic coast of northeastern Florida showing the location of collection sites for Perna viridis spat. The inlets in this area are noted as points of reference. Collection sites marked with an * denote locations of environmental data sondes maintained by the Guana Tolomato Matanzas National Estuarine Research Reserve.
processes: a Lagrangian process of advection and an Eulerian process of diffusion. The random-walk Lagrangian Parcel model was used successfully to simulate the dispersion of sulfur-hexafluoride (SF₆), drifter buoys, and clam larval biomass in a coastal lagoon (Arnold et al., 2005).

The GTM NERR lagoonal system was divided into eight segments based on consideration of hydrodynamic, morphological, and biogeochemical characteristics (Sheng et al., 2008). The flushing results indicate that tide is the most dominant flushing mechanism, while river and salinity are important flushing mechanisms for segments that are far from the tidal inlets. The normalized flushing times were used to generate a relative flushing ranking for each segment. This quantitative ranking of flushing characteristics inside the GTM is made possible because of the use of a three-dimensional numerical circulation and transport model that incorporates the effect of hydrodynamics on flushing. These results provide much more quantitative information than the simple empirical residence time indices (1–4) developed for the GTM in a previous study.

Projections of larval dispersal were made for time periods when P. viridis larvae were likely in the plankton. Collection dates on which spat were observed were considered settlement dates and birth dates were estimated by approximating the length of larval development based on the water temperatures encountered and associated growth rates as determined by Nair and Appukuttan (2003). This worked out to be approximately 28 days for larvae born in March and April and about 21 days for those born later. In most years settlement was observed from May through September. Therefore, projections were made for each of those months using tidal and wind data from 2007.

Projections consisted of tracking 1000 particles released from both St. Augustine and Matanzas Inlets from the birth date to the approximate settlement date. For each release date, projections were made for larvae released at three different time periods including during a flood tide, an ebb tide, or at peak flood tide. On the last day of a projection, the proportion of particles found in each of the eight segments encompassing the study area (see above) were determined and a Pearson Correlation was used to determine whether the proportion of particles found within a segment was positively correlated with mean settlement density observed within that region in that time period.

3. Results

Green mussel spat were rarely observed on settlement plates at any of the feeder creek collection sites. Mean settlement density over all months was significantly higher at all four of the main channel sites than at the sites within feeder creeks they were paired with (Fig. 2) (Mann–Whitney U test: CC vs. 51: P < 0.001; OC vs. 1: P < 0.001; MC vs. 46: P < 0.001; PC vs. WL: P = 0.001). This same relationship was also observed in most cases when only considering samples collected during the same month, and was especially strong during peak settlement months in the summer. Since settlement was so rare within feeder creeks, all comparisons of spatial and temporal variation among sites were limited to sites within the main channel of the ICW.

Spat settlement was considerably greater in 2007 than in the other two years and mean annual spat density differed significantly among sites in all three collection years (Fig. 3) (Kruskal–Wallis test: 2007: P < 0.001; 2008: P < 0.001; 2010: P < 0.001). Settlement appeared to be greatest at areas near the two inlets. Since there were two potential source populations for the settlers, we analyzed the relationship between settlement density and distance from both potential sources. These two analyses should provide a range of possible dispersal distances, with the distance from the nearest inlet providing the minimum distance traveled and the distance from the furthest inlet providing the maximum distance traveled. A significant negative correlation was found for spat density and distance from the nearest inlet (Pearson correlation: r = −0.70, P = 0.035), while no significant correlation was observed with distance from the furthest inlet (r = −0.16, P = 0.673). An exponential decline model fit slightly better for both data sets than did a linear model when comparing R² values (linear: nearest = 0.493, furthest = 0.027; exponential: nearest = 0.724, furthest = 0.079), although the fit was considerably better for distance from the nearest inlet than for distance from the furthest inlet.

If we assume that settlers originated from the nearest source population, then >60% of settlement occurred within 5 km of the source with >90% within 9 km. Making a similar estimate assuming that larvae originated from the furthest inlet extends dispersal distance considerably with most larvae (~54%) settling at sites 25–30 km away and >90% of total observed settlement occurring within 32 km. Therefore, the range of dispersal distances that account for 90% of all settlement is somewhere between 9 and 32 km from the source. Some settlement, however, was observed at the site furthest from either inlet at channel marker 25, which is approximately 18.4 km from the St. Augustine inlet and about 43.7 km from the Matanzas inlet. Therefore, larvae must be able to disperse at least 18.4 km and potentially even further. In fact, the best fit exponential decline model for settlement density vs. distance from nearest inlet predicts that settlement doesn’t fall below 0.05 spat per plate until the distance from the nearest inlet is >30 km.
locations with values of zero were sites where collections did not occur during that year. Some collections appeared to have a size distribution of spat that was normally distributed to approximately 4 mm in shell length and most monthly collections appeared over a relatively short period of time in that month. Some collections, with a single peak, suggesting that most of the larvae probably settled at time. Even a small fraction of the particles released from Matanzas Inlet were swept southward along the Atlantic coast and later entered the Indian River Lagoon through the Ponce De Leon Inlet and ended up in segments 6 and 7 on the last day of the development period. Even then the proportion that remained in segments 1–4 were <11% (Table 1). Observed spat density within a segment and the proportion of particles that were in the same segment at the end of the expected development period, however, were never significantly correlated and actually showed a negative trend when released at flood tide (Pearson correlation: Ebb: r = −0.032, P = 0.97; flood: r = −0.915, P = 0.08; peak flood: r = 0.0, P = 1.00). Particles were only observed in the main channel of the ICW, not in any of the larger feeder creeks included in the model.

According to the model, a substantial proportion of particles released from Matanzas Inlet were swept southward along the Atlantic coast and later entered the Indian River Lagoon through the Ponce De Leon Inlet and ended up in segments 6 and 7 on the last day of the development period. Even a small fraction of the particles released from St. Augustine Inlet could be found in segments 6, 7 and 8, after traversing the Atlantic coast spanning a distance of up to 135 km.

**4. Discussion**

Green mussel spat were found almost exclusively in the summer months at sites located within the main channel of the ICW of northeastern Florida. The timing of settlement is fairly consistent with what has been observed in previous studies around Tampa Bay, Florida. Benson et al. (2001) made monthly collections of spat between April and July in 2000 and found increasing settlement across that time period that peaked in July. Furthermore, histological work by Barber et al. (2005) suggested that *P. viridis* may have two spawning periods in Tampa Bay with one in April and another in September. Our data showed no indication of two settlement peaks except in 2008 where overall settlement was relatively high in May, decreased in June and July and peaked again in August and September. Studies of *P. viridis* in its native range have also suggested two spawning periods (Low et al., 1991; Rajagopal et al., 1998). If green mussel populations in northeastern Florida spawn twice, it seems likely that the second spawning event is typically prior to September since substantial settlement was only observed in October and November in one of the three years of the present study.

Settlement density in the present study was positively correlated with temperature but showed no relationship with salinity or chlorophyll-a concentration. Rajagopal (1991) found a similar relationship between
temperature and gonadal index but the temperature range during spawning tended to be several degrees higher (~30 °C compared to ~27 °C) where he collected in India. Since larval development takes nearly one month at the temperatures experienced in late spring in northeastern Florida, we can look at the temperatures in the month prior to the first settlement of each year to determine the temperatures that might trigger spawning in this area. Water temperatures in April 2008 were consistently above 17 °C and settlement occurred in the following month. In 2010, on the other hand, some settlement occurred in April and water temperatures in March were typically between 13–16 °C. This variation among years suggests that there may not be a specific temperature that triggers spawning. Instead, the spawning events seem to be related to substantial warming trends following the coldest wintertime temperatures. In 2008, February was the coldest month (on average) of the year and was followed by a warming trend throughout March and April. In 2010, however, January was by far the coldest month with significant warming occurring in February and March. So while the temperatures that coincided with spawning were different in each year, both spawning cycles seemed to fall approximately two months after the coldest point of the year (Fig. 6).

While Rajagopal (1991) determined that gonadal index was correlated with temperature, he found that larval abundance was related more to food availability. Other studies conducted within the native range of *P. viridis* suggested that spawning was largely influenced by temperature, salinity and chlorophyll-a concentration (Rao et al., 1975; Nagabhushanam and Mane, 1975; Qasim et al., 1977; Rajagopal et al., 1998). One of the reasons we may not have seen a relationship between spat density and salinity in the present study is because the sites where settlement was observed did not show much variation in salinity. Water quality data sondes at sites PC and 25 ranged in monthly average salinity between 5.69 ± 7.22 ppt and 27.81 ± 2.87 ppt and from 16.7 ± 5.23 ppt to 37.7 ± 0.87 ppt respectively. Neither of those locations...
showed heavy settlement and are located far from the inlets where adults are at the highest density. On the other hand, sites 1 and FM, which are located close to the highest density adult sites, showed very little variation in salinity over the course of the study with monthly mean salinities ranging from 31.51 ± 2.90 ppt to 37.10 ± 0.81 ppt and from 33.28 ± 1.32 ppt to 37.05 ± 0.31 ppt respectively. Furthermore, there were no distinct seasonal differences in salinity in the years studied resulting in no relationship between settlement density and salinity.

Spat density in the present study was also not correlated with food availability as measured by chlorophyll-a concentration. Similar to salinity, chlorophyll-a concentration did not show clear seasonal variation at any of the sites. This may be partially due to the fact that chlorophyll-a concentration was only measured on a monthly basis as opposed to the 15 minute intervals for temperature and salinity. The irregularity of collection could definitely result in large data fluctuations dependent on weather patterns immediately preceding the date of collection. So while it is unlikely that salinity is a predictor of the density of green mussel larval settlement in northeastern Florida, too little data on chlorophyll-a concentration is available to make a strong statement either way.

While salinity is not correlated with settlement density in general, the significantly lower settlement at sites within feeder creeks compared to sites within the main channel of the ICW suggests that salinity may play a role in larval survival and settlement in general. Sivalingam (1977) reported that P. viridis can survive in salinities as low as 20 ppt. Environmental parameters were only monitored at one of the sites within a feeder creek, but showed extreme fluctuations at times with salinities < 1 ppt for hours and oftentimes < 20 ppt for weeks. Therefore, it seems unlikely that green mussel larvae are able to survive consistently in many of the feeder creeks feeding the ICW. Although it is also possible that larvae rarely enter the feeder creeks during their developmental period since the hydrographic model did not predict their movement into the creeks.

Spat settlement was primarily concentrated at sites near the two inlets where previous unpublished studies have shown the highest adult densities. Still, our data showed that some settlement occurred at a site (marker 25) that was approximately 18 km from the nearest inlet. Therefore, it would seem that green mussel larvae can disperse at least up to 18 km within the ICW in northeastern Florida. It is quite possible, however, that green mussel larvae are capable of dispersing considerably greater distances. Since no sites used in the present study exceeded 18 km in distance from the nearest inlet, it was impossible to observe settlement beyond that distance. Furthermore, there is no a priori reason to assume that larvae are originating only from the nearest possible source population. If some of the larvae that settled at channel marker 25 originated from Matanzas inlet, they would have had to disperse nearly 44 km, more than doubling the distance estimate.

While it is definitely possible that P. viridis larvae may have dispersed from the further of the two likely source populations, there are at least two reasons to believe this is unlikely. First, distance from the furthest inlet was a very poor predictor of settlement density in the present study (Fig. 4, R² = 0.079). On the other hand, distance from the nearest inlet showed a reasonably strong relationship with an exponential decline in settlement density (R² = 0.724). Second, the hydrographic model showed no movement of larvae from Matanzas inlet to sites around the St. Augustine inlet (sections 1 and 2; see Table 1) and very little in the opposite direction (from the St. Augustine inlet to sections 3 and 4). Therefore, it would seem that distance from the nearest inlet would be a better predictor of typical larval movement throughout this portion of the ICW. Given that, it would seem that nearly all larvae (>90%) settle within 10 km of the two source populations with a maximum dispersal distance of approximately 20–30 km.

These estimates of dispersal distance, however, may only be accurate for the larvae that remain within the confines of the ICW. In fact, the hydrographic model used in the present study provides very different predictions than those based on settlement location. According to the model simulations few larvae are predicted to stay within the ICW. Instead, most larvae are predicted to be advected into the Atlantic Ocean and disperse to the south. If most of the larvae produced near the inlets do not remain within the ICW, then our estimates of dispersal distance based on the settlement data would be based on the movement of a minority of larvae and, therefore, may be considerably different from the actual dispersal potential of green mussel larvae. If the model is correctly predicting the movement of green mussel larvae along the Atlantic coast, then dispersal ranges would typically be >100 km. Collections along the Atlantic coastline would be necessary to determine whether
the results of the model accurately reflect the movement of larvae along the coast.

While larval dispersal exceeding 100 km is not unheard of, most estimates of larval dispersal in marine invertebrates are considerably less. McQuaid and Phillips (2000) showed that while larvae of the blue mussel *Mytilus galloprovincialis* sometimes dispersed nearly 100 km along the shore of South Africa, most successful recruits settled within 5 km of the parent population. Gilg and Hilbish (2003a) found that most blue mussel larvae in southwestern England likely dispersed between 30 and 64 km with few dispersing further than 100 km. Estimates of dispersal distance based on the width of genetic clines have suggested dispersal distances of 54–76 km per generation in the oyster *Crassostrea virginica*, and about 70 km per generation in the acorn barnacle *Balanus glandula* (Sotka and Palumbi, 2006). Similarly, dispersal estimates for larvae of the tubeworm *Riftia pachyptila* (Marsh et al., 2001) and various species of coral larvae (Lugo-Fernandez et al., 2001) were all typically less than 100 km. Therefore, it would seem unlikely that *P. viridis* larvae typically disperse over such great distances. Furthermore, a previous study in which settlement of green mussels was measured at a site within Indian River Lagoon, FL, did not find a single *P. viridis* specimen during the duration of the study (May–August, 2007) (Gilg et al., 2010). This is the same year that the hydrographic model was used to estimate larval dispersal for the present study in which it predicted that a considerable proportion of larvae would disperse into the Indian River Lagoon. Still, it is difficult to assess settlement along the Atlantic coast of northern Florida since suitable substrate for green mussels is nearly non-existent. There are few docks and the only rock substrates are jetties that are typically only found at the mouths of inlets.

Oceanographic models have been used successfully to predict larval dispersal on a number of occasions (Marsh et al., 2001; Gilg and Hilbish, 2003a, 2003b; Pedersen et al., 2003). In fact, the model used in the present study successfully predicted the movement of larvae of the hard clam *Mercenaria mercenaria* and *Mercenaria campechiensis* in the Indian River Lagoon in a previous study (Arnold et al., 2005). Still, it has been shown repeatedly that the predictions of these models can vary considerably depending on assumptions regarding larval survival, behavior, time of release, and other characteristics (DiBacco et al., 2001; Witman et al., 2003; Coscia et al., 2013). This was very true of the present study as well. Projections of larval dispersal were considerably different depending on the timing of release. More particles were retained within the ICW when the particles were released during a flood tide, whereas nearly all particles were carried into the Atlantic Ocean when released during an ebb tide. The projections used in the

Fig. 7. Representative plots of the results of a particle tracking model for a release date of April 2007. Panels A, B and C show the paths of 1000 particles released from the St. Augustine Inlet 2, 14 and 21 days after the release date. Panels D, E and F show the same for particles released from Matanzas Inlet. The area of study was subdivided into eight segments for analysis.
present study also assumed that *P. viridis* larvae would typically be near the surface and would show no vertical movement. Therefore, it is quite possible that the disagreement between our observed settlement data and the predictions of the model is due to an incomplete picture of the reproductive timing, and the survival and behavior of larval *P. viridis*. Future studies should investigate these factors in an effort to ensure that the predictive power of the oceanographic model is maximized.

Obviously, our estimates of dispersal distance are only accurate if all of the spat we collected originated from one of the two source populations we have identified. The data also beg the following question: if *P. viridis* was first reported in St. Augustine, FL in 2002 and is typically dispersing 5–10 km every generation, then why are the populations still localized around the inlets? Or are there, in fact, unidentified populations within the ICW that we are not accounting for? Previous surveys of the study area by our group and by researchers at the GTM NERR have found very few *P. viridis* adults at sites away from the inlets. Most of these surveys, however, were limited to intertidal areas and pilings on docks and bridges. In these surveys, there is definitely much greater abundance of *P. viridis* in the inlet areas, and while individual mussels exist in areas away from the inlets, no aggregates have been reported. Therefore, the only other possible source populations would be undetected sub-tidal populations. Unfortunately, water clarity is limited in this region inhibiting assessment of potential sub-tidal habitats.

One of the main reasons to expect that adult green mussels are truly rare in areas away from the inlets is because of a lack of suitable habitat both inter- and sub-tidally. *P. viridis* recruit to hard structures. In North-eastern Florida, hard structures are limited to jetties, docks and bridges. There are definitely more of these habitats near each of the inlets than at other locations throughout the ICW in the study area. This is true for both inter-tidal and sub-tidal environments. So *P. viridis* larvae have few places to settle and recruit to away from the inlets. Those that do successfully settle are often at very low population density, making successful reproduction unlikely. Even in situations where settlement density was occasionally very high, such as in the summer of 2007, winters with sustained temperatures <13 °C often result in high mortality (Firth et al., 2011; Urban et al., 2011). So populations away from the inlets have tended to be ephemeral. Therefore, we can be confident that most of the green mussel larvae in this system are produced by the populations near the inlets.

The only other known populations that could act as potential sources would be those at the mouths of the St. Johns River near Jacksonville, FL or the mouth of the St. Mary's River on the border of Florida and Georgia, approximately 60 km and 90 km to the North of St. Augustine inlet respectively. While both are a considerable distance from the locations of our study, they both fall within the range of dispersal predicted by the hydrographic model utilized in the present study. Therefore, future studies should attempt to assess movement of *P. viridis* larvae along the Atlantic coast to see how well their dispersal patterns are predicted by the local hydrography and how mean and maximum dispersal distances compare to those measured in the present study. Since green mussel populations in this area are not genetically distinct (Gilg et al., 2013), it would be necessary to investigate the potential use of chemical signatures of larvae produced at different inlets to determine if they differ enough to successfully identify larvae from different sources.

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### References


Benson, A.J., Marelli, D.C., Frischer, M.E., Danforth, J.M., Williams, J.D., 2001. Establishment and the predictions of the model is due to an incomplete picture of the reproductive timing, and the survival and behavior of larval *P. viridis*. Future studies should investigate these factors in an effort to ensure that the predictive power of the oceanographic model is maximized.

### Table 1

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<th>Section</th>
<th>Ebb</th>
<th>Flood</th>
<th>Peak flood</th>
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<td>St. Augustine Inlet</td>
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</table>

| Matanzas Inlet | 1   | 0.00  | 0.00       |
|               | 2   | 0.00  | 0.00       |
|               | 3   | 0.53  | 0.28       |
|               | 4   | 0.08  | 0.55       |
|               | 5   | 0.00  | 0.52       |
|               | 6   | 0.68  | 3.73       |
|               | 7   | 2.37  | 9.18       |
|               | 8   | 0.32  | 0.25       |
| Total         |     | 3.98  | 14.51      | 11.64 |