

# **Life History Variation in the Diamondback Terrapin**

*(Malaclemys terrapin)*

THESIS

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By

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## ABSTRACT

The adult size and propagule size of many species vary with latitude, although the reasons for these patterns are generally not well understood. Using the diamondback terrapin (*Malaclemys terrapin*), I tested whether adult female body size and hatchling fitness were related to latitude by testing various predictions, including Bergmann's Rule (BR), the optimal egg size theory, the summer length hypothesis, and the seasonality hypothesis. To test adult body size size-latitude associations, I evaluated whether terrapins follow BR, which predicts that larger body size will be found at higher latitudes. I compared average female terrapin plastron lengths from 21 sites throughout their range and found that adult female body size does not have a significant relationship with latitude. Optimal egg size theory predicts that any variation in energy expenditure for progeny will be in clutch size rather than egg size. I predicted that there would be more variation in clutch size than egg size within each population, and that egg size would be uniform within each site. I also predicted that latitude influenced egg size, and expected eggs to be larger and hatchlings to be more fit with increased latitude. To test optimal egg size theory, I collected and incubated eggs from four sites within the range of the northern diamondback terrapin (*M. t. terrapin*), and reared the hatchlings under standardized conditions in a common garden laboratory experiment to determine whether there were important genetic influences (as opposed to environmental) on egg size, hatchling size, and hatchling fitness. I found that clutch size varies more than egg size within each population; however, egg size was significantly different within each site (i.e. there was not a uniform egg size at each site). I did not find a relationship between latitude of origin and clutch size or egg size, contrary to my prediction. Hatchling fitness

was generally not associated with egg size or latitude as expected; shell abnormalities, locomotor performance, and survivorship were not related to egg size. The summer length hypothesis predicts that at higher latitudes, summer growing seasons are shorter, which selects for smaller eggs because turtle eggs incubate more quickly at higher temperatures and smaller eggs take less time to incubate. I compared summer length to initial egg mass of northern diamondback terrapins from four sites. Northern terrapins do not appear to follow the summer length hypothesis; egg mass was not related to the summer length at the site of origin. There was not a significant relationship between egg size and incubation duration. The seasonality hypothesis predicts that climatic variation selects for smaller turtle egg size. Northern latitudes tend to have higher levels of climatic variability, thus I predicted that egg size would be smaller and vary more at higher latitudes. I examined both summer and year-long temperature variation within four sites of northern diamondback terrapins, and compared it to egg size and egg size variation. Although I did not find that egg size was influenced by temporal variation, I found that egg size variation had a strong negative relationship with year-long temperature variability. However, there was no relationship between summer temperature variation and egg size variation, contrary to prediction. Important variation in terrapin reproductive characteristics remains unexplained.

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## INTRODUCTION

Several hypotheses have been proposed to explain differences in propagule size and body size among different populations of the same species distributed along a latitudinal gradient. Turtles are particularly attractive subjects to test these hypotheses because they do not provide parental care, their body and egg sizes are easily measured, and data linking egg size to offspring size and offspring fitness are accumulating. Many turtle studies have supported the following predictions in turtles: larger adult females produce larger eggs (e.g., Congdon and Gibbons, 1987; McGinley, 1989), larger eggs result in larger offspring (e.g., Congdon et al., 1983, Roosenburg, 1996), and larger offspring have higher fitness (e.g., Miller et al., 1987; Janzen, 1993; Janzen et al., 2000a). It is unclear why some organisms are larger in one population than others. Despite the overall positive relationship between body size and fitness, body size can still vary widely among populations. It is possible that there is a geographical link (e.g. latitude) or an environmental factor (e.g. productivity, climate) that may predict and influence adult turtle size, egg size, and clutch size.

### *Body Size and Latitude*

Bergmann's Rule (Bergmann, 1847) (BR) has undergone numerous interpretations since its publication (Blackburn et al., 1999). Initially, BR stated that when evaluating two "homeothermic" (i.e., endothermic) species that differ only in body size, the larger species would be expected to require a cooler environment and would live at higher latitudes (according to translation in Blackburn et al., 1999). Over time, accepted interpretation and use of BR has expanded to include the evaluation of



phylogenetic groupings at various levels (Blackburn et al., 1999) (e.g., conspecifics (e.g., Burnett, 1983; Conover and Present, 1990; Aldrich and James, 1991; Bried and Jouventin, 1997; Arnett and Gotelli, 1999) as well as ectotherms (e.g., Van Voorhies, 1996; Arnett and Gotelli, 1999; Ashton and Feldman, 2003; Litzgus et al., 2004)). Hence for this study, the following interpretation of BR will be used: the prediction that conspecific turtle adult body size is positively correlated with latitude.

As with many biological “rules”, there are exceptions to BR (Mousseau, 1997; Ashton and Feldman, 2003; Meiri and Dayan, 2003; Pincheira-Donoso et al., 2008). Currently, it appears that many endotherms and ectotherms in general follow BR; however, there are notable exceptions. For example, Ashton and Feldman (2003) found that chelonians generally follow BR, but squamates follow the converse. Ashton (2002) found that salamanders tend to follow BR, while anurans do not. Similarly, Meiri and Dayan (2003) found that although birds and mammals generally follow BR, rodents and mammalian insectivores do not.

Even for taxa that do conform to BR, the mechanism by which it might operate is disputed. Bergmann originally proposed a heat conservation hypothesis: organisms are better able to survive in higher latitudes if they have larger body sizes because of lower surface area to volume ratios, and thus lower rates of body-heat loss (Bergmann, 1847). The validity of this argument has been debated. McNab (1971) argued that the heat conservation hypothesis cannot be the mechanism behind BR because larger organisms lose more heat (in total) than smaller organisms when all else is equal. However, it is widely accepted that although large organisms lose more total heat than smaller ones, they lose a smaller percentage of heat relative to their body size, and would be more

likely to survive because it takes larger organisms longer to freeze. Large body size is advantageous in periods of extremely low temperatures during overwintering, which may result in the selection of larger bodied organisms in colder environments (Bodie and Semlitsch, 2000).

Another mechanism that might drive BR is competition and predation; high latitudes (as well as islands and high mountains) generally have low species diversity and generally larger prey body sizes, which selects for larger-bodied predators (McNab, 1971). Generally, McNab's (1971) hypothesis suggests that BR applies primarily to carnivores and granivores, and relates to latitudinal differences in prey size or the density of other organisms that utilize the same prey.

An alternative BR mechanism is the migration ability hypothesis, which states that smaller-bodied organisms occur less frequently at high latitudes because larger-bodied organisms are better able to disperse into areas made available by recent deglaciation, beginning with the Holocene epoch (Blackburn et al., 1999). This hypothesis may be particularly plausible for some vagile organisms, particularly birds. Blackburn and Gaston (1996) found on average that relatively larger bodied birds tend to live at higher latitudes. This hypothesis also may not apply to intraspecific body size variation.

For ectotherms, it has been proposed that BR could be driven by effects of developmental temperature on cell size, with lower developmental temperatures leading to larger cell size and, thus, larger body size (Partridge et al., 1994; Van Voorhies, 1996). For example, Partridge et al. (1994) allowed different *Drosophila melanogaster* populations to evolve at high and low temperatures for five years, after which the flies

reared at low temperatures had larger wing areas, the result of increased cell areas. Van Voorhies (1996) found similar results with *Caenorhabditis elegans* (increased cell areas). In contrast, Litzgus et al. (2004) showed that spotted turtles (*Clemmys guttata*) do not have significant differences in cell sizes at different latitudes. This hypothesis is controversial given the conflicting empirical findings (Mousseau, 1997).

Some BR studies have solely focused on chelonians. Ashton and Feldman (2003) evaluated geographic variation in body size in many turtle species, and found that chelonians tend to follow BR, with most species showing positive body size-latitude associations and negative body size-temperature associations, although data for many species was sparse. Litzgus and Mousseau (2003) (for spotted turtles, *Clemmys guttata*) and Ashton et al. (2007) (for gopher tortoises, *Gopherus polyphemus*) each documented turtle species that do not follow BR. In both cases, body sizes were largest at the northern and southern extremes of the species' range, and smaller towards the middle. It is not clear why these two disparate species would have the same pattern, but Litzgus and Mousseau (2003) suggested that the mid-range decrease may be due to a clutch frequency transition zone; north of this zone, turtles allocate more energy to growth and produce only one clutch per season, while south of this zone the turtles are able to produce multiple clutches while maintaining larger size due to longer growing seasons. Likewise, Ashton et al. (2007) suggested that larger body sizes were due to the adaptive need of large body size in higher latitudes and the increased productivity in southern latitudes, while smaller turtles are found in more temperate areas with moderate productivity, with most species showing positive body size-latitude associations and negative body size-temperature associations, although data for many species was sparse.

### ***Egg Size and Latitude***

In addition to adult body size, latitude has been shown to be positively associated with egg and hatchling size in some organisms, including Great Tits (*Parus major*) (Horak et al., 1995), jackdaws (*Corvus monedula*) (Soler and Soler, 1992), and Satyrine butterflies (*Nymphalidae*, *Satyrinae*) (Garcia-Barros, 1994). However, other species display a negative relationship between egg size and latitude, including a number of parasitic trematodes (Poulin and Hamilton, 2000), Chilean crabs (*Pinnaxodes chilensis*) (Lardies and Castilla, 2001), and wood frogs (*Lithobates sylvaticus*) (Berven, 1982). Chelonians vary; some species display positive correlations between egg size and latitude, while others have negative relationships, and some have no relationship at all (Iverson et al., 1993).

Total clutch investment is a product of egg size and number, and is limited by the finite quantity of resources that each female is able to allocate to reproduction. Under ideal conditions, Smith and Fretwell (1974) predicted that the resources that are expended on the propagation of young should be allocated to optimize egg size and offspring fitness in order to maximize maternal fitness. The prediction from their optimal egg size/number hypothesis is simple—all females in a population will produce offspring of the optimal size for that environment, and variation in investment will be reflected in variation in offspring number rather than variation in offspring size (Smith and Fretwell, 1974). When more energy is expended on individual progeny (i.e. larger size), fitness of the offspring increases; however, in order to ensure maternal fitness, there must be a balance between number and size of offspring (Smith and Fretwell, 1974).

Although BR and Smith and Fretwell's (1974) optimal egg size theory are separate concepts, the two may act either in conflict or concordance. For example, local selection for larger offspring in high latitude environments could drive selection for larger adult female body size. Larger female turtles may be able to lay larger eggs, and also generally have the capacity for greater total reproductive mass than smaller conspecifics (Iverson et al., 1993). Therefore, if selection for larger offspring varied positively with latitude in a particular species, resulting in larger females that are capable to pass the larger offspring, then that species would show a positive adult body size-latitude trend, consistent with BR. If selection for offspring size had a different (i.e. non-linear) relationship with latitude in a species, or none at all, then the species would not appear to follow BR, which may be the situation in the case of the body size patterns reported by Litzgus and Mousseau (2003) and Ashton et al. (2007).

Iverson et al. (1993) proposed the summer length hypothesis to explain negative correlations between egg size and latitude in turtles; they proposed that eggs are smaller at high latitudes due to shorter summers, which limit the time available for successful incubation. Turtle eggs incubate more rapidly at higher constant temperatures (e.g., Goode and Russell, 1968; Burger, 1976; Yntema, 1978; Georges et al., 1994; Roosenburg and Kelley, 1996; Booth, 1998, Booth et al., 2004; Litzgus and Mousseau, 2006; Du et al., 2007; Fordham et al., 2007); furthermore, some studies have found that larger eggs take longer to incubate than smaller eggs at a constant temperature (Ewert, 1979; Packard et al., 1987).

The shorter summers at higher latitudes may therefore present a life history challenge for oviparous ectotherms. Shine and Lee (1999) suggested that this challenge

has repeatedly led to the evolution of viviparity in squamates. However, there are no viviparous turtles; therefore, egg size may be a necessary evolutionary sacrifice at higher latitudes because it is imperative that eggs have ample time to develop before temperatures decline to a lethal level. For example, it has been shown in some turtle species (including diamondback terrapins) that egg size and latitude are negatively correlated (Zimmerman, 1992; Iverson et al, 1993; Allman, 2006; Litzgus and Mousseau, 2006). Therefore, at higher latitudes, the combination of cooler temperatures and shorter incubation periods (i.e., shorter summers) may select for smaller eggs (Iverson et al., 1993).

Iverson et al. (1993) also suggested that turtles may follow the seasonality hypothesis, suggesting that climatic uncertainty selects for smaller egg size in turtles; however, the overwhelming majority of work on environmental variation and clutch size has been done on birds (e.g., Ashmole, 1963; Cody, 1966; Ricklefs, 1980; Pendlebury and Bryant, 2005; Golawski, 2008). The seasonality hypothesis is based on the idea that in locations that experience high levels of climatic variability, such as high latitudes, resources are unreliable, which may affect competition and predation, and therefore birds lay larger clutch sizes (*r* selection) to compensate for the high risk of adverse conditions (Cody, 1966). Likewise, in areas of stable climate (such as lower latitudes, more coastal, and lowland areas as opposed to mountains), selection is driven by the carrying capacity; thus, there are smaller clutch sizes (K selection) (Cody, 1966). Iverson et al. (1993) assumed that in these situations, larger clutch sizes yield smaller eggs (and vice versa). This assumption is only valid if the resources available for reproduction are similar at different latitudes. For example, if resource levels per turtle were higher at high latitudes,

then turtles at high latitudes might produce larger clutches, but not smaller eggs. Based on the seasonality hypothesis, Iverson et al. (1993) predicted that turtle egg sizes would be smaller at high latitudes.

### ***Diamondback Terrapins***

Diamondback terrapins are brackish-water emydid turtles that inhabit a narrow coastal strip of marshes from Cape Cod, MA (42.0°N 70.2°W) to Corpus Christi, TX (27.8°N, 97.4°W) (Ernst and Barbour, 1989) (Fig. 1). There are seven subspecies of diamondback terrapin, most of which are found in Florida. Although the northeastern diamondback terrapin (*Malaclemys terrapin terrapin*) is the focus of the majority of my study, much of the available life history information for this species results from studies of southern subspecies (e.g., Coker, 1906; Cagle, 1952; Seigel, 1980; Lovich and Gibbons, 1990; Butler, 2000; Hart and McIvor, 2008).

Diamondback terrapins are sexually dimorphic; adult females are 1.5-2 times larger than adult males. Male terrapins reach sexual maturity at an earlier age than female terrapins in the same population (Lovich and Gibbons, 1990), although both sexes tend to grow at the same rate for the first three years (Seigel, 1984). After the third year, the growth rate of male terrapins decreases, while female growth continues at the same rate until approximately six years post-hatching (or maturity) (Cagle, 1952; Seigel, 1984; Lovich and Gibbons, 1990). These age estimations should be considered tentative because researchers determined the age of diamondback terrapins by counting growth rings and assume these are annual. Although these methods may be reliable in some turtle species (Wilson et al., 2003), they have not been tested in diamondback terrapins.

Also, these are broad estimates of age at maturity (at best) because there may be important inter-population differences, especially in populations that are latitudinally separated, and all studies of age of maturity in terrapins are from southern populations. Allman (2006) reported that in captivity, terrapin hatchlings from northern populations were smaller and had lower growth rates than southern conspecifics, but nevertheless reached a larger body size as adults. This suggests that high latitude populations reach sexual maturity at a much later age, which may be driven more by genetic than environmental factors.

Terrapins are both inter- and intra-annually iteroparous and may deposit up to three nests, consisting of 4-18 eggs per clutch, during each nesting season (Palmer and Cordes, 1998; Feinberg and Burke, 2003). Nesting occurs between April and August, and hatchlings typically emerge in the fall (from mid-August to mid-October) or spring (April to June) (Ultsch, 2006).

There have been no robust studies across the entire range that tested whether significant inter-population egg size differences occur in diamondback terrapins, nor whether they follow BR. However, Zimmerman (1989) and Allman (2006) found latitudinal variation in adult female size, clutch size, and egg size. Ashton and Feldman (2003) reported a qualitative trend of larger body size at higher latitudes in a small study that compared differences between terrapins from Connecticut and New Jersey, using data from Aresco (1996) and Montevicchi and Burger (1975). Zimmerman (1989) conducted a small study focused on differences between three terrapin populations (New Jersey, South Carolina, and Florida), and found no significant differences in female plastron length among sites. However, he found significant differences in clutch sizes as



well as average egg masses among sites; the New Jersey population had larger clutches of smaller eggs, in contrast to the two southern populations, which were similar (Zimmerman 1989). Allman (2006) compared terrapin eggs from Rhode Island, Maryland, and South Carolina, and found that clutch size was positively correlated with latitude and egg size was negatively associated with latitude (adult female plastron lengths were not reported in his study). In sum, based on a limited number of populations, it is unclear if diamondback terrapins are larger at higher latitudes, however two studies are consistent in demonstrating larger clutch sizes and smaller egg sizes with higher latitude.

Some turtle species have been found to follow BR (Bergmann, 1847) (larger adult females occur in populations that are at higher latitudes) (Ashton and Feldman, 2003). If larger females are found at higher latitudes and are able to produce larger eggs, it may then be predicted that larger eggs as well as larger offspring may also be found at higher latitudes. Iverson et al. (1993) discussed several hypotheses to explain inter-population differences in turtle egg size, including the spring productivity hypothesis, the size-selective predation hypothesis, the seasonality hypothesis, and the summer length hypothesis. In this study, I examined whether diamondback terrapins (*Malaclemys terrapin*) follow BR, and if so, whether egg size increases with maternal size. I tested whether egg size and hatchling fitness are positively related with latitude. I examined Iverson's (1993) summer length hypothesis and seasonality hypothesis to determine whether either of these may be the mechanism behind egg size differences among populations of terrapins.

I conducted a common garden study to evaluate body, egg, and clutch size patterns with latitude for diamondback terrapins. Specific predictions tested included:

- I. Terrapins follow BR.
  1. Adult female size increases with latitude.
- II. Terrapins follow Smith and Fretwell's (1974) optimal egg size theory (variation in offspring number will exceed variation in egg size) and when more energy is expended on individual offspring, fitness increases. When combined with the former BR prediction, fitness will increase with latitude:
  1. Clutch size will vary within each site, but there will not be significant variation in egg size.
  2. Egg size increases with latitude.
  3. Hatchling fitness increases with egg size and latitude.
    - a. Initial hatchling size increases with egg size and latitude.
    - b. Shell abnormalities decrease with egg size and latitude.
    - b. Locomotor performance increases with egg size and latitude.
    - d. Survivorship increases with egg size and latitude.
- II. Terrapins follow the summer length hypothesis:
  1. Egg size increases with growing season length.
  2. Incubation duration increases with egg size.
- III. Terrapins follow the seasonality hypothesis:

1. Egg size is negatively associated with environmental variability.
2. Egg size variation is positively correlated to environmental variation.

## METHODS

### *Body Size and Latitude*

I obtained average female terrapin plastron size data (including standard deviations and sample sizes where possible) from the primary literature as well as personal communications for 21 sites (Table 1) (Fig. 2). There were 15 different sites in Georgia that I grouped into Northern and Southern sites because of small sample size from each location. “Northern Georgia” consisted of the seven sites north of 31.5°N (range: 30.8°N-31.2°N), while “Southern Georgia” consisted of eight sites that included 31.5° and points south (range: 31.5°N-32.0°N). Latitude and longitude data points for the two Georgia points are an average of the sites that were included in each range. Peconic Bay was one of the four sites that I conducted egg and hatchling work; however there was no adult female size data available. I evaluated the data by performing a linear regression and a polynomial regression to determine whether female body size was correlated with latitude.

### *Egg Size, Hatchling Fitness, and Latitude*

#### Eggs

I collected terrapin eggs from four locations: Cape May Peninsula, NJ (39.0°N, 74.8°W), Jamaica Bay, NY (40.7°N, 73.8°W), Peconic Bay, NY (40.9°N, 72.6°W), and Barrington River, RI (41.8°, 71.3°W) (Fig. 3). Cape May Peninsula is located on the southern-most tip of New Jersey and separates the Delaware Bay from the Atlantic

Ocean. I obtained Cape May terrapin eggs near the Wetlands Institute, in a salt marsh located on the peninsula. Jamaica Bay is a 3700 ha estuarine ecosystem in the southwestern corner of Long Island, NY. I collected Jamaica Bay terrapin eggs from the island of Ruler's Bar Hassock. Peconic Bay is a tidal estuary system between the North Fork and South Fork of eastern Long Island, NY. I obtained Peconic Bay terrapin eggs near a former Suffolk County Parks hunter housing facility in Flanders, NY. Barrington River, Rhode Island is a tidal extension of the Runnins River. I collected Barrington River terrapin eggs from the Nockum Hill area of Hundred Acre Cove.

In June and July 2007, I collected thirteen to fifteen naturally oviposited clutches from each site. All eggs were treated identically. I removed eggs from nests and randomly chose three eggs to freeze for other analyses. I wrote identification numbers on the remainder of the eggs with a pencil, and placed the eggs into plastic containers containing vermiculite (1 part vermiculite: 2 parts water by mass). Within three days of being laid eggs were placed into incubators that were maintained at 29°C. After I collected all of the eggs, they were randomly sorted among containers, shelves, and incubators. I monitored vermiculite moisture weekly and water was added as needed to maintain constant container weight (g).

I weighed eggs at 3, 5, 10, and 30 days post-oviposition. I discarded moldy eggs. After 45 days of incubation, I put the eggs into individual cups with moistened vermiculite, and observed them daily until hatching. After each turtle completely exited its shell, I recorded the hatch date and discarded the egg shell. Change in egg mass was determined by calculating the percentage of mass gained  $((\text{mass at 30 days} - \text{mass at 3 days}) / \text{mass at 30 days} * 100)$ .

### Hatchling Fitness

Hatchling fitness was determined indirectly by examining hatchling size, righting response, shell abnormalities, and survivorship. Size and survivorship (for hatchlings) are commonly used to evaluate fitness (Janzen 1993; Bodie and Semlitsch, 2000; Janzen et al., 2000a; Janzen et al., 2000b). Shell abnormalities are used as an indirect measure of fitness, as anomalies in the shell may be indicative of genetic (e.g., inbreeding) or environmental (e.g., pollutants) instability (Velo-Anton et al., 2011), which may result in decreased fitness (Clarke, 1995). The amount of time that a turtle takes to right itself after being inverted (righting response time) may be important to its survival because prolonged periods of inversion may lead to predation, desiccation, and overheating (Steyermark and Spotila, 2001), which may result in decreased fitness (Janzen et al., 2000a; Delmas et al., 2007).

### Hatchling Size

All hatchlings were treated identically. At three days post-hatching (initial measurement), I rinsed, dried, weighed, measured carapace and plastron lengths (with digital calipers), photographed, and placed terrapins back into their individual cups of vermiculite. When the hatchlings were seven days post-hatching, I rinsed them and subsequently maintained them in individual containers, which had approximately 2 cm of lukewarm dechlorinated brackish tap water (12-15ppt salt (Instant Ocean)). I exposed the terrapins to 12 hours of UVA/UVB light each 24 hour period. When hatchlings were 15, 45, 75, and 105 days post-hatching, I weighed and measured turtles as described above.

## *Husbandry*

Hatchlings were always fed individually and to satiation. After the turtles reached five weeks post-hatching, I began to feed them turtle brittle (Nasco) daily (seven days/week). At three months post-hatching, I fed the hatchlings turtle brittle five days/week and thawed seafood (supplemented with Reptivite and Herptivite) two days/week (mysis, silversides, squid, prawn, or krill) until hibernation (see below). After hibernation, turtles were fed brittle four days/week and thawed seafood (supplemented with Reptivite and Herptivite) two days/week until the end of the experiment. I gave turtles a minimum of one hour to eat before food was removed and a complete water change was done.

At approximately two months of age, I individually tagged turtles for identification. I sewed small (1/8"x1/4") shellfish tags onto the L10 scute with monofilament (8 lb test). If the tag later ripped through the scute, I attached it to the R10 scute. After tagging, turtles remained in individual containers for an additional 24 hours to ensure the tagging caused no ill effects. Next, I matched terrapins by hatch date and distributed them among nine tubs (122cm x 61cm with approximately 1-1.5cm of de-chlorinated brackish tap water (12-15ppm salt) water. Every two months, the hatchlings were redistributed based on mass. Tubers were equipped with submersible filters, heaters, basking stations, and 12 hours of UVA/UVB lighting. I removed turtles from the tubs and placed them into the cups daily 6-7 days/week for feeding (7 days/week until hibernation, 6 days/week post-overwintering). Tubers received 50% water changes and filter cleaning twice a week.

### *Hibernating*

Before hibernation, I fasted terrapins for two weeks and then placed them into individual containers (473 mL plastic deli cups), which I maintained at approximately 20-21°C. I saturated sphagnum moss with de-chlorinated tap water, and placed it into the cups (approximately 2.54-3.81cm) with the hatchlings. I placed each hatchling in a cup and covered it with a lid with air holes, and randomly distributed them throughout four incubators. I reduced the incubation temperature (originally 19°C) by 1°C every hour until I reached the final overwintering temperature of 4°C. I chilled (hibernated) the hatchlings for 25 days in January 2008 (when the turtles were 4-5 months post-hatching). Temperature was monitored every third day in various places throughout the incubators. Every third day, moisture was monitored by checking randomly distributed containers throughout all incubators. The sphagnum moss maintained moisture throughout the month, so there was never a need to re-hydrate. Twenty-five days after hibernation, hatchlings were warmed up as they were chilled: temperature was increased at no more than 1°C per hour over a period of two days (approximately 9-10°C each day) until 19°C was reached. Hatchlings were then rinsed, dried, weighed, and measured (carapace and plastron length) before being returned to their tubs.

### *Righting Response*

When terrapins were 15 days post-hatching (and subsequently at 45, 75, and 105 days post-hatching), locomotor performance was tested by conducting righting tests. Righting tests occurred after the turtles received food. I towel-dried them and placed them upside down on a paper towel on a flat surface. Using a stopwatch, I measured the



time that elapsed until each turtle turned itself right side up. Turtles were allowed a maximum of two minutes to complete each trial. I conducted three trials on each turtle with a minimum of 20 seconds between each trial. The shortest time out of the three trials was used for analysis. Turtles that failed to right themselves were assigned a value of 200 seconds for analysis.

### *Shell Abnormalities*

At two months of age, I examined each terrapin's carapace for shell abnormalities, defined as a deviation from the standard (1 nuchal, 5 vertebral, 4 left costal, 4 right costal, 12 left marginal, and 12 right marginal scutes). I summed the number of abnormalities for each terrapin and computed the average number of abnormalities per site. The carcasses of turtles that had died prior to two months were also evaluated.

### *Survivorship*

The number of possible days of survival depended on the date of hatch, and ranged from 170-205 days. Survivorship was determined as the percentage of days that each hatchling survived out of the total possible number of days that the hatchling could have survived (end of study). For terrapins that survived to the completion of the study, a value of 100% survival was given. For those that died prior to the end of the experiment, the number of days that the terrapin survived was divided by the number of days that it could have possibly survived (difference of the end of study date and hatch date) and multiplied that number by 100. It is not clear what day turtles died if they died during

hibernation; therefore, their date of death was considered to be the day that they were removed from hibernation. After the completion of the study, terrapins were uniquely marked using transponders and released at their location of origin after receiving appropriate permissions.

### ***Testing the Summer Length Hypothesis***

I obtained long-term (1949-2008) climate data from National Oceanic and Atmospheric Administration (NOAA), using the closest weather stations to the four egg collection locations (Cape May, NJ, Jamaica Bay, NY (JFK International Airport), Peconic Bay, NY (Riverhead), and Barrington River, RI (Providence). I used only climate records for the months of June, July, and August (92 summer days) because typically these are the months that terrapin eggs incubate. I used 21°C as the minimum threshold temperature because Ewert (1979) found that this was generally the minimum temperature that turtle eggs will incubate; below 21°C, many eggs either fail to develop and/or die. I evaluated the average percentage of the 92 days that each site was  $\geq 21^\circ\text{C}$  for all of the available years for each site and compared it with egg size.

I calculated degree-days by subtracting 21°C (threshold temperature) from the maximum temperature for each summer day that had a maximum temperature above 21°C (e.g., a day with a high temperature of 31°C would have 10 degree days) (similar to Iverson, 1991). I calculated the average number of degree-days per year for each site and compared it with average egg size for that site.

### ***Testing the Seasonality Hypothesis***

Available climate records (1949-2008) for the entire year at the same NOAA stations that were evaluated for the summer length hypothesis (see above) were used to test for the effects of seasonality on terrapin egg size. I compared the standard deviation of the median daily temperature (median calculated as the difference between the daily maximum temperature and the daily minimum temperature) for the summer months for each site averaged over 49 years to initial egg mass. Next, I averaged the standard deviation of the median temperature of the entire year averaged over 49 years for each site, and compared this to the initial egg mass of the corresponding site.

### ***Statistical Analyses***

I performed statistical analyses using SPSS for Windows version 15 and Microsoft Excel. I calculated coefficients of variation for egg size and clutch size for each of my four study sites, with data pooled for each site. I conducted linear regressions to test relationships between terrapin body size and latitude, clutch size vs. latitude, egg size vs. latitude, egg growth vs. egg size, hatchling mass vs. carapace and plastron lengths, hatchling size vs. egg size, shell abnormalities vs. latitude, shell abnormalities vs. egg size, righting response vs. egg size, righting response vs. hatchling size, egg mass vs. survivorship, egg size vs. threshold temperature (Summer Length Hypothesis), egg size vs. summer degree days (Summer Length Hypothesis), incubation period vs. latitude (Summer Length Hypothesis), egg size vs. incubation period (Summer Length Hypothesis), egg size vs. summer temperature variation (Seasonality Hypothesis) and egg size vs. annual temperature variation (Seasonality Hypothesis). I also conducted a

polynomial regression to test for relationships between terrapin body size and latitude, similar to those seen by Litzgus and Mousseau (2003) and Ashton et al. (2007). I used analysis of variance (ANOVA) single factor tests to evaluate the differences among sites in hatchling growth, incubation duration, locomotor performance, and shell abnormalities. I performed post hoc analyses, using Bonferroni tests. I used chi-square tests to test for differences in hatching success rate, locomotor performance, shell abnormalities, and survivorship among sites. For all tests,  $\alpha=0.05$ .

## RESULTS

### *Body Size and Latitude*

Adult female body size was not related to latitude for diamondback terrapins (linear  $r^2=0.058$ ;  $F_{1,19}=0.058$ ;  $p=0.291$ ) (polynomial  $r^2=0.160$ ;  $F_{1,19}=1.713$ ;  $p=0.208$ ) (Fig. 4) or when considering only northern diamondback terrapins (*Malaclemys terrapin terrapin*) (including data from Barrington, RI to NC), (linear  $r^2=0.318$ ;  $F_{1,6}=2.791$ ;  $p=0.146$ ) (polynomial  $r^2=0.354$ ;  $F_{1,6}=1.367$ ;  $p=0.336$ ) (Fig 5). Maryland terrapins appeared to be an outlier, and when the northern subspecies of terrapins were examined without the MD data, there was a significant polynomial size-latitude relationship (polynomial  $r^2=0.917$ ;  $F_{1,5}=22.223$ ;  $p=0.007$ ) (Fig. 6).

My primary study sites (Cape May, NJ, Jamaica Bay, NY, Peconic Bay, NY, and Barrington, RI) are located in the northern part of *Malaclemys terrapin terrapin* range. Little work has been done at Peconic Bay, NY and there were no female size data available; therefore, that site was not included in the evaluation. However, when the other three sites were evaluated adult female plastron length and latitude were positively correlated (linear  $r^2=0.997$ ;  $F_{1,1}=286.314$ ;  $p=0.038$ ) (Fig. 7).

### *Egg Size, Hatchling Fitness, and Latitude*

#### Eggs

I obtained fifty-five terrapin clutches from the four sites (Table 2), a total of 732 eggs from all sites combined, and froze 165 eggs for future analyses, leaving 567 eggs to

incubate. Clutch size varied within each site (ranged from 7-12 eggs from NJ, 8-18 eggs from JB, 7-19 eggs from PB, and 13-20 eggs from RI). Average clutch sizes were significantly different among sites ( $p < 0.001$ ;  $n = 55$ ;  $df = 3$ ;  $F = 16.306$ ) (Fig. 7). RI clutches were significantly larger than those of all of the other sites ( $p \leq 0.001$ ) (Table 3). NJ had the smallest clutches, both RI ( $p < 0.001$ ) and PB ( $p = 0.035$ ) had clutch sizes significantly larger than NJ (Table 3). There was not a significant relationship between average clutch size and latitude ( $r^2 = 0.866$ ;  $F_{1,2} = 12.932$ ;  $p = 0.069$ ) (Fig. 8). The coefficients of variation of clutch sizes from each site were higher than the coefficients of variation of egg size from each site (Table 4).

Initial average egg masses significantly differed among clutches from all four sites (NJ ( $p < 0.001$ ;  $df = 13$ ;  $F = 66.430$ ); JB ( $p < 0.001$ ;  $df = 12$ ;  $F = 29.028$ ); PB ( $p < 0.001$ ;  $df = 14$ ;  $F = 42.015$ ); RI ( $p < 0.001$ ;  $df = 12$ ;  $F = 26.708$ )), although there appeared to be little variation within individual clutches (Fig. 9-12). Among the four sites, there was not a correlation between egg mass and latitude ( $r^2 = 0.066$ ;  $F_{1,2} = 0.141$ ;  $p = 0.744$ ) (Fig. 13). However, initial egg mass significantly differed among sites ( $df = 3$ ;  $F = 26.369$ ;  $p < 0.001$ ) (Fig. 13, Table 5). Bonferroni post hoc analyses revealed that some sites were not significantly different from others, although RI terrapin eggs were significantly smaller ( $p < 0.001$ ) than all other sites (Table 6).

Eggs from all sites increased in mass over incubation time (Fig. 14). Average egg masses significantly differed among the sites at all four measurement times during incubation ( $p < 0.001$ ) (Table 6) (Fig 14). Total change in egg mass was significantly different among all sites ( $p < 0.001$ ;  $df = 3$ ;  $F = 21.852$ ), although post hoc tests determined that not all sites were significantly different from each other (NJ and JB were similar,

while RI and PB were similar) (Fig. 14). Total increase of egg mass was influenced by initial egg size ( $r^2=0.133$ ;  $F_{1,491}=75.487$ ;  $p<0.001$ ) (Fig 15A). The percentage of egg mass gained had a significant relationship with initial egg size ( $r^2=0.056$ ;  $F_{1,491}=29.142$ ;  $p<0.001$ ) (Fig. 15B).

Of the 567 eggs that were incubated, 496 successfully hatched (an overall hatching success rate of 87.48%) (Table 2). Hatching success rates were not significantly different among sites ( $\chi^2=0.834$ ;  $p=1.0$ ). One entire clutch from Cape May Peninsula failed to hatch, whereas all other clutches had at least some successful hatching. Eggs from Cape May Peninsula had the lowest hatch success rate (83.33%) even when the failed clutch was eliminated from the analysis. Eggs from Jamaica Bay had the highest hatching success rate (92.19%) (Table 2).

### Hatchling Fitness

#### *Size*

Initial hatchling mass was significantly related to initial carapace length ( $r^2=0.742$ ;  $F_{1,492}=1779.662$ ;  $p<0.001$ ) (Fig. 16) and initial plastron length ( $r^2=0.704$ ;  $F_{1,492}=846.907$ ;  $p<0.001$ ) (Fig. 17). Hatchling mass was chosen to represent hatchling size because its correlation to carapace and plastron length and also because it may best indicate the overall health of individuals. Soft hatchlings may be unhealthy and have less mass than healthy hatchlings of the same carapace or plastron length because healthy turtles form a fully keratinized shell, giving them larger mass values. Burke (pers.

comm.) observed a large die-off of other captive hatchlings after their shells went soft for unknown reasons.

Initial egg mass was significantly related to initial hatchling mass ( $r^2=0.827$ ;  $F_{1,493}=2357.686$ ;  $p<0.001$ ) (Fig. 18). Initial hatchling mass was significantly different among sites ( $p<0.001$ ;  $df=3$ ;  $F=22.296$ ). RI hatchlings were significantly smaller than those from every other site ( $p<0.001$ ) and JB hatchlings were significantly larger than NJ hatchlings ( $p=0.031$ ); however, the remainder of sites were not significantly different from each other. Hatchlings from Jamaica Bay had larger average body size and mass than the other hatchlings at every measurement interval throughout the experiment, although there were high levels of variation within all four sites (Fig. 19). There was a significant relationship between hatchling mass at 105 days (the last measurement time point in which all terrapins were the same age) and initial egg mass ( $r^2=0.209$ ;  $F_{1,470}=124.502$ ;  $p<0.001$ ) (Fig. 20).

### *Shell Abnormalities*

Most hatchlings (56.7%) (from all sites) had at least one shell abnormality (Fig. 21). Cape May Peninsula hatchlings had the lowest frequency of shell abnormalities (33.7% had abnormalities), followed by Barrington River hatchlings (57.4% had abnormalities). Turtles from New York (both Jamaica Bay and Peconic Bay) had the highest total frequency of shell abnormalities (63.6% and 64.2% respectively). There were significant differences among sites in the number of shell abnormalities when compared to those with no abnormalities ( $n=490$ ;  $df=3$ ;  $\chi^2=11.76$ ;  $p=0.008$ ). There was no relationship between the prevalence of shell abnormalities and latitude of origin



( $r^2=0.6514$ ;  $F_{1,2}=3.737$ ;  $p=0.193$ ) (Fig. 21). Initial egg size also was not significantly associated with the prevalence of abnormalities ( $r^2=0.4053$ ;  $F_{1,2}=1.363$ ;  $p=0.363$ ) (Fig. 22). There was not a significant relationship between shell abnormalities (present vs. not present) and survivorship (survived experiment or did not survive) ( $\chi^2=0.09$ ;  $DF=2$ ;  $p=0.76$ ).

### *Locomotor Performance*

Righting response performance dramatically improved with age for terrapins from all sites (Figs. 23-26). At 15 days old, over half the terrapins from Barrington River and Peconic Bay did not right themselves within two minutes; Jamaica Bay terrapins had the fastest performance rates (34.8% righted themselves within 30s) (Fig. 23). At 45 days of age, 58.3% of Cape May Peninsula hatchlings righted themselves within 30s, while over half of the turtles from Peconic Bay were still not successful in righting themselves within two minutes (Fig. 24). When the hatchlings reached 75 days old, righting response times were much faster than at younger ages, with Jamaica Bay with the highest percentage of hatchlings that righted within 30 seconds (Fig. 25). The last righting response test was at 105 days post-hatching because most hatchlings at this age were able to right themselves within 30s; there were no significant differences among sites (Table 7) (Fig. 26). There were some significant differences at 15 and 45 day old turtles in righting response times between sites for the fastest and slowest turtles ( $p=0.04$ ;  $df=3$ ;  $\chi^2=8.18$ ) (Table 7). Initial egg size ( $r^2=0.0045$ ;  $F_{1,487}=2.186$ ;  $p=0.140$ ) (Fig. 27) and hatchling size ( $r^2=0.003$ ;  $F_{1,487}=1.267$ ;  $p=0.261$ ) (Fig. 28) did not influence righting response.

Righting response improved with age at all sites, although turtles from differing sites did not improve at the same rate (Figs. 23-26). Peconic Bay hatchling performance remained poor through 45 days post-hatching, and then improved greatly at 75 days post-hatching (Figs. 24-25).

### *Survivorship*

There was no significant relationship between site of origin and survivorship ( $\chi^2=4.46$ ,  $DF=3$ ,  $P=0.215886$ ) nor was survivorship influenced by initial egg mass ( $r^2=0.001$ ;  $F_{1,495}=0.702$ ;  $p=0.403$ ) (Fig. 29).

### *Summer Length Hypothesis*

Among the four focal sites, there was no relationship between the average percentage of days above 21°C and average initial egg mass ( $r^2=0.0001$ ;  $F_{1,2}=0.0002$ ;  $p=0.989$ ) (Fig. 30) or the average number of summer degree days and initial egg mass ( $r^2=0.3652$ ;  $F_{1,2}=1.151$ ;  $p=0.396$ ) (Fig. 31). Incubation duration was significantly different among sites ( $p<0.001$ ); however, there was not a significant relationship between incubation duration and latitude of origin ( $r^2=0.403$ ;  $F_{1,2}=1.349$ ;  $p=0.365$ ) (Fig. 32). Post hoc tests revealed that incubation durations of eggs from JB and RI were similar, and that eggs from PB and NJ had similar incubation periods. There was no relationship between initial egg mass and incubation duration ( $r^2=0.005$ ;  $F_{1,495}=2.424$ ;  $p=0.120$ ) (Fig. 33).

### *Seasonality Hypothesis*

Among the four focal sites, there was no significant relationship between initial egg mass and average summer temperature variability ( $r^2=0.498$ ;  $F_{1,2}=1.980$ ;  $p=0.295$ ) (Fig. 34), average yearly temperature variability ( $r^2=0.221$ ;  $F_{1,2}=0.568$ ;  $p=0.530$ ) (Fig. 35), or initial egg size variation and summer temperature variation ( $r^2=0.863$ ;  $F_{1,2}=12.554$ ;  $p=0.791$ ) (Fig. 36). However, initial egg size variation was negatively correlated with the annual seasonal variability of the site of origin; there was a strong relationship between egg mass variability and year-long variability ( $r^2=0.995$ ;  $F_{1,2}=422.504$ ;  $p=0.002$ ) (Fig. 37).

## DISCUSSION

### *Body Size and Latitude*

Diamondback terrapins are ideal for testing Bergmann's Rule (BR) because their habitat is narrowly constricted to the oceanic coast, and consists of a considerable linear range (N-S) along the eastern seaboard of the United States. This is particularly useful when looking at trends associated with latitude, as there is no need to compensate for inland vs. coastal differences (i.e. coastal areas are often more stable than inland habitats, which can result in differing selective pressures and ultimately different life history strategies (Cody, 1966)). Terrapins also have an east-west range along the Gulf Coast, which may be useful for examining differences along a fairly constant longitudinal gradient; however, there are few data points currently available for this part of the terrapin range. Future study of terrapins along the Gulf Coast would be informative.

Diamondback terrapin adult female body size does not increase with latitude. My finding, based on a much larger data set, are in contrast to the qualitative trend of larger body size for this species suggested by Ashton and Feldman (2003), and consistent with the small study by Zimmerman (1992).

Although most of the research done on body size-latitude associations has examined linear relationships between size and latitude (e.g. Ashton et al, 2000; Meiri and Dayan, 2003; Ashton and Feldman, 2003), some recent studies of turtles have found a polynomial relationship between body size and latitude (Litzgus and Mousseau, 2003; Ashton et al., 2007; Greaves and Litzgus, 2009). In these studies, turtles were largest at both the lowest and highest latitudes, with smaller sizes found in middle latitudes. Two of

these studies focused on small freshwater turtle species (*Clemmys guttata* and *Glyptemys insculpta*) and the other was a large tortoise species (*Gopherus polyphemus*), whereas my evaluation focused on a medium-sized brackish-water turtle that does not appear to show a polynomial relationship of body size and latitude. These turtle species are ecologically diverse and future work should be done to incorporate additional species for which there are robust data (e.g. *Chelydra serpentina* (e.g.. Steyermark et al. 2008), *Chrysemys picta* (e.g.. Moll, 1973; Rowe, 1994; Lindeman, 1996), and *Sternotherus oderatus* (e.g. Tinkle, 1961); to determine the breadth of polynomial trends for Chelonians.

Although diamondback terrapin body size was not associated with latitude across the entire species' range, relationships might be different within smaller sections of the range, especially when data were collected within individual subspecies or over restricted longitudinal ranges. Therefore, I also evaluated size-latitude differences within the diamondback terrapin subspecies that was the focus of my lab studies, the northern diamondback terrapin (*M. terrapin terrapin*). Again, there was no significant relationship between terrapin size and latitude, and this appears to be due in part to MD terrapins; they were much larger than expected. Since MD terrapins appeared to be an outlier, I also tested for an association between body size and latitude in northern terrapins, excluding the MD data point, and I found a very strong polynomial trend, like that seen by Litzgus and Mousseau (2003) and Ashton et al. (2007). It is unclear why MD terrapins are more similar in size to those from the northern-most population that I tested, Barrington, RI. Both Litzgus and Mousseau (2003) and Ashton et al. (2007) attributed large body size in spotted turtles at high latitudes to climatic uncertainty and seasonality because larger turtles are better able to survive food shortages and longer, harsher

winters. They both also proposed that turtles at lower latitudes are larger due to the presumption that the warmest areas are also those with the highest productivity, permitting larger body size. Neither of these theories seems to be a plausible explanation for the size of MD terrapins because MD is neither at the highest or lowest latitude of the northern diamondback terrapin. A number of hypotheses should be tested to see if there is something different about MD terrapins in relation to other northern diamondback terrapins. For example, further work should be done to determine other differences across the range of the subspecies to see if there are differences in diet, predation, environment, and anthropogenic threats that would select for larger terrapins in MD. It also may be interesting to test for similar patterns in other subspecies of terrapins.

My focal study sites were in the northern range of the northern diamondback terrapin subspecies (*M. terrapin terrapin*) range. When including only three of my primary sites (adult size data was not available for Peconic Bay, NY), I found larger adult female body size with latitude. However, it should be noted that this analysis consists of only three populations. Nonetheless, it is possible that various environmental factors at the northern end of their range, such as resource availability and predation, proportionally change with latitude. It would be interesting to see whether trends would remain when incorporating data from the northernmost population of terrapins (Cape Cod, MA).

I tested whether diamondback terrapins follow BR (defined previously as the intraspecific positive correlation of body size and latitude). When looking at terrapins as a species, they do not appear to follow BR. I applied BR to a subspecies of diamondback terrapin, and found that there is not a significant correlation, but there appears to be a stronger trend than for the entire species, and when one outlier was removed from data

analysis, a significant polynomial relationship was found (larger terrapins were found at higher and lower latitudes with smaller terrapins in the middle). When examining the northern range of the subspecies, I found that there was a correlation that strongly agrees with BR; however, I only evaluated three sites and although this is a reasonable starting point, further work should examine more sites within the range. It appears that BR may apply to smaller groupings of a species, such as a subspecies or individuals within a smaller defined geographic area.

### ***Egg Size, Hatchling Fitness, and Latitude***

#### *Eggs*

Smith and Fretwell (1974) predicted that energy resources would be allocated toward optimizing individual egg size to maximize offspring and maternal fitness, and variation in energy investment within populations would result in differences in clutch size. There was more clutch size variation than egg size variation within each site, supporting Smith and Fretwell's prediction. However, egg size varied significantly within each population of diamondback terrapins in my study. Roosenburg and Dunham (1997) reported similar results from a large population of terrapins in Maryland.

The variation in egg size within each population may be due to morphological constraints, specifically overall body size and the size of the pelvic girdle, which may limit smaller turtles from producing optimally-sized eggs (Congdon and Gibbons, 1987; Wilkinson and Gibbons, 2005). Rowe (1994) found that reproductive output (egg mass, clutch mass, and clutch size) increased with maternal body size within some populations

of painted turtles *Chrysemys picta bellii*. However, the average size of adult female terrapins in Rhode Island (the study site at the highest latitude) was much larger than those at lower latitudes, suggesting that morphological pelvic size constraints are not responsible for egg size in diamondback terrapins. Roosenburg and Dunham (1997) found that there does not appear to be a correlation between adult female plastron size and egg size in diamondback terrapins, suggesting that maternal size is not associated with maximum egg size; however, more evidence across the entire range is needed before this may be ruled out.

The variation in egg size among populations may also be due to the age of the adult females that were laying the eggs; Bowden et al. (2004) found that younger painted turtles (*Chrysemys picta*) laid eggs that were 20% smaller than older turtles (even when they had similar body size). If there was a wide age distribution of egg-laying turtles within a population, and diamondback terrapins also followed the trend seen by Bowden et al. (2004) for painted turtles, then this may be an explanation for egg size variation. The predictions that maternal size and age may affect egg size are not mutually exclusive; Wilkinson and Gibbons (2005) found that there is a positive relationship between age and plastron length in the eastern mud turtle (*Kinosternon subrubrum*). Further work on the effects of age and size on reproductive output of the diamondback terrapin would be interesting.

I found a significant positive relationship between clutch size and latitude among four sites, consistent with other geographical comparisons of terrapins (Zimmerman, 1992; Allman, 2006). Egg size was not correlated with latitude of origin, failing to support the prediction that eggs from higher latitudes would be larger as a consequence of



larger females being able to carry larger eggs and maternal body size increasing with latitude. Rhode Island (the site at the highest latitude) eggs were significantly smaller than those from all other sites. The largest eggs were from the two NY sites. However, it is interesting to note that clutches from the northernmost population were significantly larger and egg size was significantly smaller than those from the other populations I tested, which was similar to the findings of Zimmerman (1992) and Allman (2006). A robust study of terrapin eggs and clutches across the entire range of diamondback terrapins as well as the entire range of the northern diamondback terrapins should be conducted to determine whether there is a relationship between these variables and latitude. Data are especially needed from the northernmost population (Cape Cod, Massachusetts).

### Hatchling Fitness

I evaluated whether hatchling fitness increases with egg size using four indices of fitness: hatchling size, frequency of shell abnormalities, speed of righting response, and survivorship. I combined data from all four sites to determine relationships between egg size and hatchling fitness. I also looked at differences among sites to determine whether there were relationships between fitness and latitude.

### *Size*

Initial terrapin egg mass was a good indicator of initial hatchling size, supporting the hypothesis that hatchling size is correlated with egg size, similar to the findings of Burger (1977), Roosenburg and Kelley (1996), Ashmore and Janzen (2003), and Herlands et al. (2004). I expected to find the largest hatchlings at the highest latitudes

(based on my prediction about egg size). However, hatchling terrapins from Rhode Island were significantly smaller than those from all other sites, due to their small egg size.

Hatchling size may be an important factor for fitness; some manipulative field studies have found that larger hatchlings have higher survivorship (Janzen, 1993; Janzen et al., 2000a; Janzen et al., 2000b). Some studies have shown that larger hatchlings walk faster (Burger et al., 1998), may be better able to evade predators (or less likely to be eaten due to predator gape limits) (Miller et al., 1987; Janzen, 2000b), and larger hatchlings may be better able to survive overwintering by being more cold-tolerant (Bodie and Semlitsch, 2000). Larger turtles have higher surface area to volume relationships, potentially resulting in lower rates of body heat loss (Bergmann, 1847). Ironically, the smallest hatchlings are found at the highest latitudes, suggesting that Bergmann's heat loss theory may not be relevant to hatchling terrapins. Average adult female size in Rhode Island was larger than at lower latitudes, but average hatchling size was much smaller compared to lower latitudes. Both are counterintuitive.

### *Shell Abnormalities*

I hypothesized that terrapins that hatched from larger eggs would be less likely to have shell abnormalities simply on the basis that larger hatchlings tend to have higher fitness (Janzen, 1993; Janzen et al., 2000a; Janzen et al., 2000b) and hatchlings that have lower levels of deformity also tend to have higher fitness (Clarke 1995; Velo-Anton et al., 2011). This hypothesis was not supported; there was no significant relationship between initial egg size and the frequency of shell abnormalities. Also, there was no

relationship between shell abnormalities and latitude, although for unknown reasons hatchlings from Cape May Peninsula had fewer abnormalities when compared to the other sites.

There have been numerous hypotheses about the possibility of environmental factors that cause deformities in turtles, including exposure to pollutants (ex: Bell, 2005; Bell et al., 2006), inbreeding depression due to small population size (Fernandez and Rivera, 2004), and suboptimal incubation conditions (i.e., temperature and humidity) (MacCulloch, 1981; Fernandez and Rivera, 2004; Davy and Murphy, 2009). There are few data available on pollutant levels in the marshes at my four study sites. Some may have had substantial pollution levels, particularly Jamaica Bay (Tanacredi, 1990; Seidemann, 1991; Bopp et al., 1993; Bopp et al., 1998; Ferguson et al., 2003; Ferguson and Brownawell, 2003; Litten, 2003; Reddy and Brownawell, 2005).

It is not clear whether inbreeding depression could be affecting the presence of shell anomalies in the four diamondback terrapin populations I studied. Because terrapin populations in many places were hunted to near extinction for food in the early 1900s, it is possible that inbreeding occurred, resulting in a proliferation of mutations that affected shell formation, and these genes have proliferated throughout the generations.

There was not a significant relationship between the occurrence of shell abnormalities and latitude. MacCulloch (1981) hypothesized that turtle eggs at higher latitudes may be more likely to have a higher incidence of shell abnormalities because of cold, dry incubation conditions. Hewavisenthi and Paramenter (2001) found that hatchlings from eggs incubated at lower temperatures had a higher incidence of shell abnormalities. Furthermore, Davy and Murphy (2009) found that there is a significant

relationship between latitude and shell abnormalities in painted turtles, but not in snapping turtles. Because I incubated all eggs under the same conditions, randomly distributed in the incubators, and had high hatch rates (minimum 83%), I conclude that incubation conditions were good. Therefore, I conclude that shell abnormalities in this case are either caused by maternally-transmitted pollutants or by a developmental factor that is not attributable to the incubation environment. Further studies should be conducted to investigate the causes and effects of shell abnormalities in turtles.

I included shell abnormalities as a measure of fitness; however, the correlation between the two has never been shown empirically. I did not find that there was a significant relationship between the presence of shell abnormalities and survivorship in captivity. Future studies, including field work, at multiple sites over many years would be helpful to understand whether shell abnormalities are an appropriate indirect measure of fitness.

### *Righting Response*

In nature, turtles, especially hatchlings, may be flipped onto their carapaces, perhaps because of falling over an obstacle or being attacked by a predator. If they are unable to right themselves promptly, their chances of predation, desiccation, starvation, or overheating are greatly increased (Steyermark and Spotila, 2001). Based on work done by Janzen et al. (2000a) and Delmas et al. (2007), I assumed that turtles with the shortest righting response times had highest fitness. I hypothesized that terrapins that hatched from larger eggs would have shorter righting response times; however, my hypothesis was not supported. There was no significant relationship between righting

response time and initial egg size (similar to findings of Steyermark and Spotila (2001)) or initial hatchling size.

I did find that locomotor performance greatly increased with hatchling age for hatchlings from all sites. For some hatchlings, it can be argued that locomotor performance at 15-days post-hatching (the first time righting response was tested) is the most ecologically significant time point measured because this is closest to the time period during which a hatchling in the wild would be most exposed, while seeking shelter. If young hatchlings are unable to right themselves within two minutes, they are unlikely to survive because they would not flee from predators or could die from starvation or dehydration (Finkler, 1999; Steyermark and Spotila, 2001). However, some terrapin hatchlings often do not emerge for long periods of time (some even overwinter in the nest) (Baker et al., 2006), suggesting that for some hatchlings, locomotor performance after longer periods of time are more relevant.

Other locomotor studies have shown that turtle hatchling performance can be affected by hydric conditions (Miller et al., 1987; Finkler, 1999), incubation temperature (Du and Ji, 2003; Freedburg et al., 2004), incubation temperature variation (Ashmore and Janzen, 2003), ambient temperature at performance time (Freedburg et al., 2004; Delmas et al., 2007), and maternal identity (Steyermark and Spotila, 2001; Delmas et al., 2007). All of these factors, except for maternal identity, were held constant in my experiment; therefore, maternal identity may have been important to the variation in righting response time that I detected. Steyermark and Spotila (2001) found that clutch identity affected righting response in snapping turtles (*Chelydra serpentina*), and suggested that clutch may be an important variable when examining turtle behavior.

### *Survivorship*

I hypothesized that hatchlings from larger eggs would have higher survivorship; however, this hypothesis was not supported. There was not a significant relationship between initial egg mass and survivorship, although there was a significant relationship between initial hatchling mass and survivorship. Because I found a significant relationship between initial egg mass and initial hatchling mass, it was surprising these relationships were correlated when comparing these two variables to survivorship, and there is no obvious explanation. The relationship between initial hatchling mass and survivorship concurs with some studies (e.g., Janzen, 1993; Janzen et al., 2000a), but not with all (Congdon et al., 1999). Janzen (1993), Janzen et al. (2000a), and Congdon et al. (1999) studied turtle hatchlings in much more natural settings than I did; their method of evaluating survivorship was concentrated on the release and recapture of hatchlings in the field, whereas my study was conducted in a very controlled environment, free from predators and environmental variability. It is difficult to assess the meaning of these short term studies when evaluating survivorship in long-lived organisms such as turtles. Future work should evaluate life-long effects of initial egg and hatchling size on adult survivorship in diamondback terrapins and other turtles.

### *Summer Length Hypothesis*

Temperature is an important challenge for ectotherms because some metabolic processes cease (e.g., embryo development during incubation) or are changed (e.g., species with temperature dependent sex determination) at a threshold temperature. A standard measure for the effect of temperature on ectotherms is average degree-days

(Schwarzkopf and Brooks, 1987; Frazer et al., 1993; Valenzuela et al., 1997; Charnov and Gillooly, 2003, Walde et al., 2007). Average degree days is a measure of heat units or heat availability, which is important in the incubation and development of ectotherms.

I hypothesized that diamondback terrapins would follow the summer length hypothesis (i.e., egg size increases with increased growing season length and incubation duration increases with egg size). I measured growing season length two ways: the average percentage of days above 21°C and the average number of summer degree days. Surprisingly, neither of these factors had a significant relationship with egg sizes from the four sites. Numerous studies have shown that eggs incubate more quickly at higher temperatures (Goode and Russell, 1968; Burger, 1976; Yntema, 1978; Georges et al., 1994; Roosenburg and Kelley, 1996; Booth, 1998, Booth et al., 2004; Du et al., 2007; Fordham et al., 2007), which led me to believe that eggs from lower latitudes may incubate quicker because of longer summers. New Jersey is much warmer than the other three sites; there was a much higher average percentage of days above 21°C (twice as many as the other three sites). However, it does not appear that summer length alone has an effect on egg size.

I predicted a linear positive relationship between egg size and incubation duration, and for smaller eggs to come from higher latitudes. For example, I expected for eggs from Rhode Island to be the smallest (because the length of the growing season is shorter at higher latitudes), and for eggs from Rhode Island to incubate more quickly than larger eggs from lower latitudes (because of studies done that stated that smaller eggs incubate more quickly than larger eggs (Ewert, 1979; Packard et al., 1987)), although Burger (1977) found an inverse relationship between egg size and incubation duration.

Surprisingly, I did not find any correlation between egg size and incubation duration. Rhode Island eggs were significantly smaller than those from the other three sites, but incubation duration was not affected. Although there was not a significant relationship between initial egg mass and incubation duration, there were significant differences in incubation duration among sites, but these differences were not related to latitude of origin or egg size.

Roosenburg and Dennis (2005) suggested that diamondback terrapin eggs may be smaller at higher latitudes due to decreased need for post-natal lecithotropy during overwintering. It has been suggested that terrapins probably do not eat in the wild until the spring following hatching (Brennessel, 2006). At lower latitudes, there is a longer growing season, and terrapins require more energy (temperature dependent consumption) than terrapins that undergo the facultative overwintering that is required much sooner for hatchlings at higher latitudes (Roosenburg and Dennis, 2005). Allman (2006) found that terrapin eggs from lower latitudes were larger and contained more energy reserves than those at higher latitudes. It is suggested that turtles at higher latitudes overwinter in the nest and do not need the large amount of lipids afforded by larger eggs, while those from lower latitudes emerge immediately after hatching need those energy reserves (Allman, 2006).

My analysis suffers from a small sample size (four sites, two of which were close together) with little variation in summer length among sites for the three sites at the highest latitudes. Future work should be done to compare the relationship between egg size and summer length across the diamondback terrapin's entire range to test whether



there may be a general trend across a larger latitudinal gradient, and whether summer length might only affect turtle egg sizes at the farthest extremes of latitude.

### *Seasonality Hypothesis*

I hypothesized that initial egg mass would be correlated with seasonality as measured by average temperature variation, therefore larger eggs would be associated with lower levels of temperature variability. I measured variability two ways: the average standard deviation of the difference between the daily maximum and minimum temperatures over the entire year as well as the average standard deviation for just the summer months. I found no significant relationship between egg size and either variability measure.

Interestingly, while there was no significant relationship between average summer temperature variation and average egg size variation, average year-long temperature variation and average egg size variation were strongly and significantly related. This is interesting because it may be logical to assume that summer temperature variation may be more important than annual variation because eggs are laid and incubate during the summer months; however, this does not appear to be the case. I did not find that summer lengths at the site of origin for the eggs that I examined had an effect on size, as discussed previously.

Burger (1977) found an inverse relationship between egg size and incubation period in diamondback terrapins. She attributed the difference in development rates to the possibility that larger eggs retained more heat during cooler incubation periods. Smaller eggs have higher surface area to volume ratios, resulting in an increased rate of heat loss,

which may have delayed development during periods of lowered temperature).

However, such incubation temperature variation was not a factor in my common garden study; environmental variability was eliminated and incubation temperature was held constant. Perhaps year-long temperature variation is more important than summer length when it comes to selection of egg size.

If an organism is in an area of high environmental uncertainty or temporal fluctuation, egg size variation (as opposed to simply egg size) may be favored because there may be a higher probability of survivorship for larger eggs in some years, while smaller eggs may have a higher probability of survivorship in other years. This may help to explain the variation of propagule size within sites. However, there is little variation in egg size within individual clutches of diamondback terrapins (Roosenburg and Dennis, 2005). It is possible that selection on egg size and offspring size is weak, allowing variation in these traits to persist. For example, reproductive fitness may be influenced more strongly by the number of eggs per clutch, the number of clutches per year, or the number of clutches laid over a lifetime.

## CONCLUSION

I tested a number of differing predictions about geographical size differences among populations of diamondback terrapins. There was no straightforward relationship between size and latitude in terrapins. Adult size does not have a linear relationship with latitude. A positive polynomial relationship between adult female body size and latitude in northern diamondback terrapins was observed, but only after removing the population from Maryland. More data from across the entire range is needed, particularly in the farthest northern portion of the terrapin range (Cape Cod), as well as along the Gulf Coast. Other environmental parameters, including temperature, seasonality, and productivity, as well as pollutants and fishery impacts should be evaluated for terrapin populations throughout their range to help understand why populations differ in body size.

Smith and Fretwell's (1974) optimal egg size theory states that organisms produce eggs of the optimal size in order to maximize offspring and maternal fitness and that more deviation in reproductive output within a population is in clutch size, not egg size. I found that there was more variation in clutch size than in egg size within each population. However, I found that there is not a uniform, optimal egg size within each population of northern diamondback terrapins. I predicted that larger egg size would translate to higher fitness, but instead found that egg size affected hatchling size but not locomotor performance, shell abnormalities, or survivorship.

Summer (growing season) length and summer temperature variation were not associated with diamondback terrapin egg size. However, the amount of annual temporal variation had a significant relationship with egg size when comparing four sites in the

northern part of the terrapin's range. Annual temperature variation should be compared with egg size throughout the entire range of the diamondback terrapin.

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Table 1: Average female diamondback terrapin plastron lengths (mm) by latitude (Lat.)

(°N). (\*=Sites that were used for further analyses.)

Site	Lat.	Average Plastron Length (mm)	s.d.	n	Source
Barrington, RI*	41.8	196	11.0	343	Sorenborger, pers. comm.
CT	41.1	169	15.4	27	Chambers, pers. comm.
Oyster Bay, NY	40.9	180	-	80	Bauer, 2004
Jamaica Bay, NY*	40.7	176	1.0	440	Burke, pers. comm.
Little Beach, NJ	39.5	154	9.9	221	Montevecchi and Burger, 1975
Cape May, NJ*	39.0	151	1.7	128	Wood, pers. comm.
Poplar Island, MD	38.3	190.0	9.9	5667	Roosenburg, pers. comm.
NC	34.8	150.5	13.5	33	Hart, pers. comm.
Kiawah, SC	32.6	157	12.1	40	Zimmerman, 1992
Northern GA	31.8	152	-	36	Grosse, pers. comm.
Southern GA	31.1	165	-	26	Grosse, pers. comm.
Northeastern FL	30.6	162.2	8.7	378	Butler, 2002
Alabama	30.3	168.9	1.1	28	Coleman, pers. comm.
Grand Bay, MS	30.3	176	-	13	Watters, pers. comm.
Mississippi	30.2	170.2	-	13	Mann, 1995
LA	29.4	176.5	-	2	Cagle, 1952
South Deer Island, TX	29.2	178	-	56	Hogan, 2003
Merritt, FL	28.6	154	10.0	113	Seigel, 1984
Everglades, FL	25.3	160	1.2	139	Hart and McIvor, 2008
Florida Bay	24.8	181	-	445	Baldwin et al., 2005
Florida Keys	24.6	156	-	46	Wood, pers. comm.

Table 2: Diamondback terrapin egg collection data and hatching success from each of the four focal sites. The number of eggs represented here does not include the three eggs that were frozen from each clutch for future testing.

Site	# of Clutches	# of Eggs	# of Hatchlings	Unhatched Eggs	Hatch Success (%)
Cape May Peninsula	14	106	85	21	80
Jamaica Bay	13	128	118	10	92
Peconic Bay	15	153	134	19	88
Barrington River	13	180	159	21	88
Total	55	567	496	71	87

Table 3: Results from Bonferonni post hoc tests to evaluate significance of differences in clutch size among the four focal sites.

					95% Confidence Interval	
(I) Site	(J) Site	Mean Difference (I-J)	Std. Error	Sig.	Upper Bound	Lower Bound
Jamaica Bay , NY	Barrington River, RI	-4.1538	0.9374	<0.001	-6.7271	-1.5806
	Peconic Bay, NY	-0.3538	0.9056	1.000	-2.8399	2.1322
	Cape May, NJ	2.2033	0.9205	0.122	-0.3236	4.7302
Barrington River, RI	Jamaica Bay, NY	4.1538	0.9374	<0.001	1.5806	6.7271
	Peconic Bay, NY	3.8000	0.9056	0.001	1.3140	6.2860
	Cape May, NJ	6.3571	0.9205	<0.001	3.8302	8.8841
Peconic Bay, NY	Jamaica Bay, NY	0.3538	0.9056	1.000	-2.1322	2.8399
	Barrington River, RI	-3.8000	0.9056	0.001	-6.2860	-1.3140
	Cape May, NJ	2.5571	0.8881	0.035	0.1191	4.9951
Cape May, NJ	Jamaica Bay, NY	-2.2033	0.9205	0.122	-4.7302	0.3236
	Barrington River, RI	-6.3571	0.9205	<0.001	-8.8841	-3.8302
	Peconic Bay, NY	-2.5571	0.8881	0.035	-4.9951	-0.1191

Table 4: Comparison of the coefficient of variation (CV) of clutch size and egg size from each site.

	CV Clutch	CV EGG
Cape May, NJ	0.2199144	0.149853
Jamaica Bay, NY	0.1875982	0.1191662
Peconic Bay, NY	0.1967198	0.1231602
Barrington, RI	0.1270733	0.1113546

Table 5: Results of ANOVA testing for differences in egg mass among the four focal sites at four different egg ages.

Egg Mass	n	Sum of Squares	D.f.	Mean Square	F	P
3 Days	567	81.772	3	27.257	26.359	<0.001
5 Days	567	67.11	3	22.37	19.955	<0.001
10 Days	567	98.96	3	32.987	25.046	<0.001
30 Days	547	106.873	3	35.624	22.377	<0.001

Table 6: Results of Bonferroni post hoc analyses testing for differences in initial egg mass among the four focal sites.

(I) Site	(J) Site	Mean Difference (I-J)	Std. Error	Sig.	95% Confidence Interval	
					Upper Bound	Lower Bound
Jamaica Bay, NY	Barrington River, RI	.9673(*)	0.117	<0.001	0.657	1.277
	Peconic Bay, NY	0.2762	0.1215	0.141	-0.046	0.598
	Cape May, NJ	.4393(*)	0.1336	0.006	0.086	0.793
Barrington River, RI	Jamaica Bay, NY	-.9673(*)	0.117	<0.001	-1.277	-0.657
	Peconic Bay, NY	-.6910(*)	0.1124	<0.001	-0.989	-0.393
	Cape May, NJ	-.5279(*)	0.1253	<0.001	-0.86	-0.196
Peconic Bay, NY	Jamaica Bay, NY	-0.2762	0.1215	0.141	-0.598	0.046
	Barrington River, RI	.6910(*)	0.1124	<0.001	0.393	0.989
	Cape May, NJ	0.1631	0.1295	1.000	-0.18	0.506
Cape May, NJ	Jamaica Bay, NY	-.4393(*)	0.1336	0.006	-0.793	-0.086
	Barrington River, RI	.5279(*)	0.1253	<0.001	0.196	0.86
	Peconic Bay, NY	-0.1631	0.1295	1.000	-0.506	0.18

Table 7: Significance of differences in righting speed among sites. The top half of the table compares righting times for those hatchlings that righted in 30 seconds or less, the bottom half compares righting times for those hatchlings that failed to right within 120 seconds.

Age	Righting Time (s)	p-Value
15 Days	1-30	0.014
45 Days	1-30	<0.001
75 Days	1-30	0.536
105 Days	1-30	0.946
15 Days	>120	0.066
45 Days	>120	0.005
75 Days	>120	0.279
105 Days	>120	0.297

Figure 1: Range of *Malaclemys terrapin*: Cape Cod, MA to Corpus Christi, TX (based on Ernst and Barbor, 1989).





Figure 2: Geographic representation of the 21 sites used to compare adult female plastron size in order to test Bergmann's Rule.

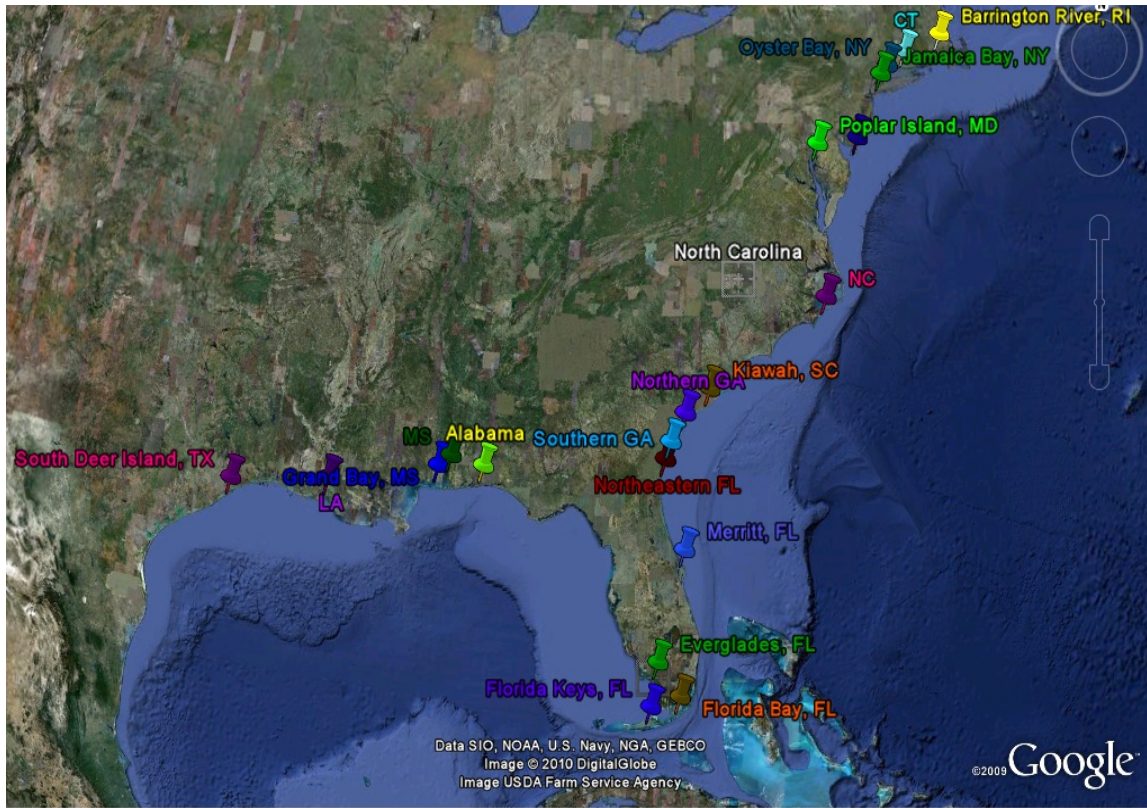


Figure 3: Geographic representation of the four sites from which eggs were collected for analysis.



Figure 4: Average adult female diamondback terrapin plastron length in relation to latitude. (Note: s.d. was not available for the following sites: Oyster Bay, NY( 40.9°N), Northern GA (31.8°N), Southern GA (31.1°N), Grand Bay, MS(30.3°N), Mississippi (30.2°N), Louisiana (29.4°N), South Deer Island, TX (29.2°N), Florida Bay (24.8°N), and the Florida Keys (24.6°N).

# Adult Female Body Size vs. Latitude

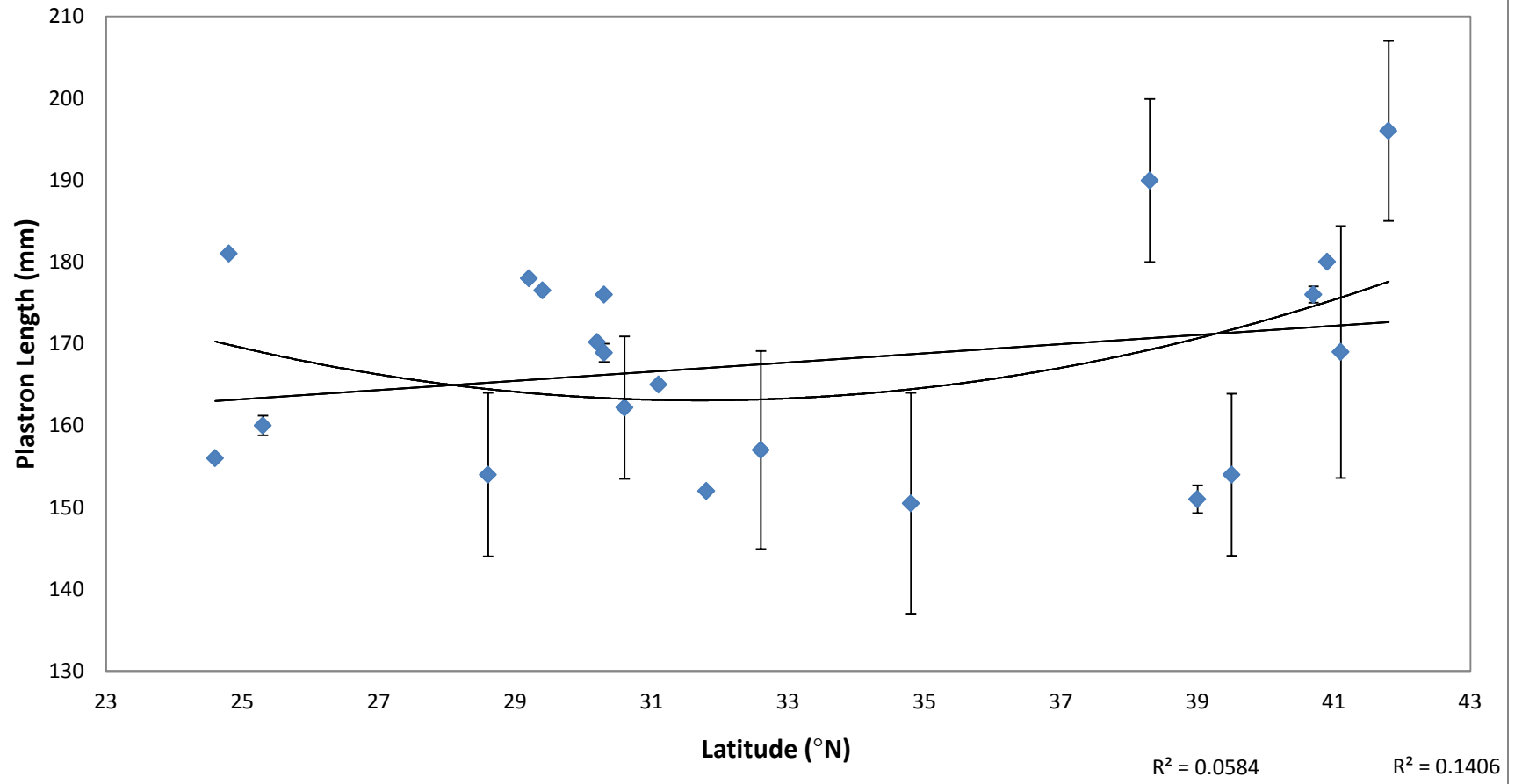


Figure 5: Average adult female plastron length of northern diamondback terrapins (*Malaclemys terrapin terrapin*) in relation to latitude. (Note: s.d. was not available for Oyster Bay, NY (40.9°N).)



## Northern Adult Female Size vs. Latitude

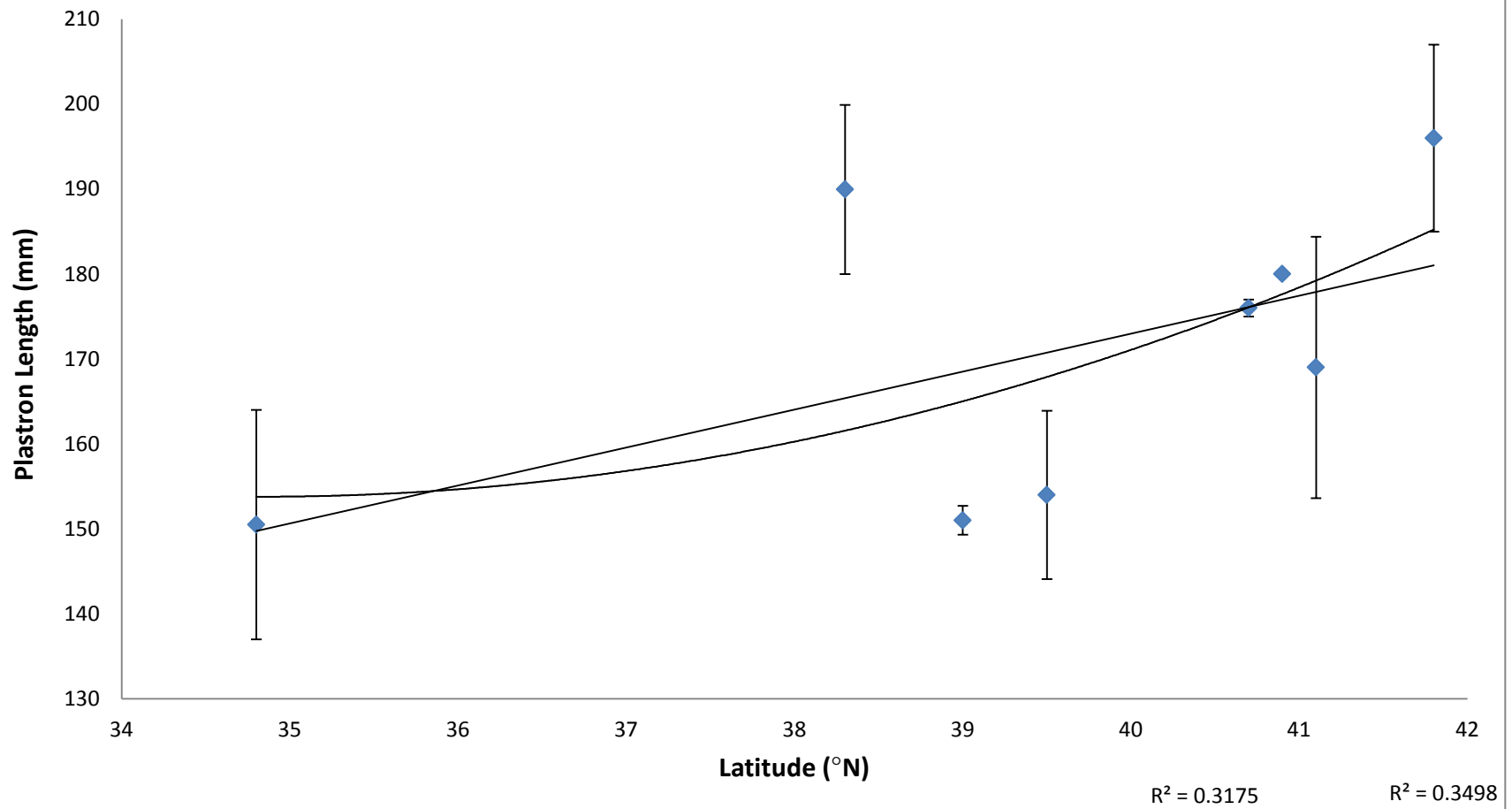


Figure 6: Average adult female plastron length of northern diamondback terrapins (*Malaclemys terrapin terrapin*) in relation to latitude, excluding the population from MD. (Note: s.d. was not available for Oyster Bay, NY (40.9°N).)

### Northern Adult Female Size Exlcuding MD vs. Latitude

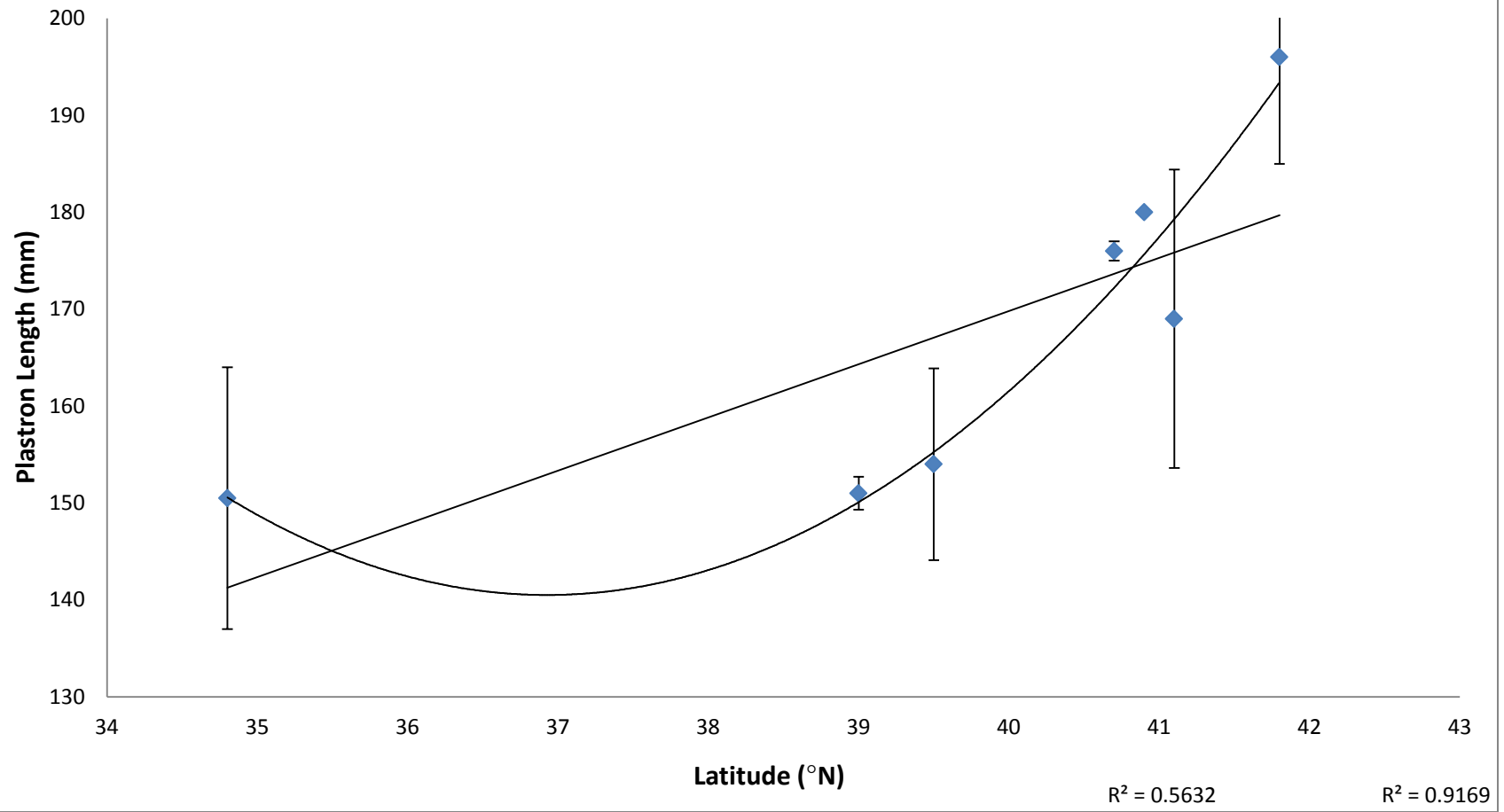


Figure 7: Average adult female plastron length of northern diamondback terrapins (*Malaclemys terrapin terrapin*) from three sites (Barrington, RI, Jamaica Bay, NY, and Cape May, NJ). Peconic Bay, NY turtles were not included in this analysis because no data on adult terrapins were available.

### Average Adult Female Size (Primary Sites) vs. Latitude

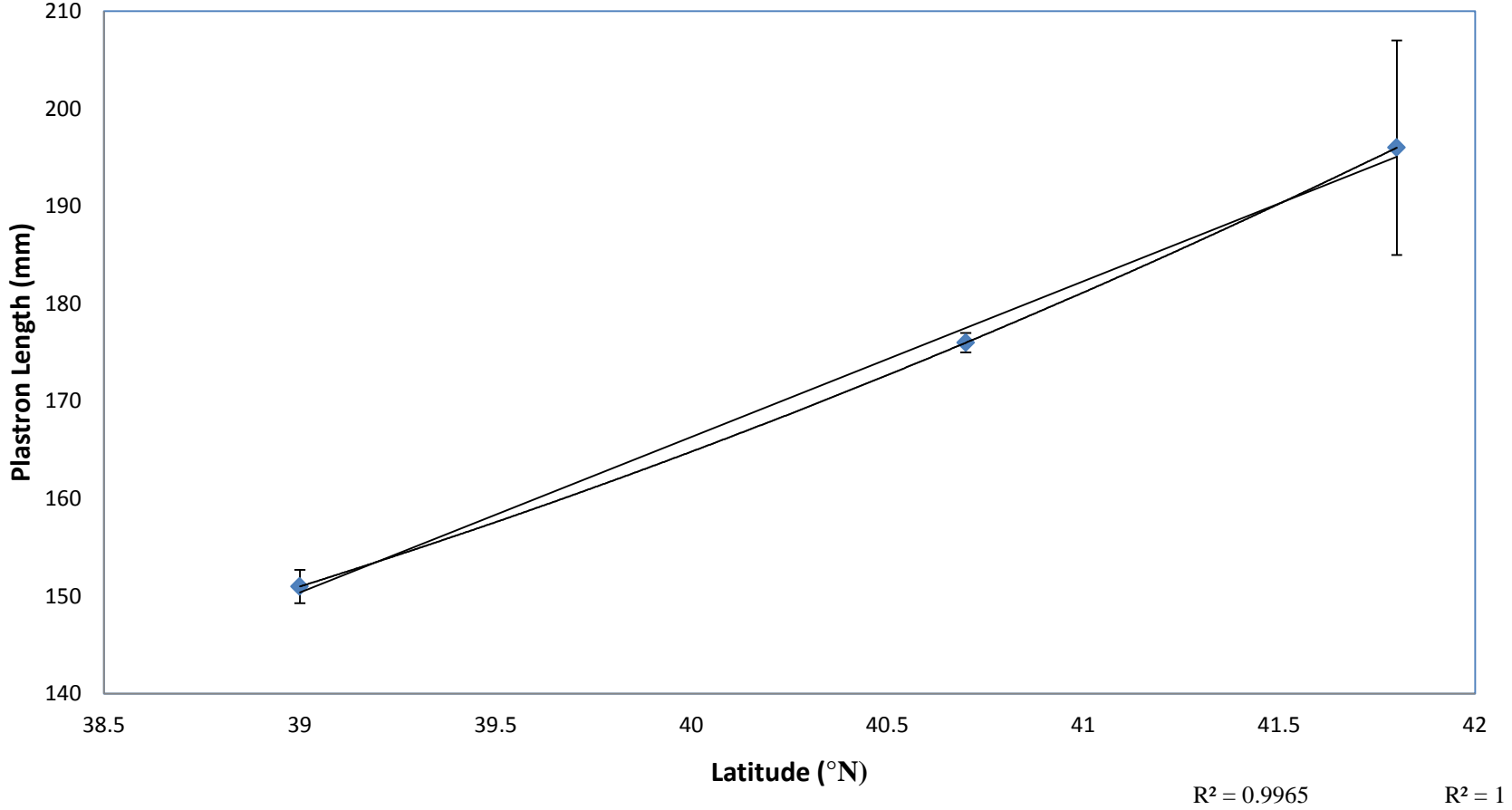


Figure 8: Average clutch size of northern diamondback terrapins (*Malaclemys terrapin terrapin*) from four sites (Barrington, RI, Jamaica Bay, NY, Peconic Bay, NY, and Cape May, NJ). The three eggs that were frozen from each clutch were included to determine the average number of eggs per clutch.

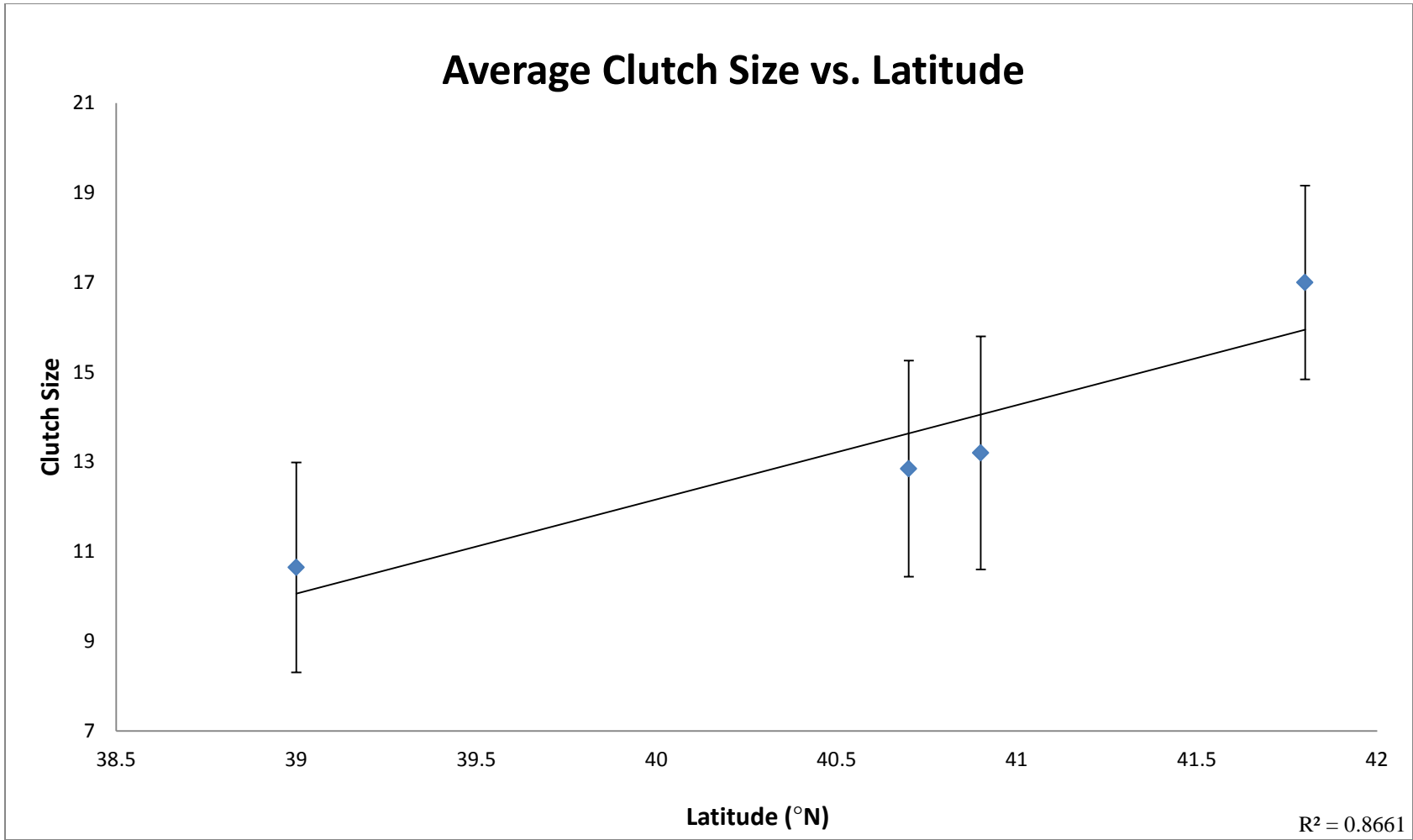


Figure 9: Average initial egg mass of diamondback terrapin clutches from Cape May, NJ.



### Initial Egg Mass: Cape May, NJ

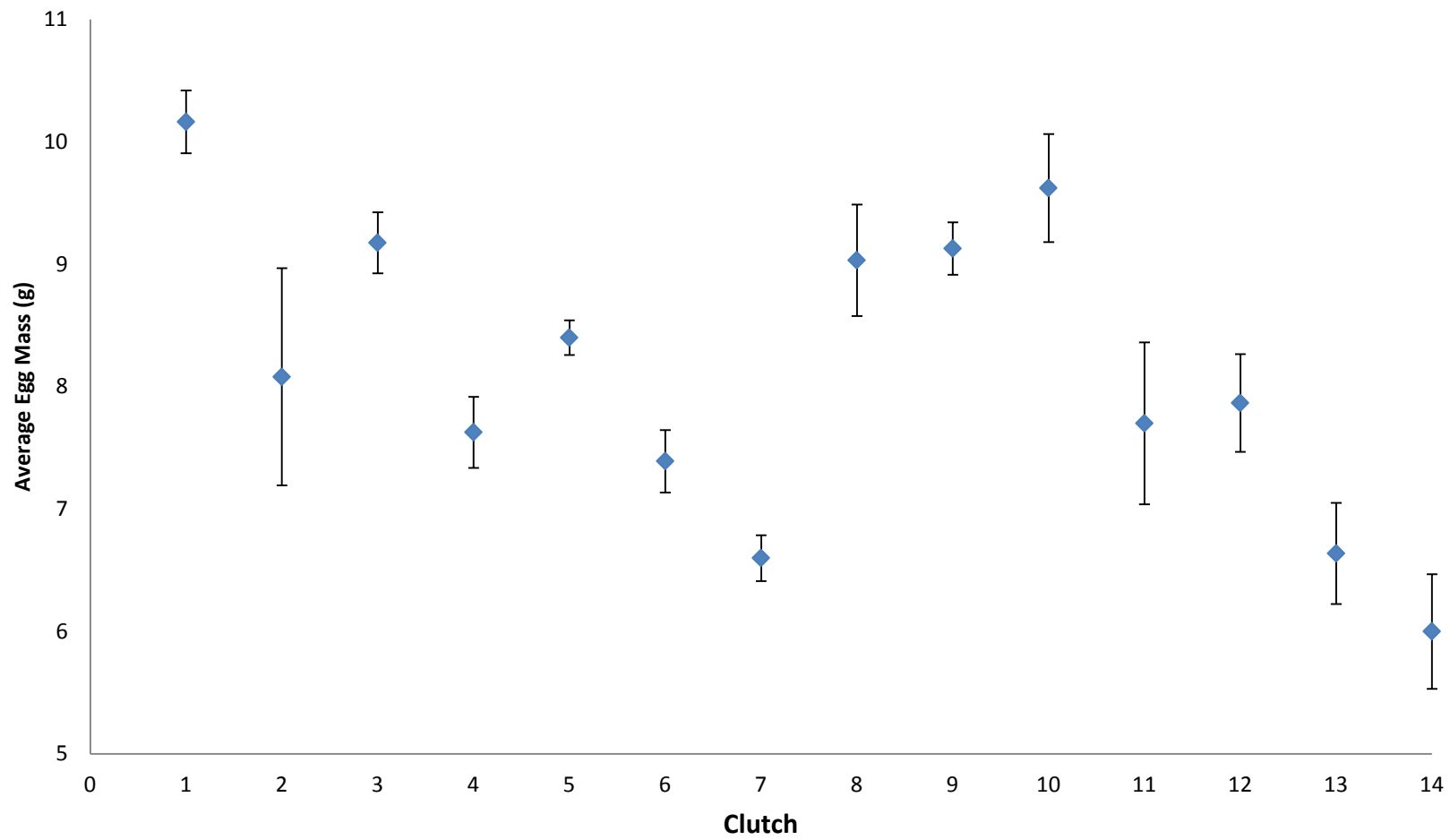


Figure 10: Average initial egg mass of diamondback terrapin clutches from Jamaica Bay, NY.

# Initial Egg Mass: Jamaica Bay, NY

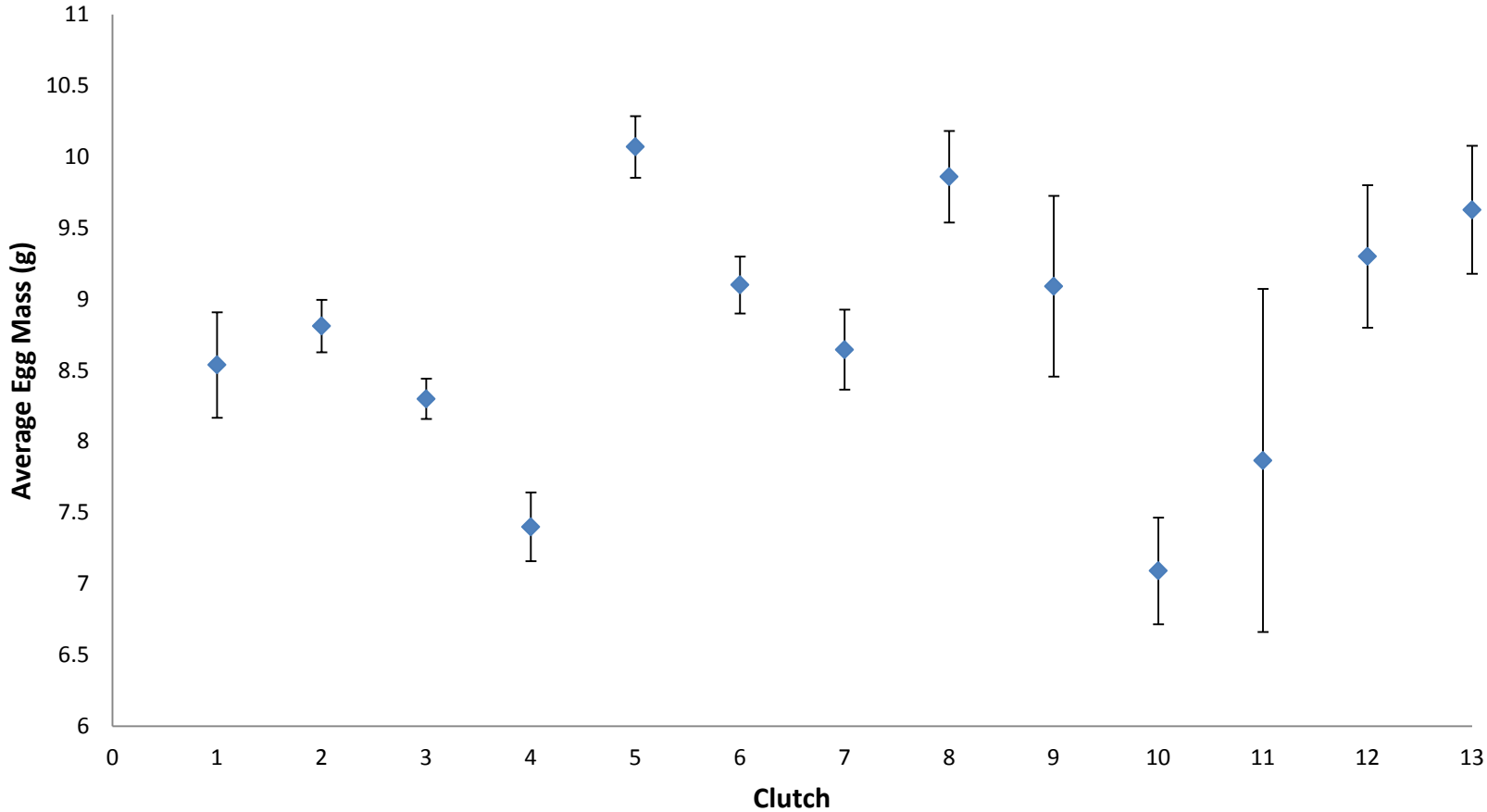


Figure 11: Average initial egg mass of diamondback terrapin clutches from Peconic Bay, NY.

## Initial Egg Mass: Peconic Bay, NY

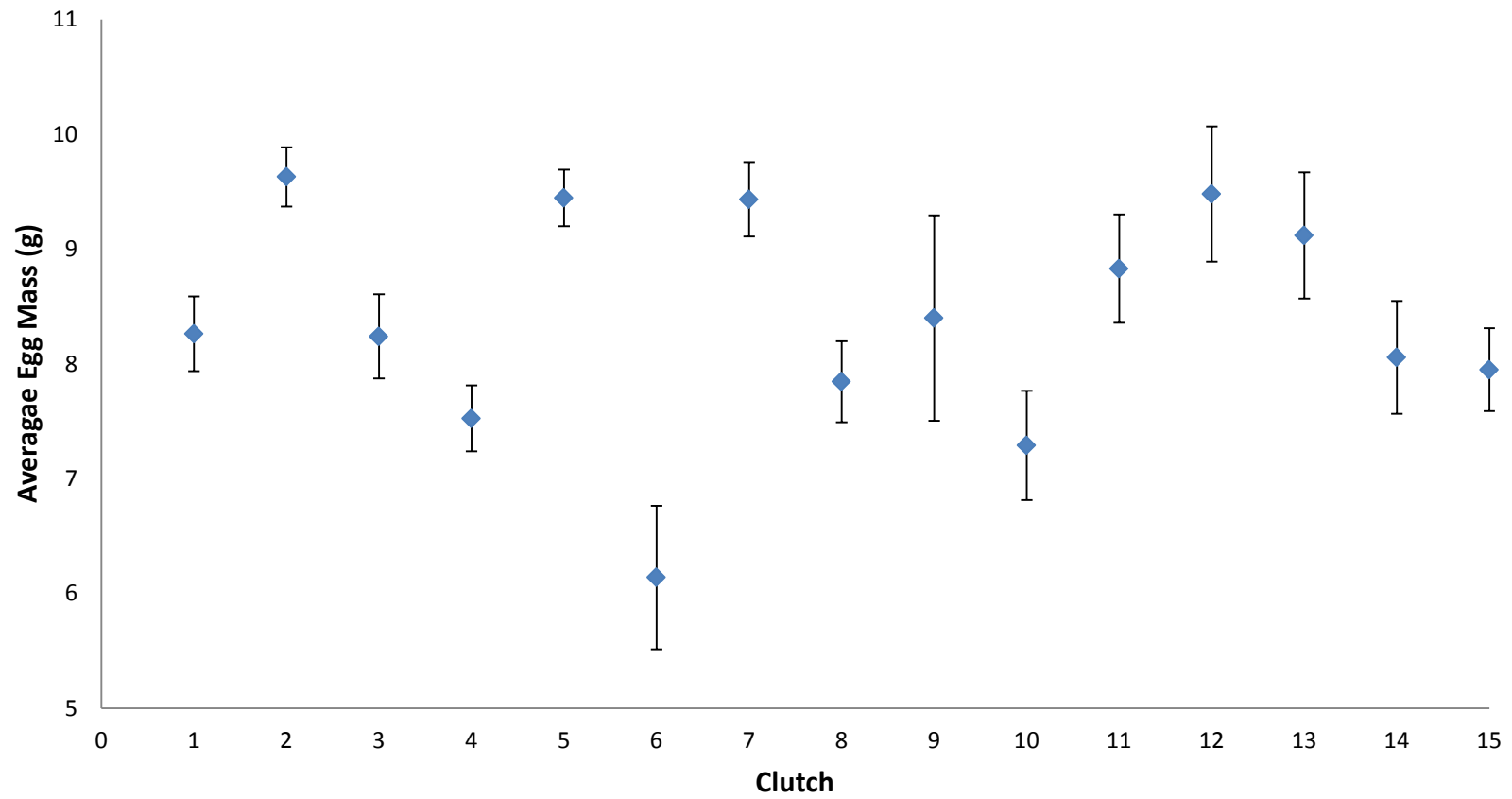


Figure 12: Average initial egg mass of diamondback terrapin clutches from Barrington River, RI.

## Initial Egg Mass: Barrington River, RI

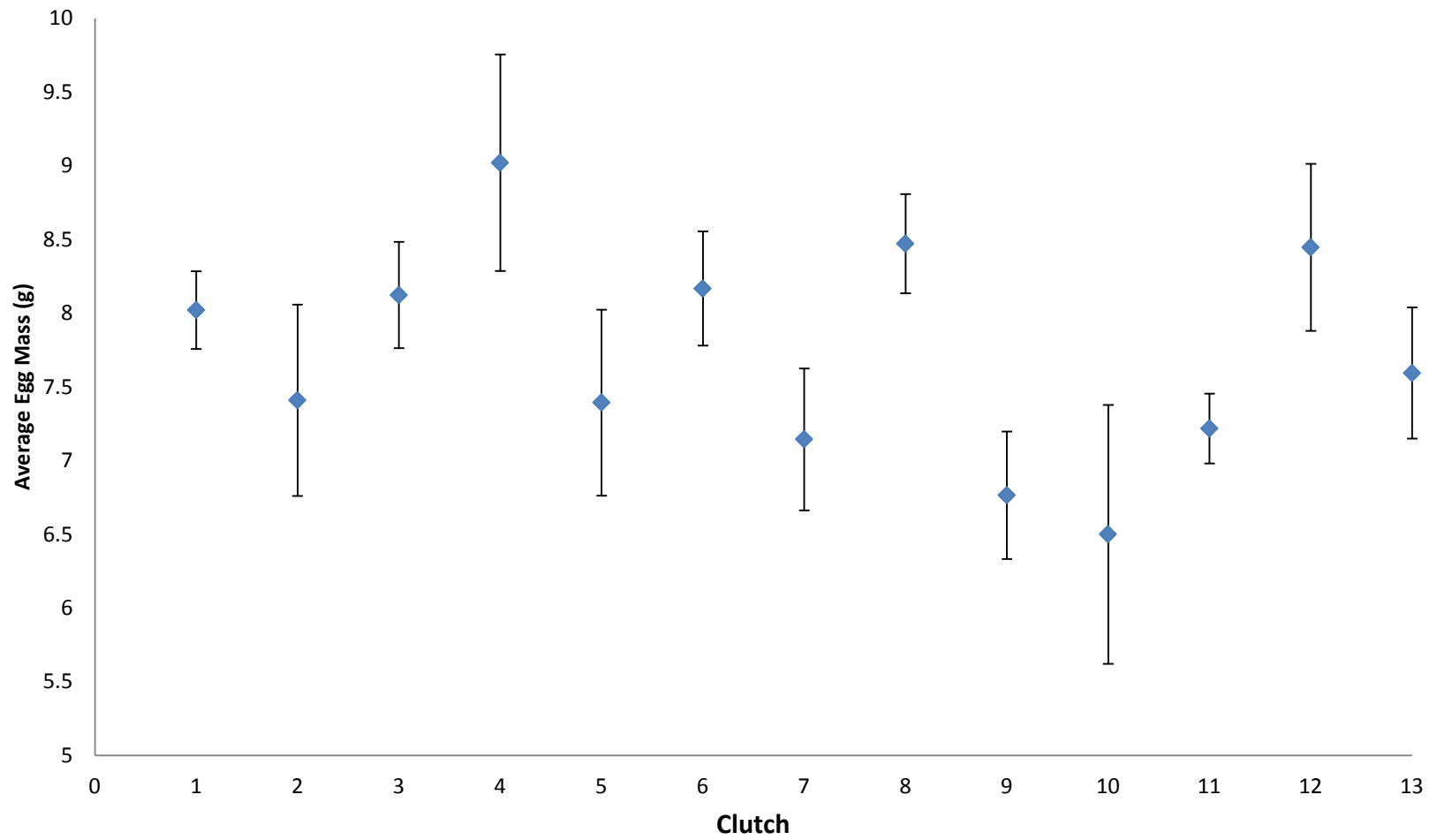


Figure 13: Relationship of average initial egg mass and latitude for northern diamondback terrapins (*Malaclemys terrapin terrapin*) from four sites (Barrington, RI, Jamaica Bay, NY, Peconic Bay, NY, and Cape May, NJ).



# Initial Egg Mass vs. Latitude

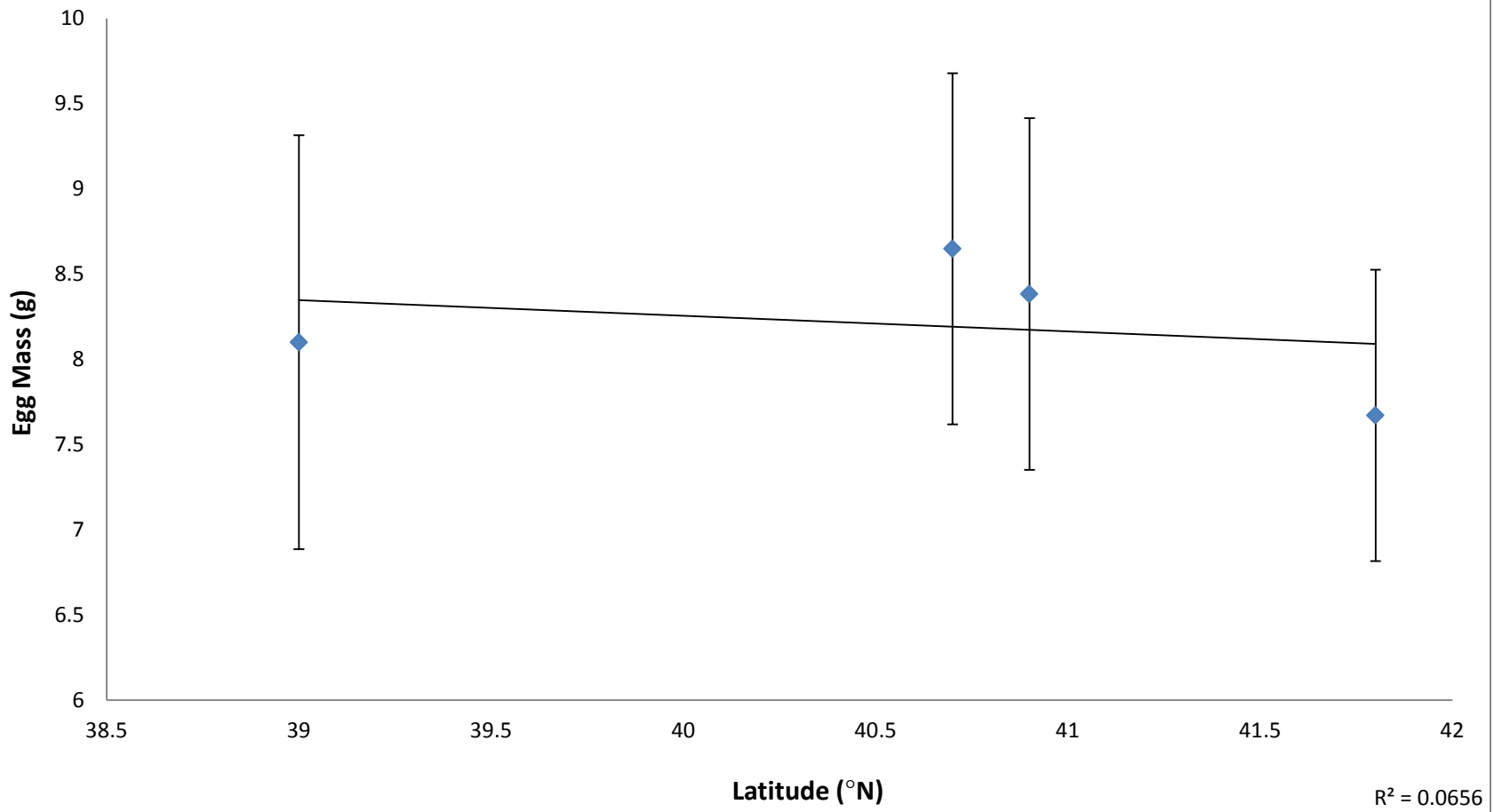


Figure 14: Change in egg mass over 30 days of northern diamondback terrapins (*Malaclemys terrapin terrapin*) from four sites (Barrington, RI, Jamaica Bay, NY, Peconic Bay, NY, and Cape May, NJ). Eggs were incubated in the same lab environment.

## Change in Egg Mass

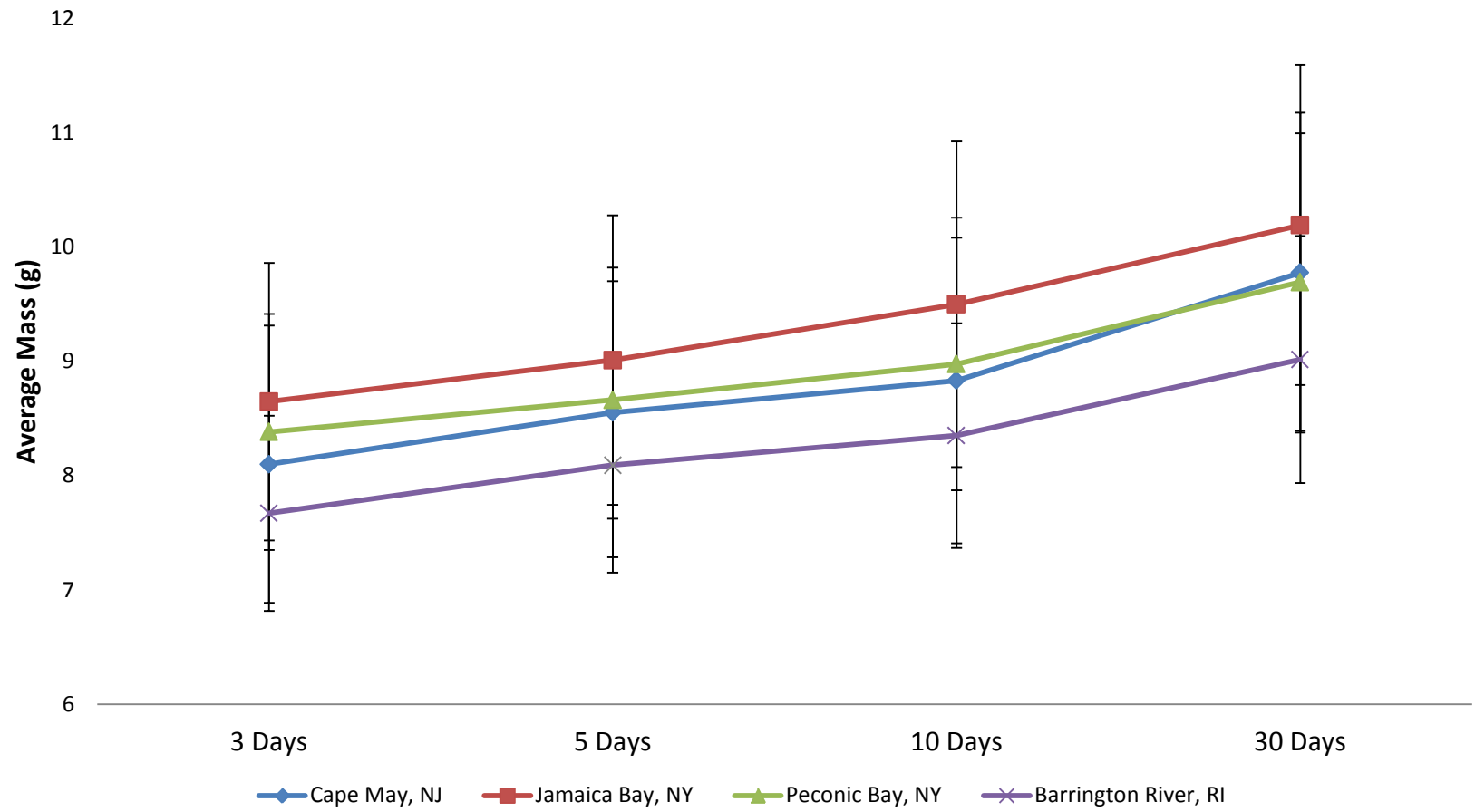
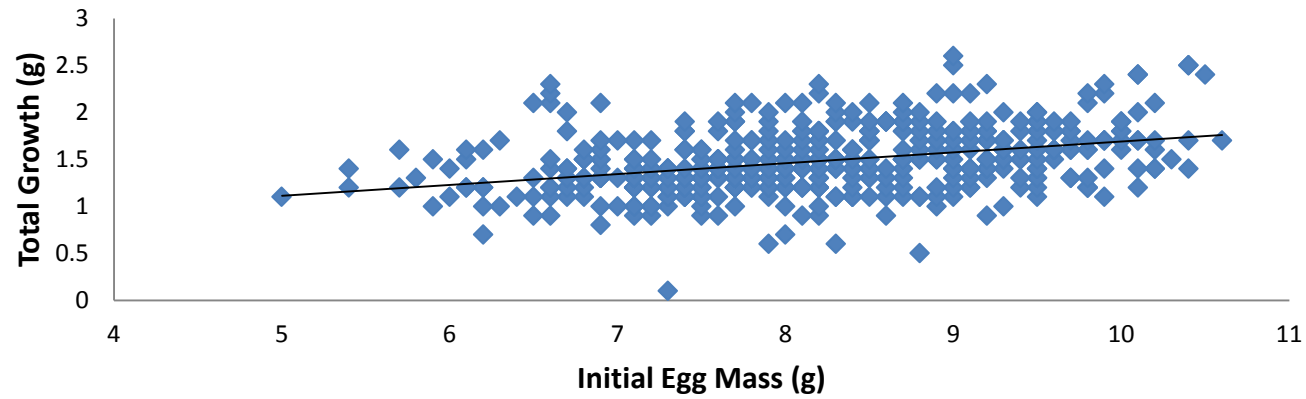


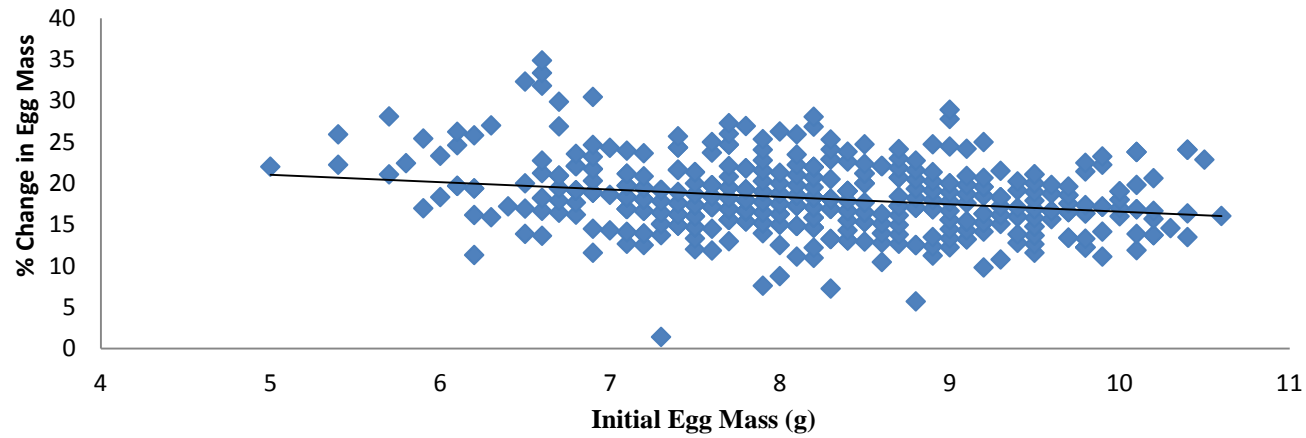
Figure 15A, B: Relationship of initial egg mass and egg growth from all sites. *A*) Total growth (change in egg mass) from initial measurement (3 days post-oviposition) to final egg measurement (30 days post-oviposition). *B*) Percentage of egg mass change from initial measurement to final measurement. (Note: Only eggs that hatched were used in these analyses.) Eggs were incubated in the same lab environment.

**A: Change in Egg Mass vs. Initial Egg Mass**



$R^2 = 0.1333$

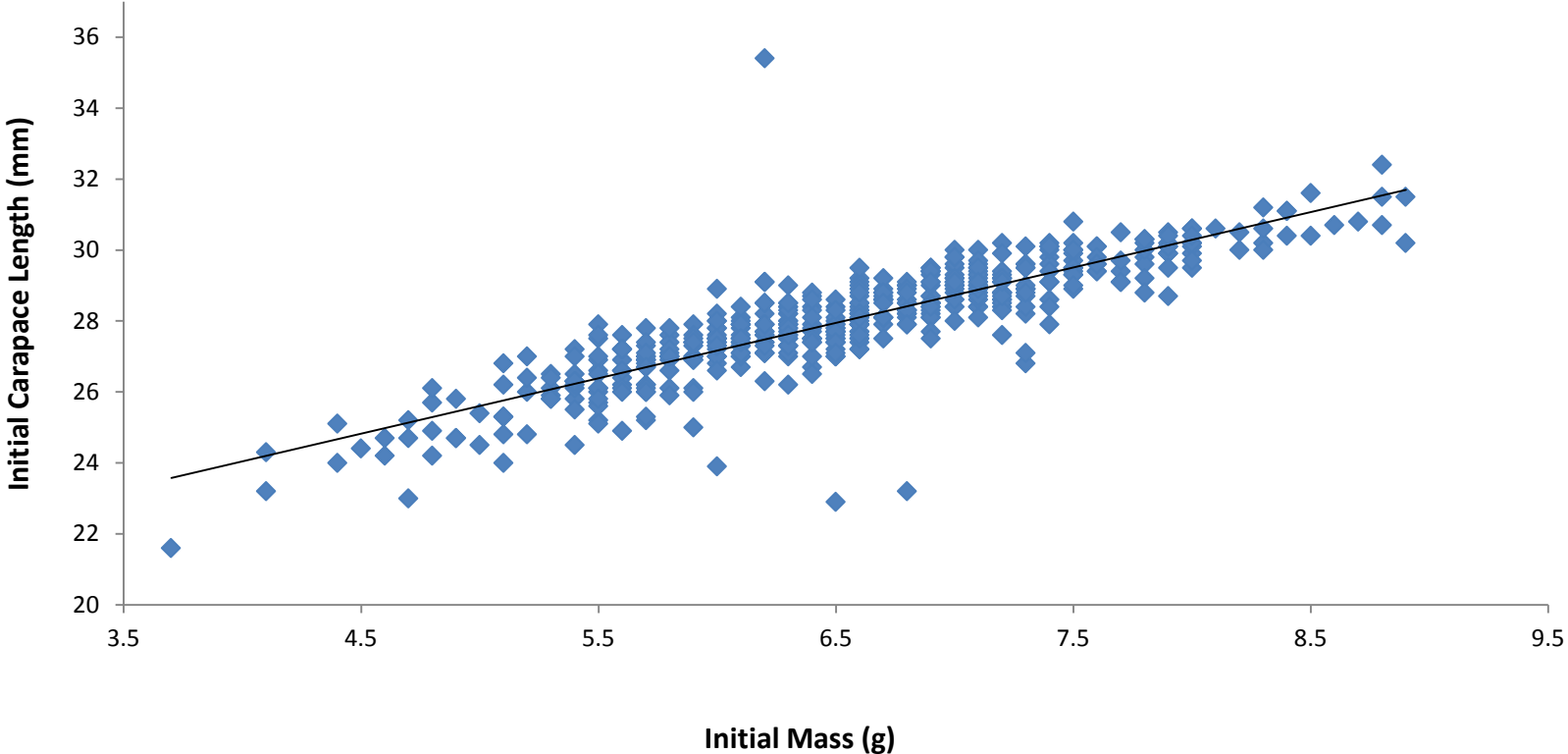
**B: Percent Change in Egg Mass vs. Initial Egg Mass**



$R^2 = 0.056$

Figure 16: Relationship of initial hatchling mass and initial hatchling carapace length of northern diamondback terrapins (*Malaclemys terrapin terrapin*) from four sites (Barrington, RI, Jamaica Bay, NY, Peconic Bay, NY, and Cape May, NJ).

# Initial Hatchling Mass vs. Carapace Length

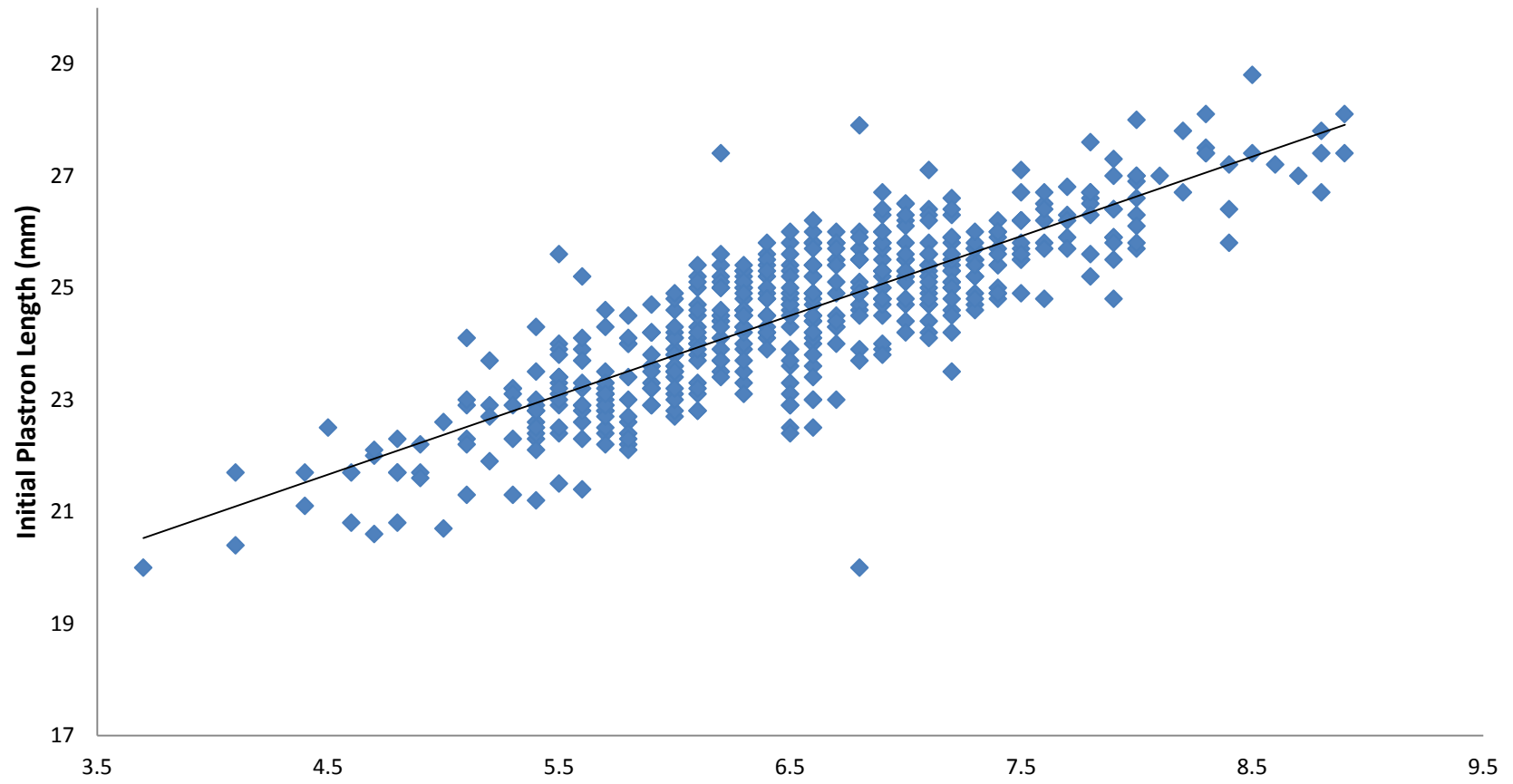


$R^2 = 0.7422$

Figure 17: Relationship of initial hatchling mass and hatchling plastron length of northern diamondback terrapins (*Malaclemys terrapin terrapin*) from four sites (Barrington, RI, Jamaica Bay, NY, Peconic Bay, NY, and Cape May, NJ).



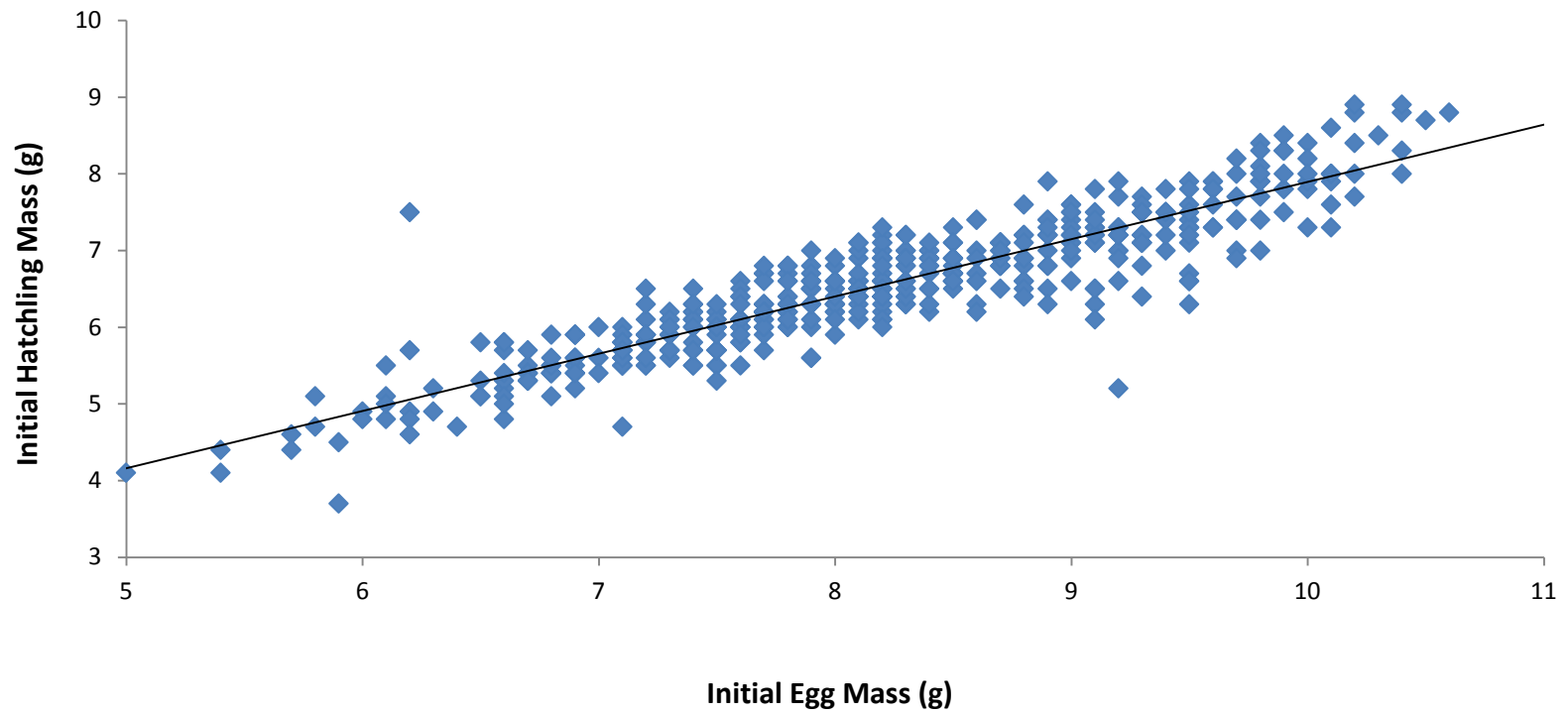
# Initial Hatchling Mass vs. Plastron Length



R<sup>2</sup> = 0.7035

Figure 18: Relationship of initial egg mass and initial hatchling mass of northern diamondback terrapins (*Malaclemys terrapin terrapin*) from four sites (Barrington, RI, Jamaica Bay, NY, Peconic Bay, NY, and Cape May, NJ).

## Initial Egg Mass vs. Initial Hatchling Mass



$R^2 = 0.8271$

Figure 19: Change in hatchling mass of northern diamondback terrapins (*Malaclemys terrapin terrapin*) from four sites (Barrington, RI, Jamaica Bay, NY, Peconic Bay, NY, and Cape May, NJ) throughout the first 75 days of the experiment. Terrapins were incubated and reared in the same lab environment.

# Hatchling Mass

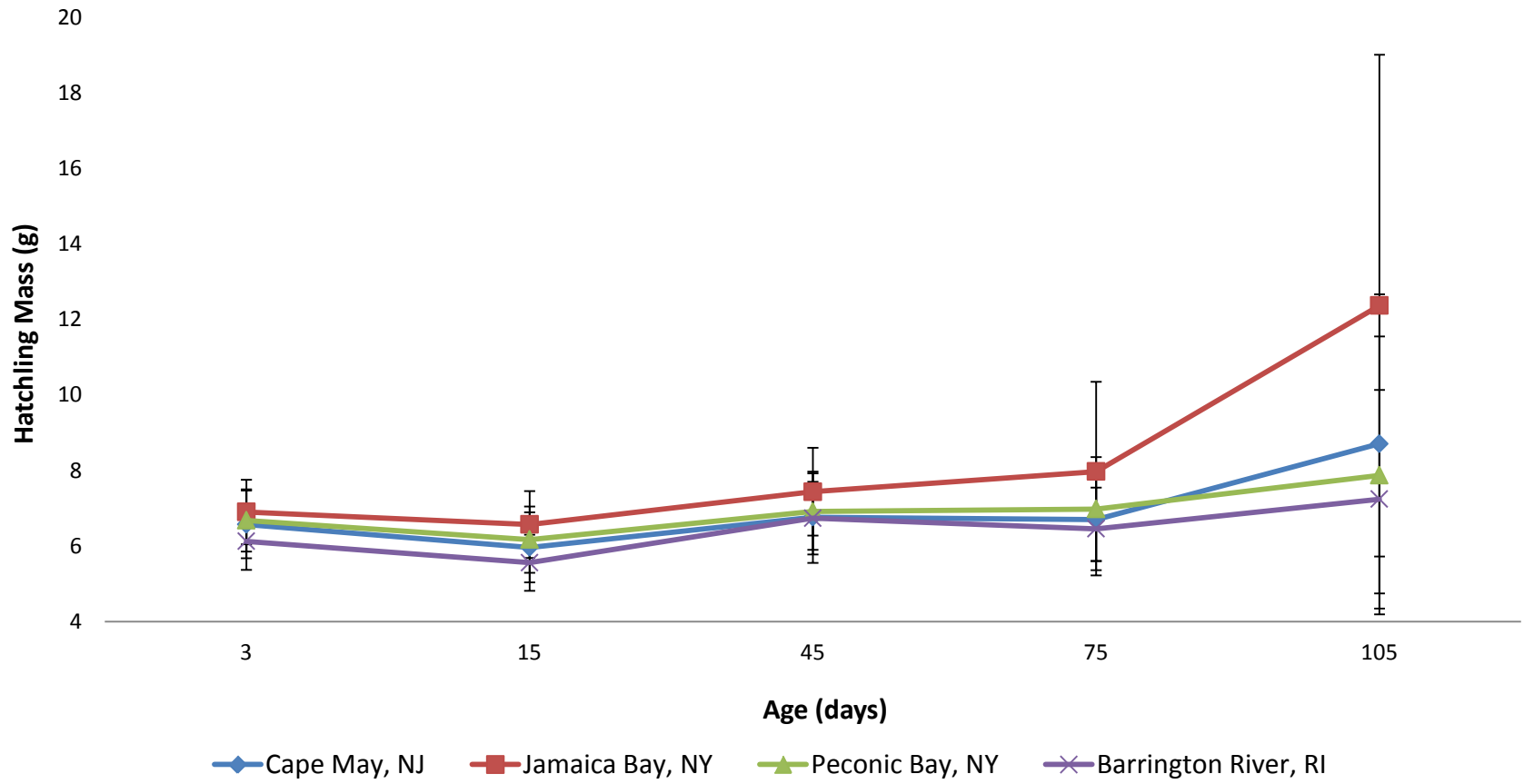


Figure 20: Relationship between initial egg mass and hatchling mass at 105 days post-hatching in northern diamondback terrapins (*Malaclemys terrapin terrapin*) from four sites (Barrington, RI, Jamaica Bay, NY, Peconic Bay, NY, and Cape May, NJ).  
Terrapins were incubated and reared in the same lab environment.

# Initial Egg Mass vs. Hatchling Mass at 105 Days

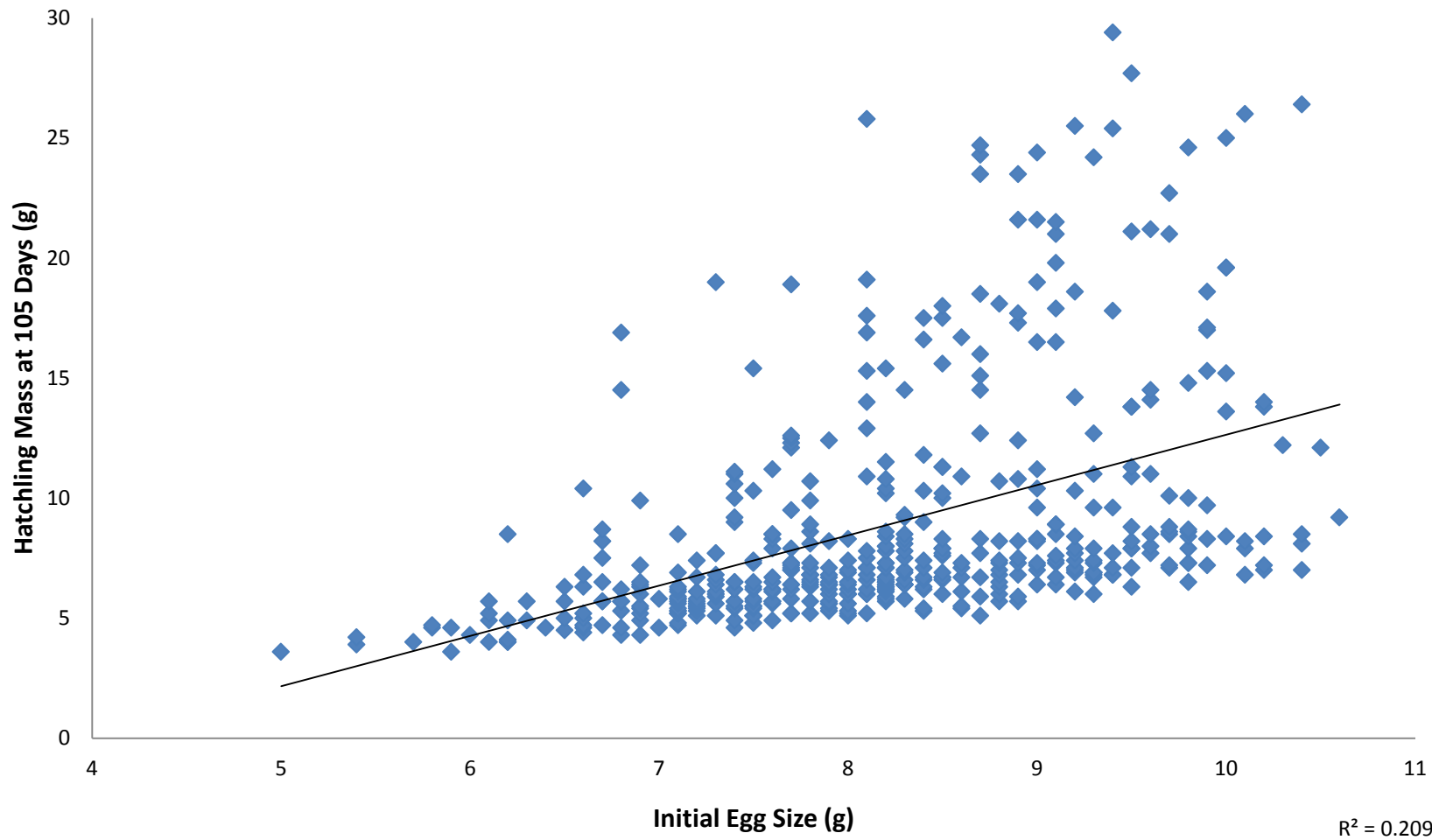


Figure 21: Relationship of the percentage of shell abnormalities and latitude of origin for northern diamondback terrapins (*Malaclemys terrapin terrapin*) from four sites (Barrington, RI, Jamaica Bay, NY, Peconic Bay, NY, and Cape May, NJ).



## Shell Abnormalities vs. Latitude

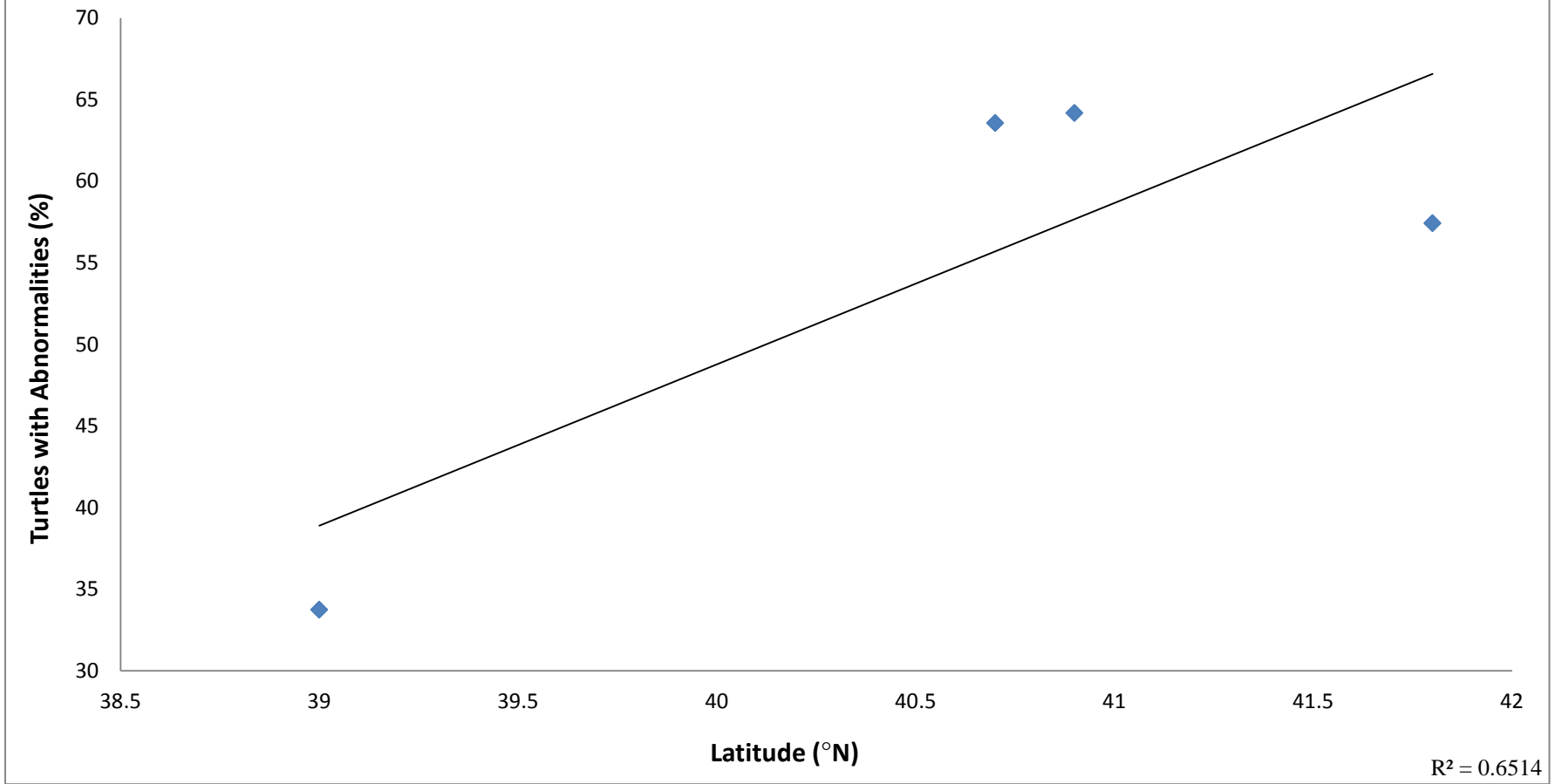
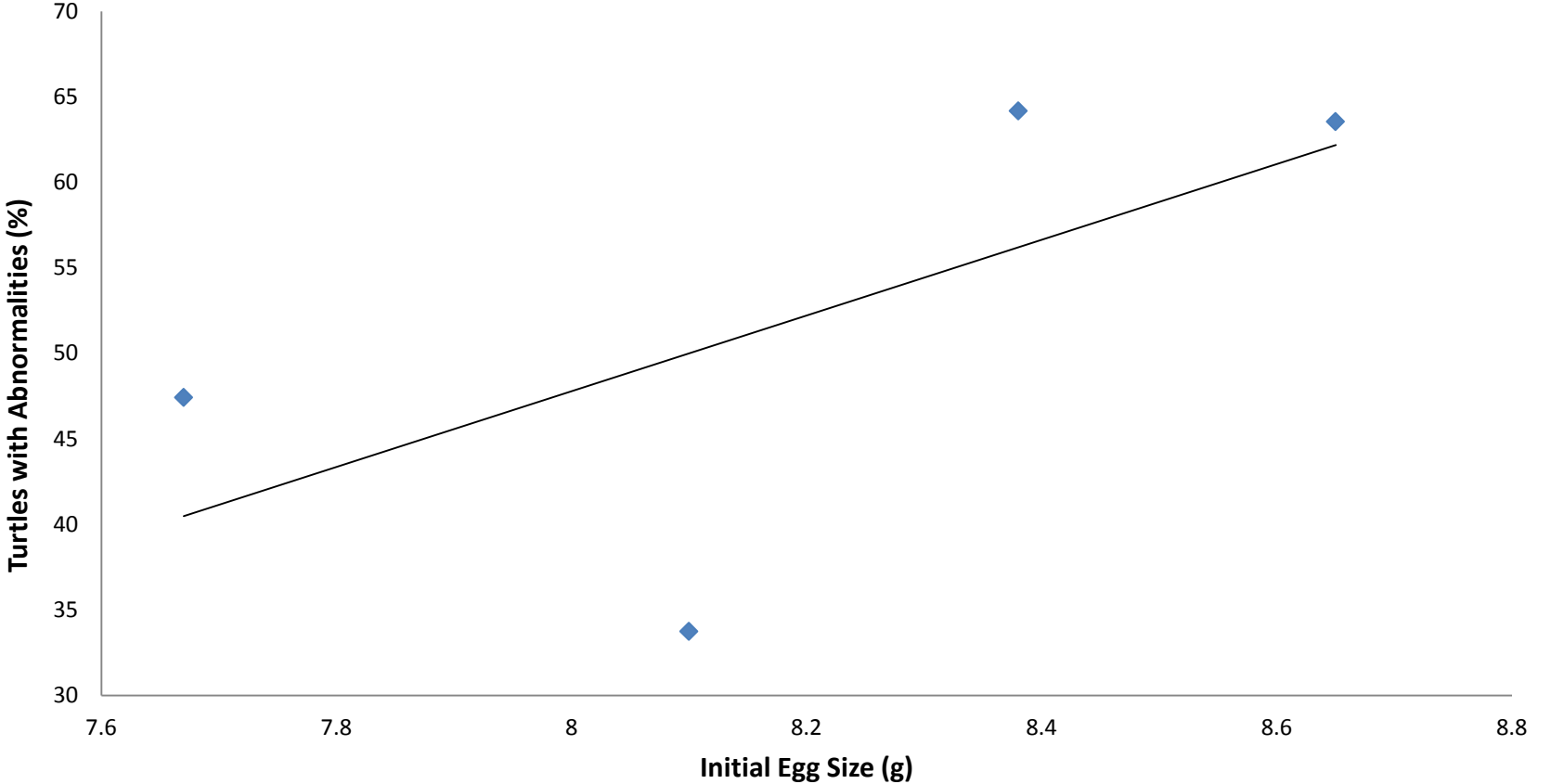


Figure 22: Relationship between initial egg size and percentage of shell abnormalities in northern diamondback terrapins (*Malaclemys terrapin terrapin*) from four sites (Barrington, RI, Jamaica Bay, NY, Peconic Bay, NY, and Cape May, NJ).

### Shell Abnormalities vs. Initial Egg Size



R<sup>2</sup> = 0.4053

Figure 23: Righting speed frequency percentages at 15 days post-hatching for northern diamondback terrapins (*Malaclemys terrapin terrapin*) from four sites (Barrington, RI, Jamaica Bay, NY, Peconic Bay, NY, and Cape May, NJ). Terrapins were incubated and reared in the same lab environment.

### Righting Response: 15 Days Old

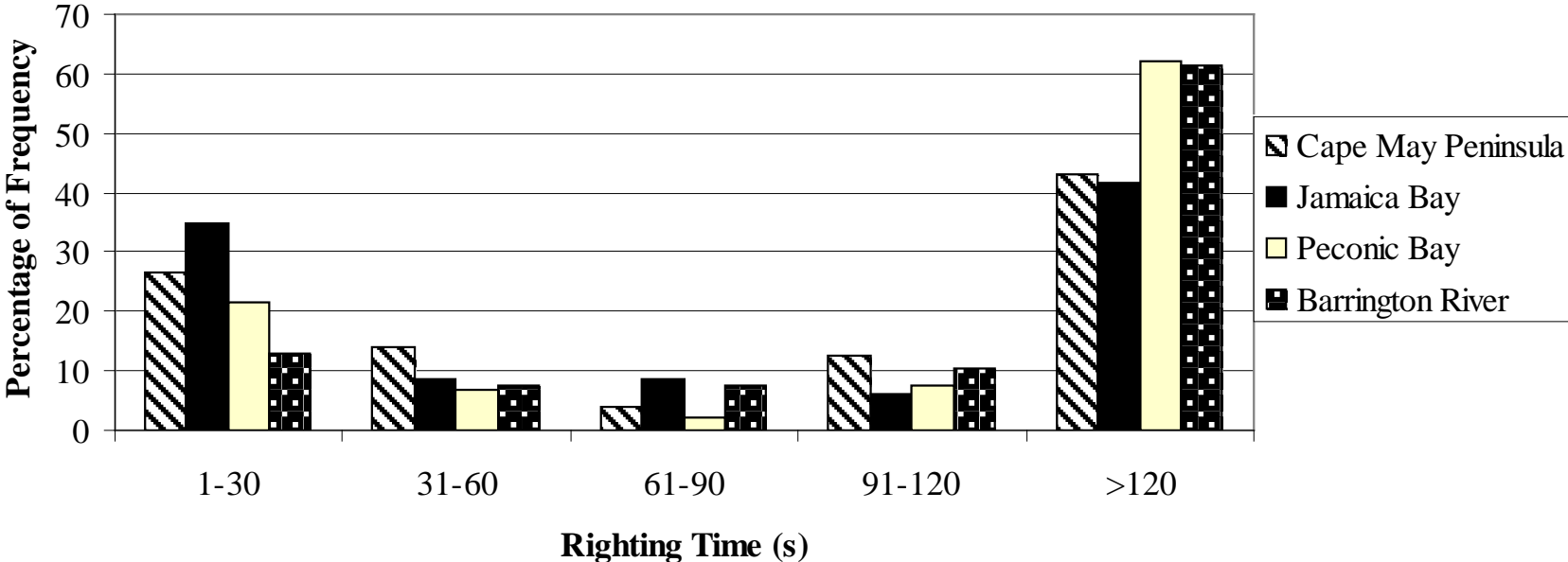


Figure 24: Righting speed frequency percentages for each site at 45 days post-hatching northern diamondback terrapins (*Malaclemys terrapin terrapin*) from four sites (Barrington, RI, Jamaica Bay, NY, Peconic Bay, NY, and Cape May, NJ). Terrapins were incubated and reared in the same lab environment.

### Righting Response: 45 Days Old

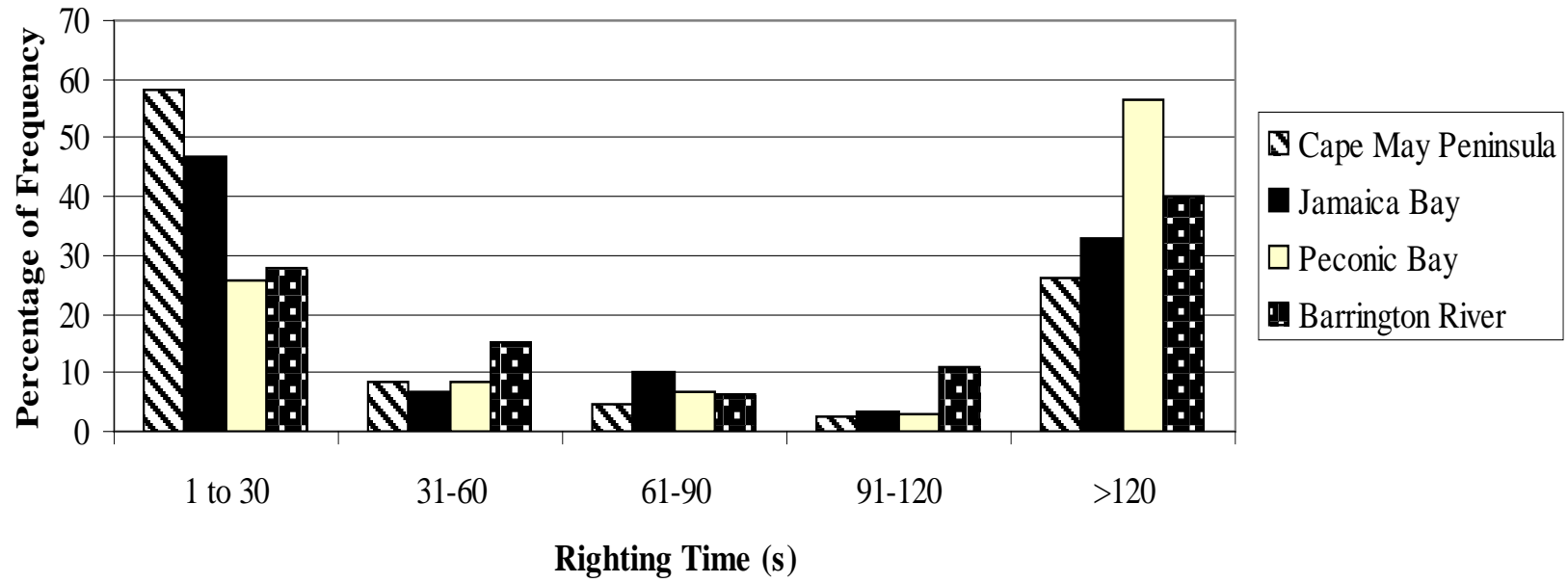


Figure 25: Righting speed frequency percentages for each site at 75 days post-hatching for northern diamondback terrapins (*Malaclemys terrapin terrapin*) from four sites (Barrington, RI, Jamaica Bay, NY, Peconic Bay, NY, and Cape May, NJ). Terrapins were incubated and reared in the same lab environment.



### Righting Response: 75 Days Old

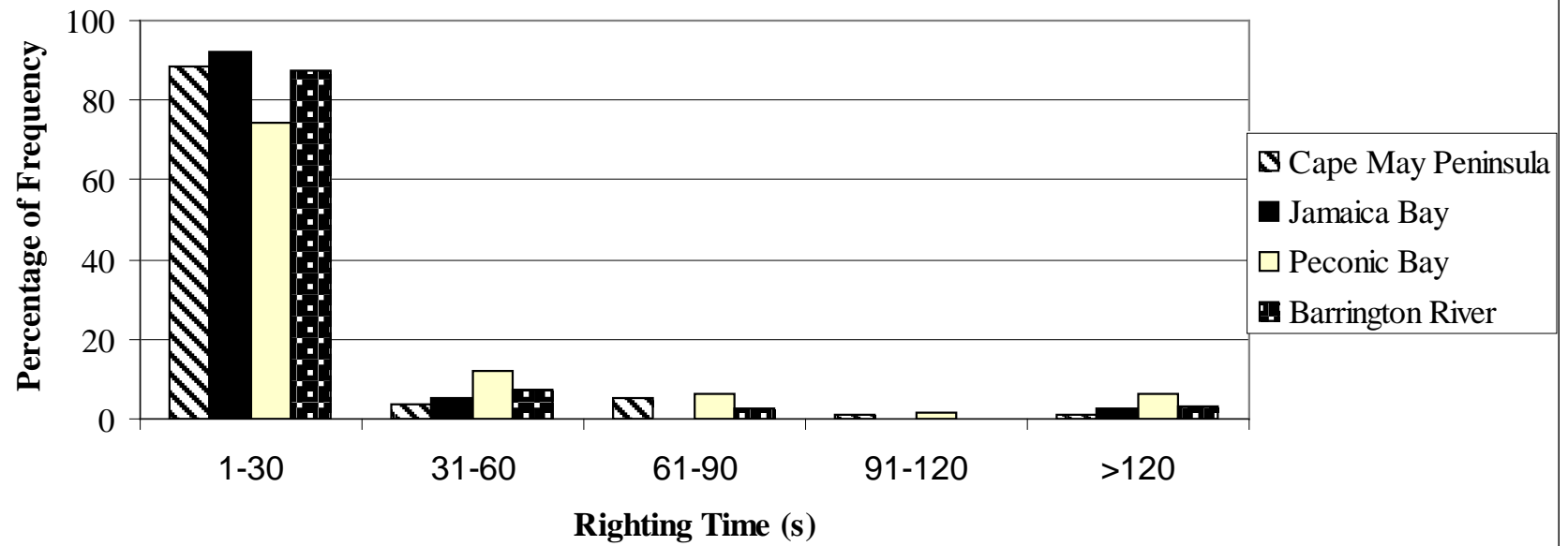


Figure 26: Righting speed frequency percentages for each site at 105 days post-hatching for northern diamondback terrapins (*Malaclemys terrapin terrapin*) from four sites (Barrington, RI, Jamaica Bay, NY, Peconic Bay, NY, and Cape May, NJ). Terrapins were incubated and reared in the same lab environment.

### Righting Response: 105 Days

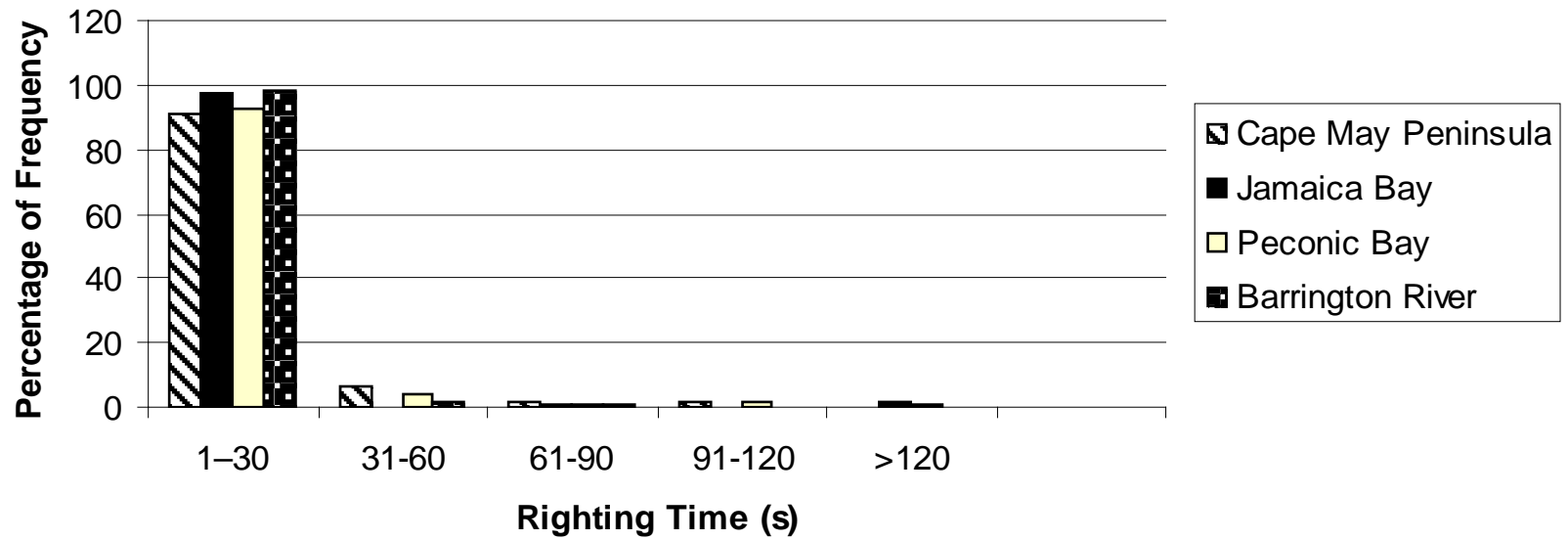
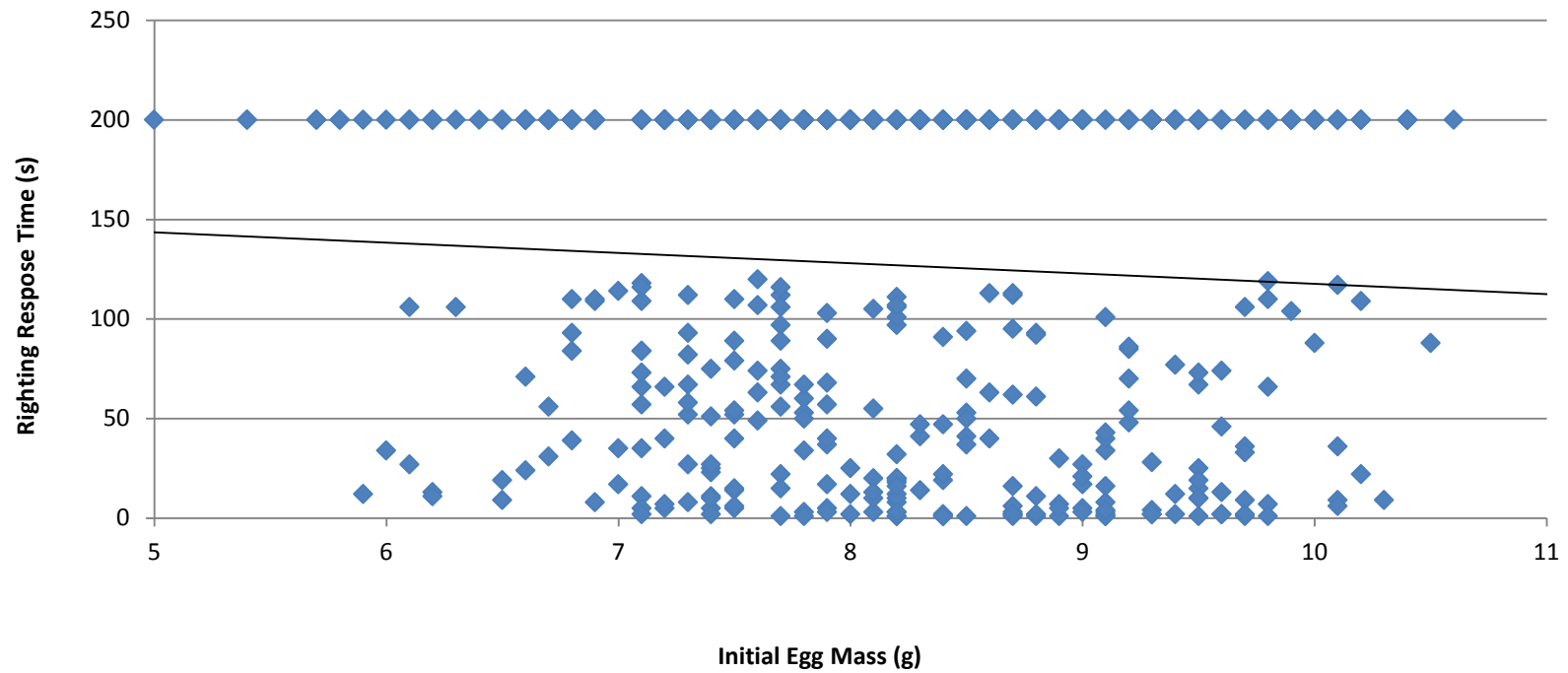


Figure 27: Relationship between righting response and initial egg size for northern diamondback terrapins (*Malaclemys terrapin terrapin*) from four sites (Barrington, RI, Jamaica Bay, NY, Peconic Bay, NY, and Cape May, NJ). Terrapins were incubated and reared in the same lab environment.

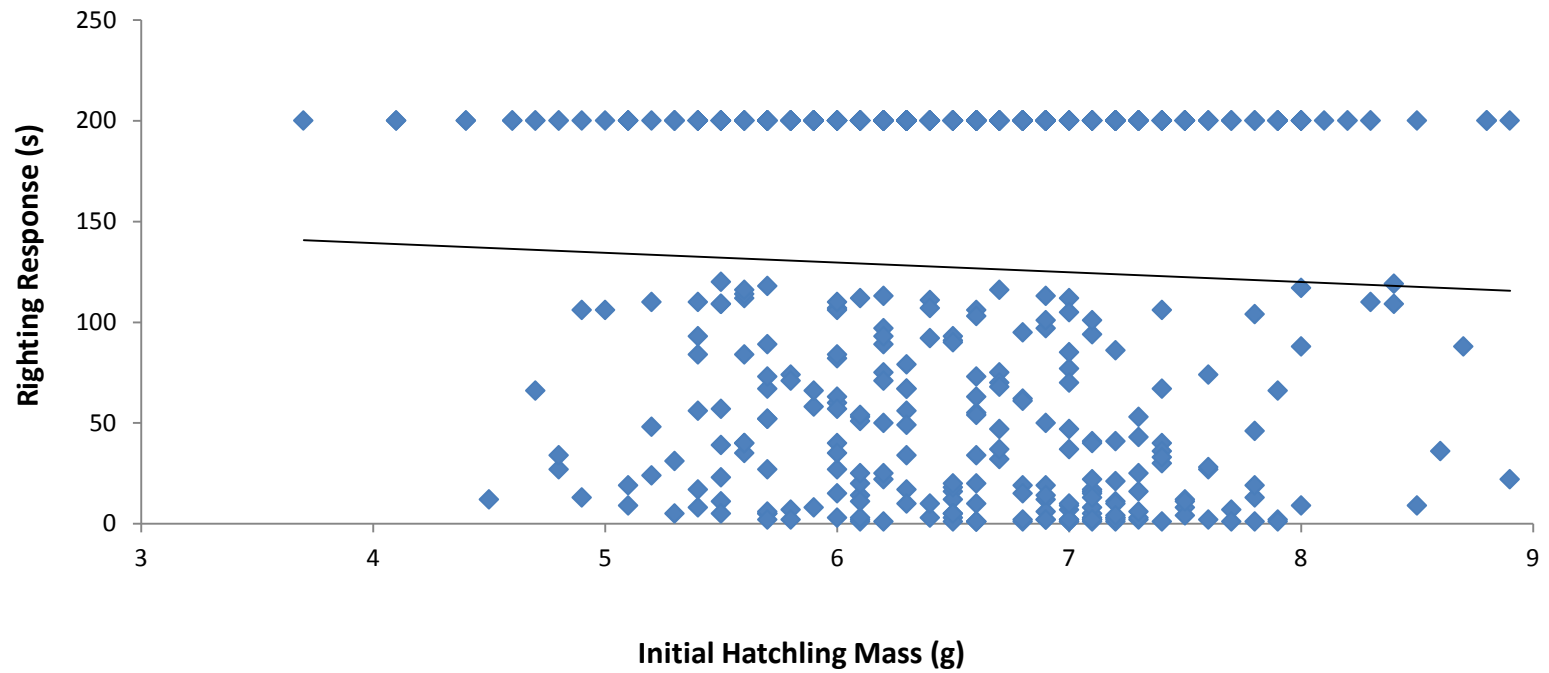
## Initial Egg Mass vs. Righting Response at 15 Days



$R^2 = 0.0045$

Figure 28: Relationship between righting response and initial hatchling size for northern diamondback terrapins (*Malaclemys terrapin terrapin*) from four sites (Barrington, RI, Jamaica Bay, NY, Peconic Bay, NY, and Cape May, NJ). Terrapins were incubated and reared in the same lab environment.

## Initial Hatchling Mass vs. Righting Response at 15 Days



$R^2 = 0.0026$

Figure 29: Relationship between percent of days survived (survivorship) and initial egg mass for northern diamondback terrapins (*Malaclemys terrapin terrapin*) from four sites (Barrington, RI, Jamaica Bay, NY, Peconic Bay, NY, and Cape May, NJ). Terrapins were incubated and reared in the same lab environment.



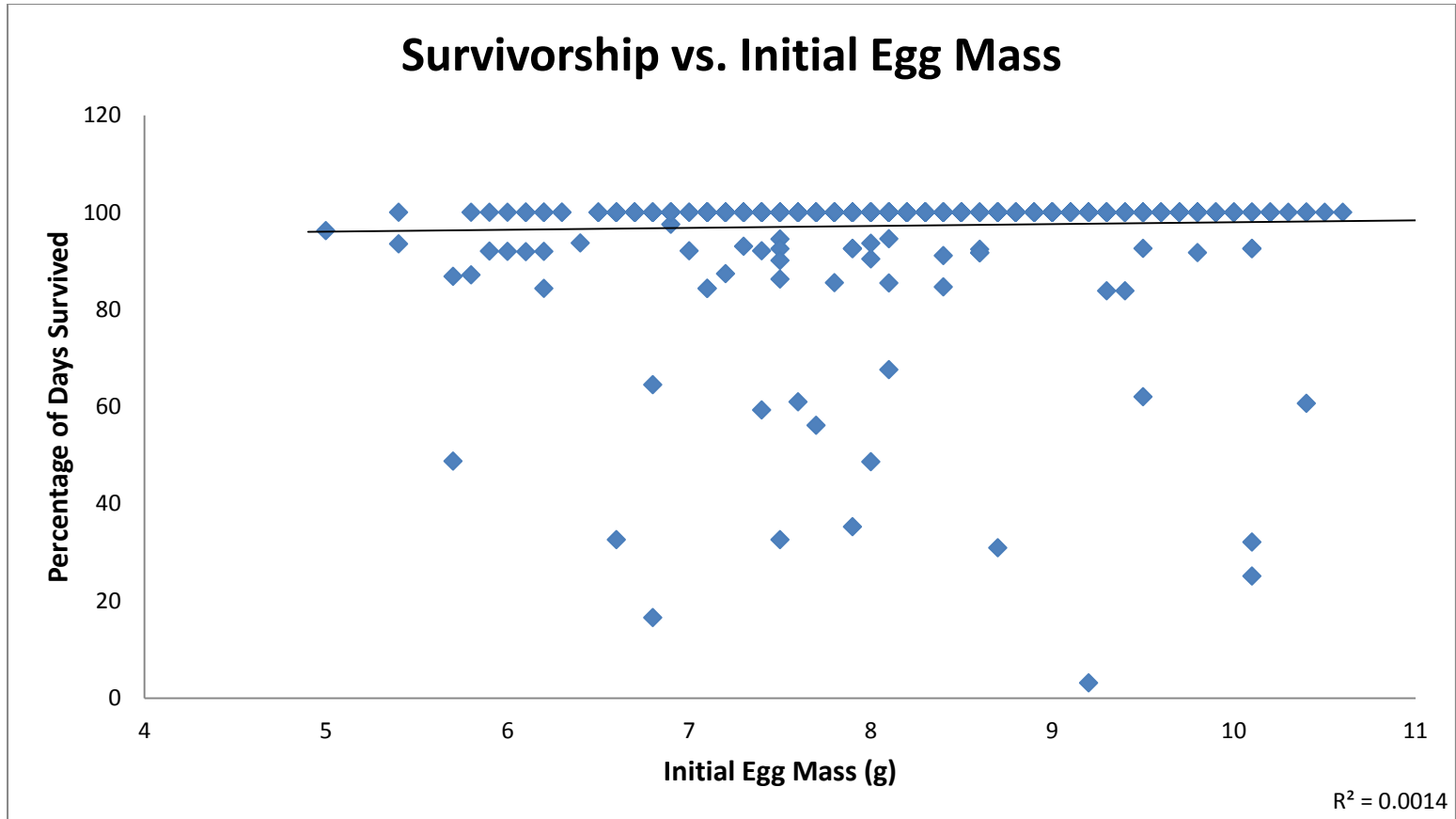
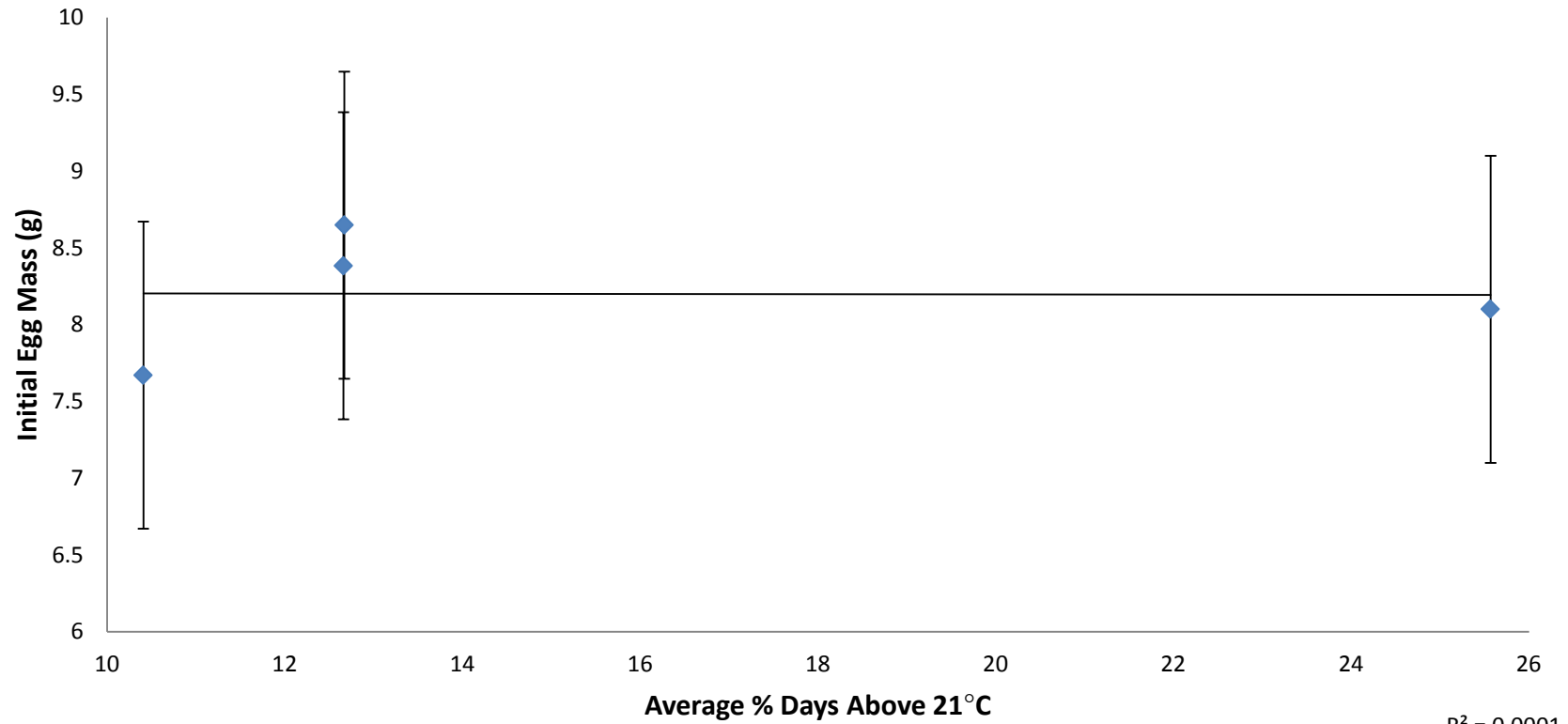


Figure 30: Relationship between the average percentage of summer days above 21°C and initial egg size for northern diamondback terrapins (*Malaclemys terrapin terrapin*) from four sites (Barrington, RI, Jamaica Bay, NY, Peconic Bay, NY, and Cape May, NJ).

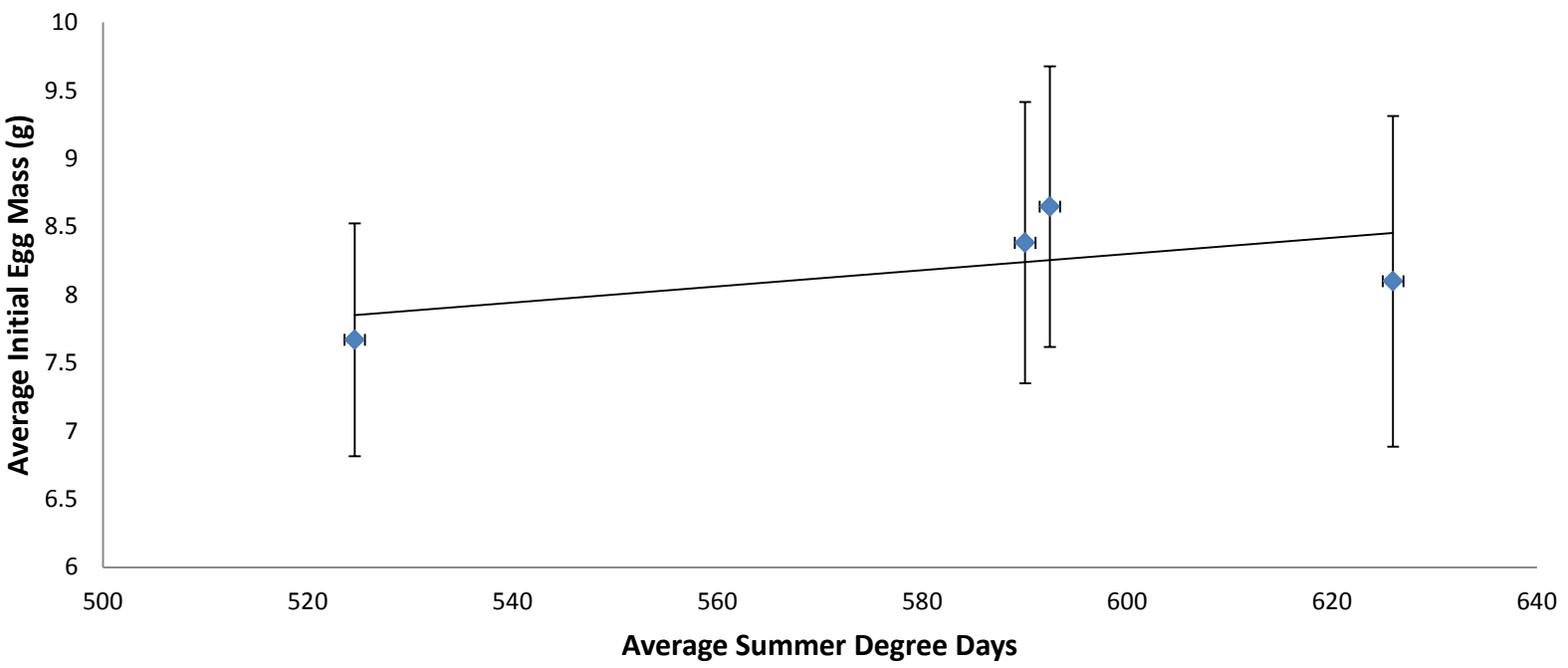
# Initial Egg Size vs. Days Above Threshold Temperature



R<sup>2</sup> = 0.0001

Figure 31: Relationship between average number of summer degree days and initial egg size for northern diamondback terrapins (*Malaclemys terrapin terrapin*) from four sites (Barrington, RI, Jamaica Bay, NY, Peconic Bay, NY, and Cape May, NJ).

# Initial Egg Size vs. Summer Degree Days



$R^2 = 0.3652$

Figure 32: Relationship between average incubation duration and latitude for northern diamondback terrapins (*Malaclemys terrapin terrapin*) from four sites (Barrington, RI, Jamaica Bay, NY, Peconic Bay, NY, and Cape May, NJ). Eggs were incubated in the same lab environment.

## Incubation Period vs. Latitude

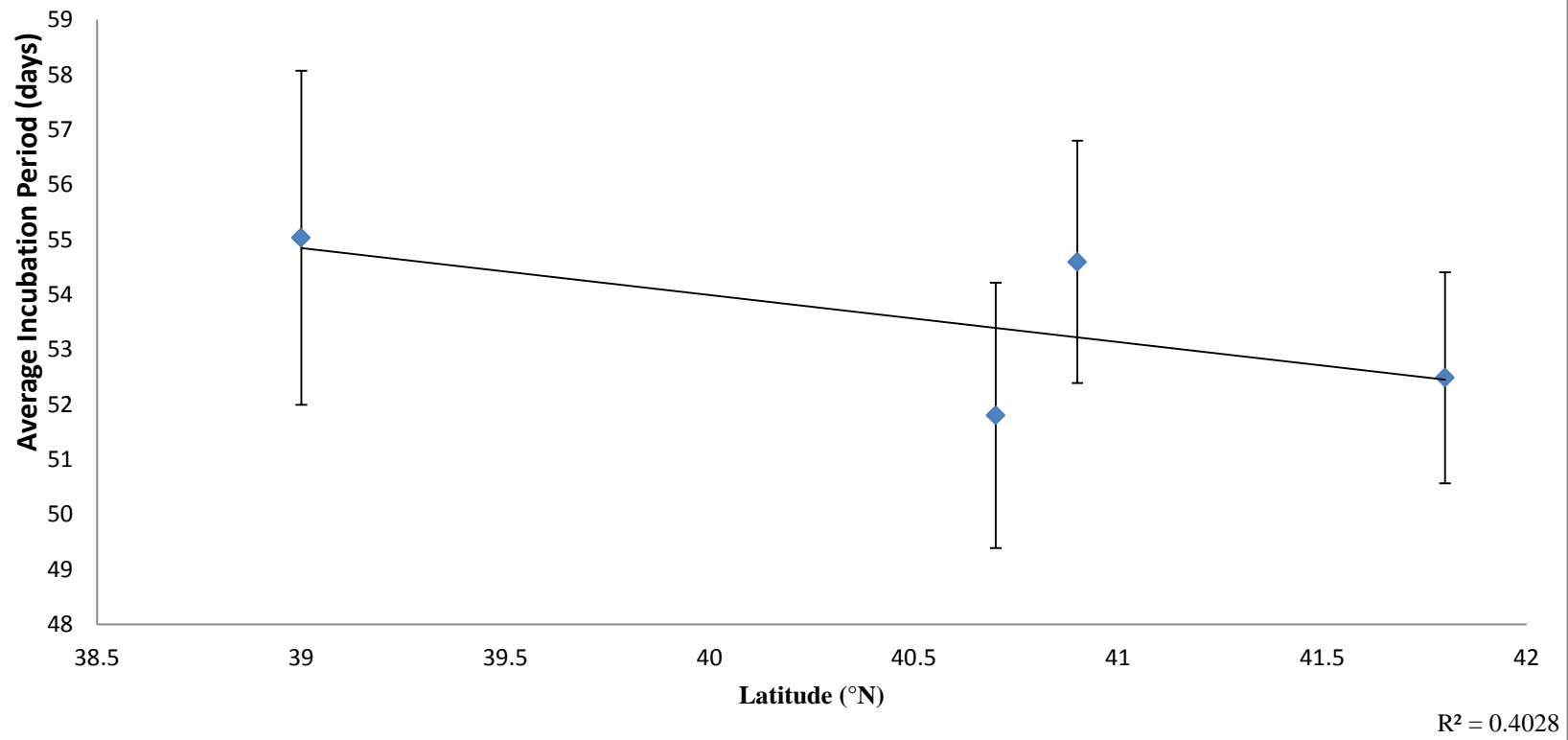
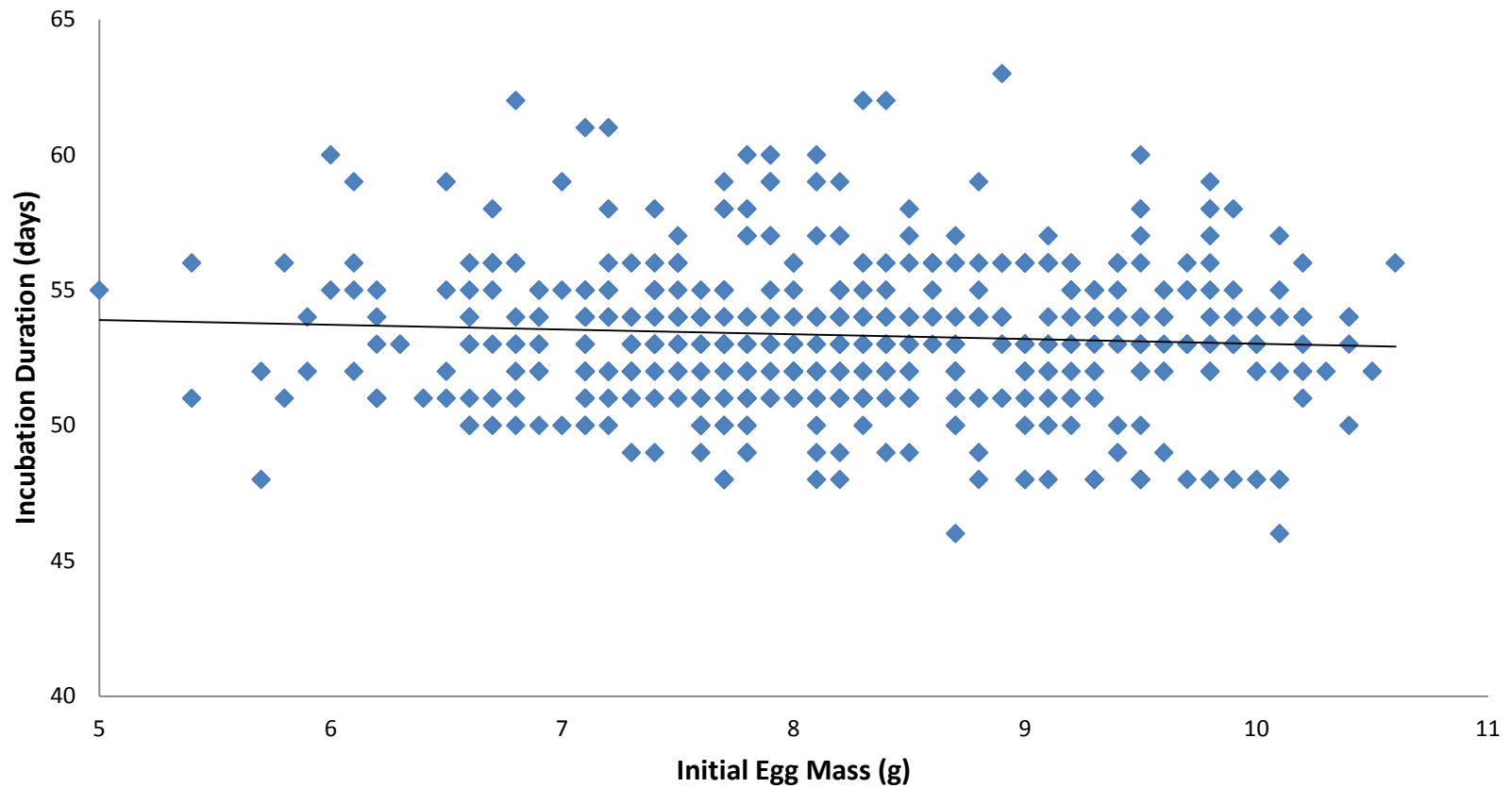


Figure 33: Relationship between incubation duration and initial egg size for northern diamondback terrapins (*Malaclemys terrapin terrapin*) from four sites (Barrington, RI, Jamaica Bay, NY, Peconic Bay, NY, and Cape May, NJ). Eggs were incubated in the same lab environment.



# Initial Egg Mass vs. Incubation Duration



R<sup>2</sup> = 0.0049

Figure 34: Relationship between summer temperature variability and average initial egg size northern diamondback terrapins (*Malaclemys terrapin terrapin*) from four sites (Barrington, RI, Jamaica Bay, NY, Peconic Bay, NY, and Cape May, NJ).

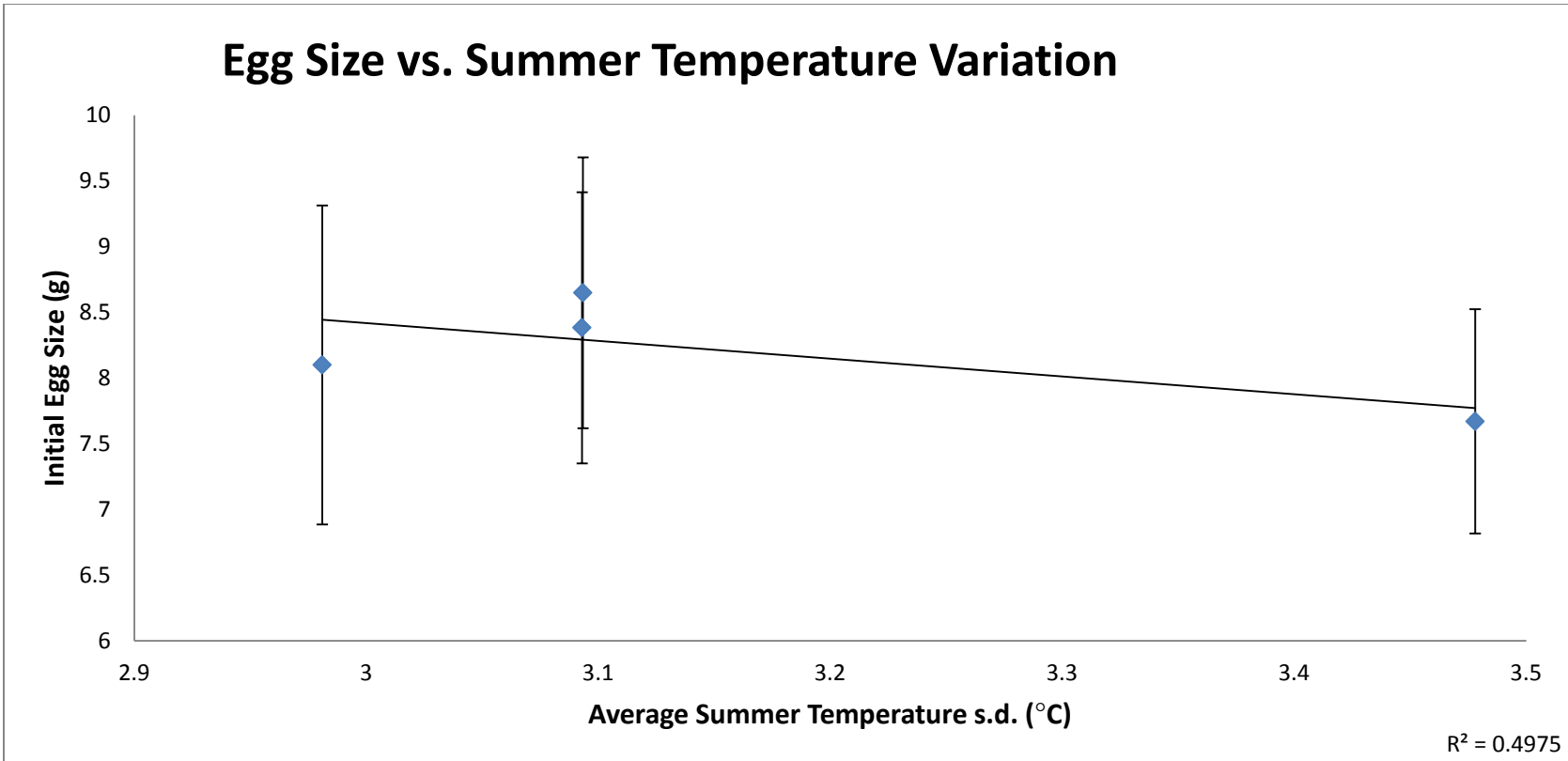
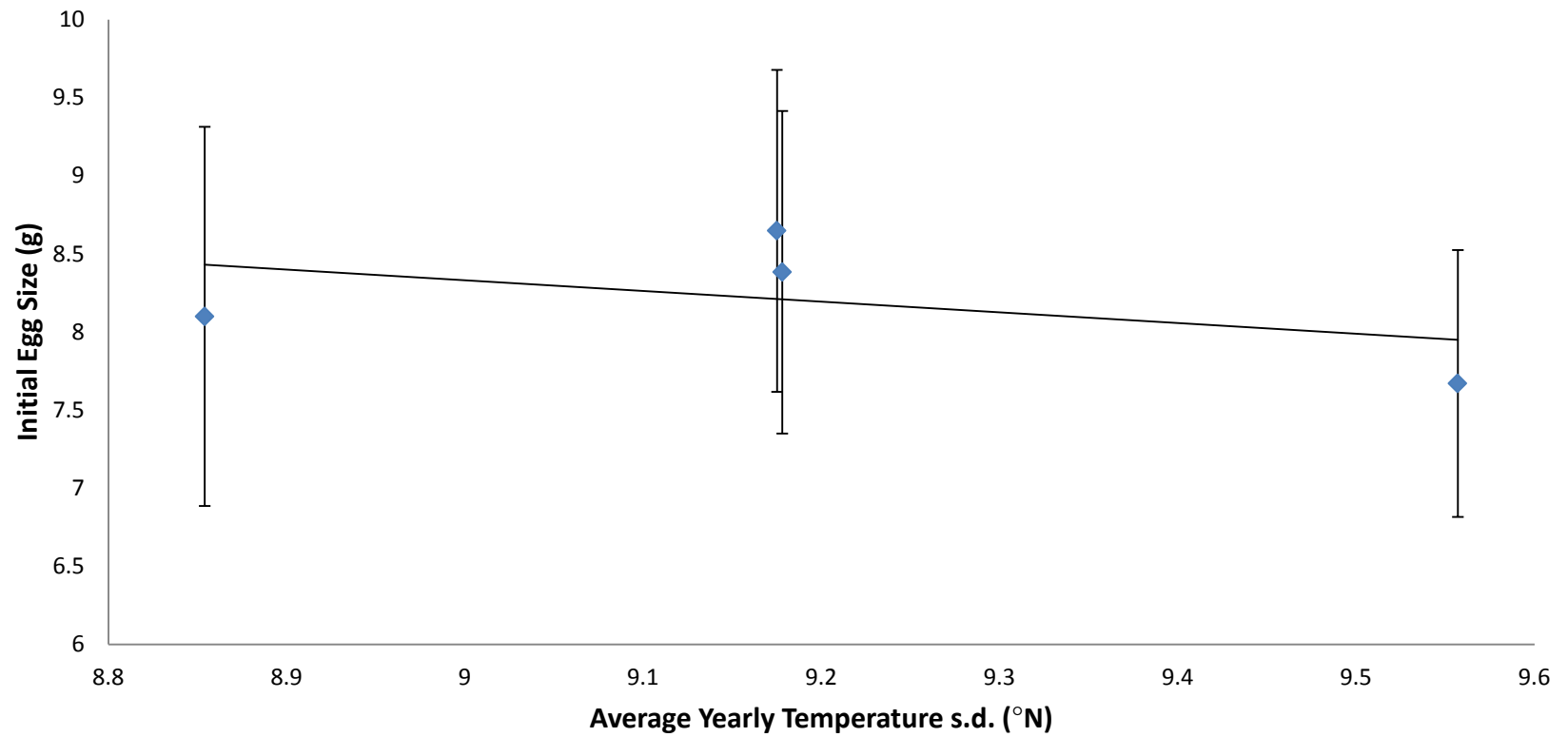


Figure 35: Relationship between average annual temperature variability and average initial egg size northern diamondback terrapins (*Malaclemys terrapin terrapin*) from four sites (Barrington, RI, Jamaica Bay, NY, Peconic Bay, NY, and Cape May, NJ).

## Egg Size vs. Yearly Temperature Variation



$R^2 = 0.2212$

Figure 36: Relationship between average summer temperature variability and egg size variability for northern diamondback terrapins (*Malaclemys terrapin terrapin*) from four sites (Barrington, RI, Jamaica Bay, NY, Peconic Bay, NY, and Cape May, NJ).

## Egg Size Variation vs. Summer Temperature Variation

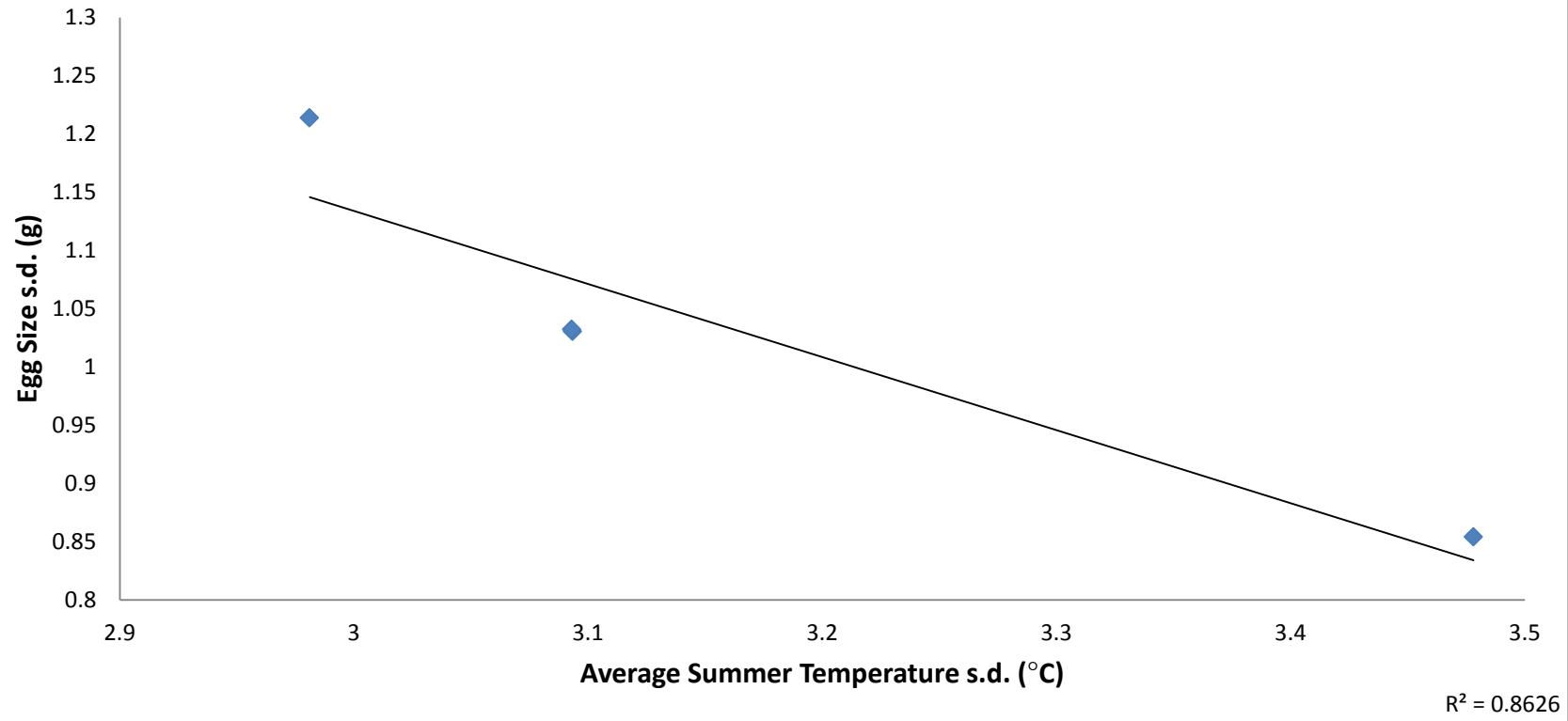
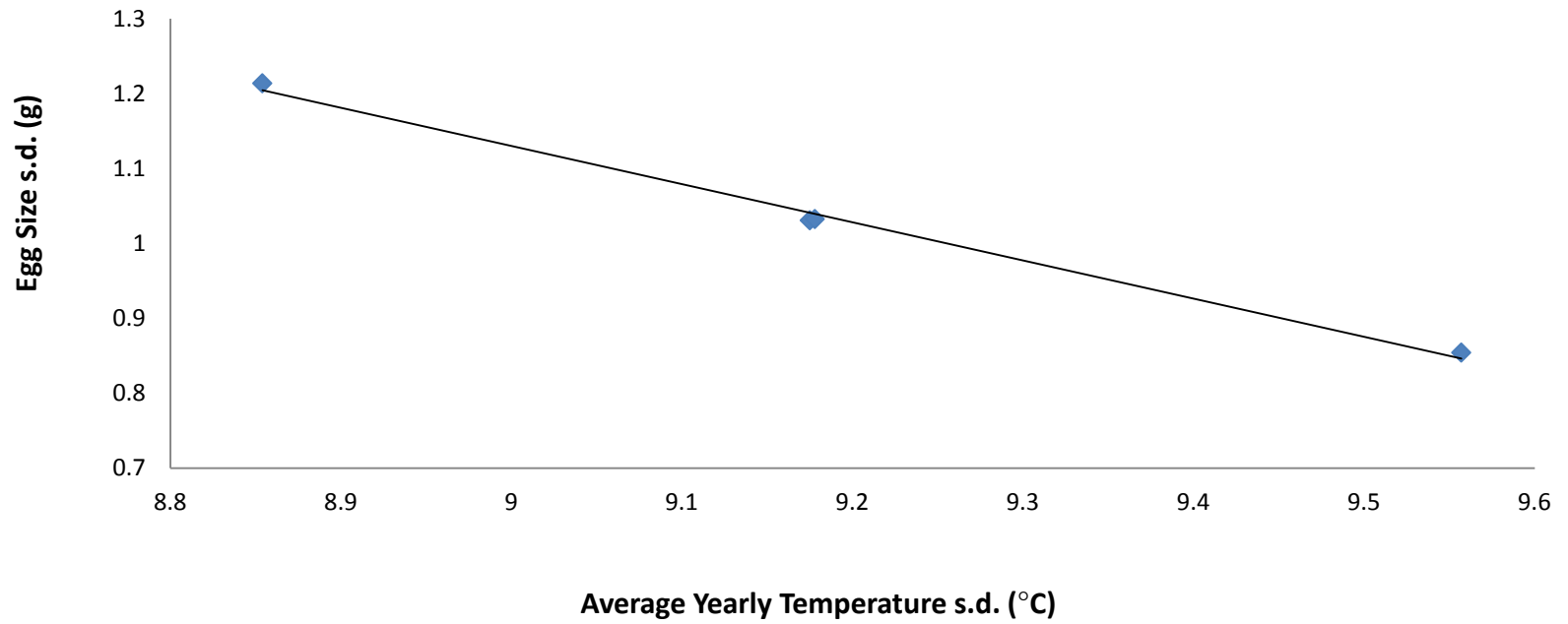


Figure 37: Relationship between average annual temperature and egg size variability for northern diamondback terrapins (*Malaclemys terrapin terrapin*) from four sites (Barrington, RI, Jamaica Bay, NY, Peconic Bay, NY, and Cape May, NJ).



## Egg Size Variation vs. Yearly Temperature Variation



$R^2 = 0.9953$