

Errata

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Graham, Larissa J., Mark L. Botton, David Hata, Robert E. Loveland, and Brian R. Murphy

Prosomal-width-to-weight relationships in American horseshoe crabs (*Limulus polyphemus*): examining conversion factors used to estimate landings

Page 238, Equation 1. The y -intercept variable reads " b " and it should read " $\log_e(b)$."

Page 241, Table 3. The third entry horizontally in the boxhead of the table reads " b " and it should read " $\log_e(b)$." Likewise, " $SE(b)$ " should read " $SE[\log_e(b)]$."

The table should read as follows:

	n	a	$\log_e(b)$	$SE(a)$	$SE[\log_e(b)]$	r^2
Female (all)	1025	2.98	-15.71	0.02	0.10	0.96
Females (mature)	802	2.65	-13.85	0.04	0.21	0.86
Females (immature)	223	2.85	-15.10	0.05	0.23	0.95
Males (all)	1055	2.89	-15.39	0.02	0.12	0.94
Males (mature)	931	2.97	-15.80	0.02	0.13	0.94
Males (immature)	124	2.58	-13.81	0.10	0.50	0.85

Abstract—Horseshoe crabs (*Limulus polyphemus*) are valued by many stakeholders, including the commercial fishing industry, biomedical companies, and environmental interest groups. We designed a study to test the accuracy of the conversion factors that were used by NOAA Fisheries and state agencies to estimate horseshoe crab landings before mandatory reporting that began in 1998. Our results indicate that the NOAA Fisheries conversion factor consistently overestimates the weight of male horseshoe crabs, particularly those from New England populations. Because of the inaccuracy of this and other conversion factors, states are now mandated to report the number (not biomass) and sex of landed horseshoe crabs. However, accurate estimates of biomass are still necessary for use in prediction models that are being developed to better manage the horseshoe crab fishery. We recommend that managers use the conversion factors presented in this study to convert current landing data from numbers to biomass of harvested horseshoe crabs for future assessments.

Prosomal-width-to-weight relationships in American horseshoe crabs (*Limulus polyphemus*): examining conversion factors used to estimate landings

Larissa J. Graham (contact author)¹

Mark L. Botton²

David Hata¹

Robert E. Loveland³

Brian R. Murphy¹

Email address for contact author: Ljg85@cornell.edu

¹ Department of Fisheries and Wildlife Sciences
Virginia Polytechnic Institute and State University
100 Cheatham Hall
Blacksburg, Virginia 24061

Present address for contact author: New York Sea Grant
Stony Brook University
146 Suffolk Hall
Stony Brook, New York 11794-5002

² Department of Natural Sciences
Fordham University, College at Lincoln Center
113 West 60th Street
New York, New York 10023

³ Department of Ecology, Evolution, and Natural Resources
Cook College, Rutgers University
New Brunswick, New Jersey 08901

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Horseshoe crabs (*Limulus polyphemus*) are considered a multiple-use resource. They are valued by many stakeholders, including the commercial fishing industry, biomedical companies, and environmental interest groups (Berkson and Shuster, 1999). Horseshoe crabs are commercially harvested and sold as bait for whelk (*Busycon* spp. and *Busycotypus* spp.) and American eel (*Anguilla rostrata*) fisheries. This species is also gathered for biomedical companies because its copper-containing blood is used to create a pharmaceutical product, *Limulus* amoebocyte lysate (LAL) that is used to detect pathogenic endotoxins on medical devices and in injectable drugs (Novitsky, 1984; Mikkelsen, 1988; Levin et al., 2003). The mortality associated with the handling and bleeding of horseshoe crabs is minimized (i.e., 8–20% [Rudloe, 1983; Kurz and James-Pirri, 2002; Walls and Berkson, 2003; Hurton and Berkson, 2004]) because the animals are

required to be returned to the water within 72 hours. Horseshoe crabs are ecologically important because their eggs serve as a food source for migrating shorebirds most notably in Delaware Bay (Tsipoura and Burger, 1999; Botton et al., 2003; Karpanty et al., 2006; Haramis et al., 2007).

In 1998, a fishery management plan was developed for the horseshoe crab. However, before this plan, most states did not require the mandatory reporting of harvested horseshoe crabs. NOAA Fisheries collected commercial landing data by state, year, and gear type, but these data were incomplete and disjunct. To estimate reference period (or a basis for reductions in landing data), the Horseshoe Crab Technical Committee asked state agencies to provide their best estimate of the number of horseshoe crabs harvested before 1998. These numbers were converted to pounds using various conversion factors. The number of horseshoe

crabs harvested in Delaware and Virginia waters were converted to biomass using conversion factors derived from fishery-independent and fishery-dependent data (i.e., Delaware: 1.05 kg/male, 2.32 kg/female, 1.69 kg/combined catch; Virginia: 1.8 kg/horseshoe crab or 2.27 kg/horseshoe crab depending on the composition of the catch). The landing data from all other states were converted to pounds using a NOAA Fisheries conversion factor (i.e., 1.21 kg/horseshoe crab). These data have since been used to generate estimates of total landings, to set state-by-state quotas, and to manage the stock (Fig. 1).

Once the horseshoe crab fishery management plan was initiated, all landings were required to be reported by sex, harvest method, and the number and pounds of harvested horseshoe crabs. However, many fishermen reported their catch in numbers of harvested horseshoe crabs, and state agencies used conversion factors to convert harvests from numbers to pounds. Because of the uncertainty in these conversion factors and resulting biomass estimates, state agencies are no longer required to report the pounds of horseshoe crabs landed. The Atlantic States Marine Fisheries Commission (ASMFC) and state agencies now assess and manage stocks using only the number of horseshoe crabs (not pounds) harvested.

ASMFC currently uses trend analysis to manage horseshoe crab populations, but numerous prediction models are being developed for future, more accurate management. For some of these models, landing data are required to be reported in pounds, not numbers. Because all state landings are currently reported by numbers of landed horseshoe crabs, conversion factors need to be derived to estimate pounds of landed

horseshoe crabs. The availability of accurate conversion factors will serve as a factor in choosing an appropriate model to better manage horseshoe crab populations.

The objective of our study was to derive prosomal-width-to-weight equations to calculate alternative sex-specific conversion factors based on the average width of horseshoe crabs from each state. We also tested the NOAA Fisheries conversion factor by comparing the observed total biomass of horseshoe crabs to the total biomass that was estimated with the conversion factor.

Materials and methods

Data collection

Data were collected during three spawning surveys in the Mid-Atlantic (i.e., Delaware Bay, NJ, sampled in 1997 and 2000 [$n=379$]; Raritan Bay, NJ, sampled in 1988 [$n=297$]) and southern New England (i.e., Great Bay, NH, sampled in 1988 [$n=131$]) and from the Delaware commercial fishery (i.e., Delaware Bay, DE, sampled in 1999, 2003, and 2004 [$n=348$]) (Fig. 2). The sex, prosomal width (PW; to the nearest 1 mm), and weight (to the nearest 10 g) were recorded from a sample of individuals that were collected from the vicinity of each breeding beach. During spawning surveys, animals were collected as either mated pairs (a male coupled to a female) or as unpaired (or satellite males) because previous studies (Botton and Loveland, 1989) have shown that there is no significant size difference between unattached males within a population. The majority of the samples collected from the commercial

fishery were harvested by hand during spawning events. All samples were mature individuals because only mature horseshoe crabs visit beaches during spawning events.

Measurements also were recorded for horseshoe crabs in coastal waters (i.e., within 12 nautical miles from shore) between New York and Virginia (Fig. 2). In September, October, and November of 2005 and 2006, 743 individuals were collected and measured during the Horseshoe Crab Research Center (HCRC) trawl survey (for methods see Hata and Berkson, 2004). In June of 2006, an additional 182 horseshoe crabs were sampled aboard a commercial trawl vessel harvesting crabs for a biomedical company off the coast of Ocean City, Maryland. Trawling gear, specifically a flounder net, was used to collect all horseshoe

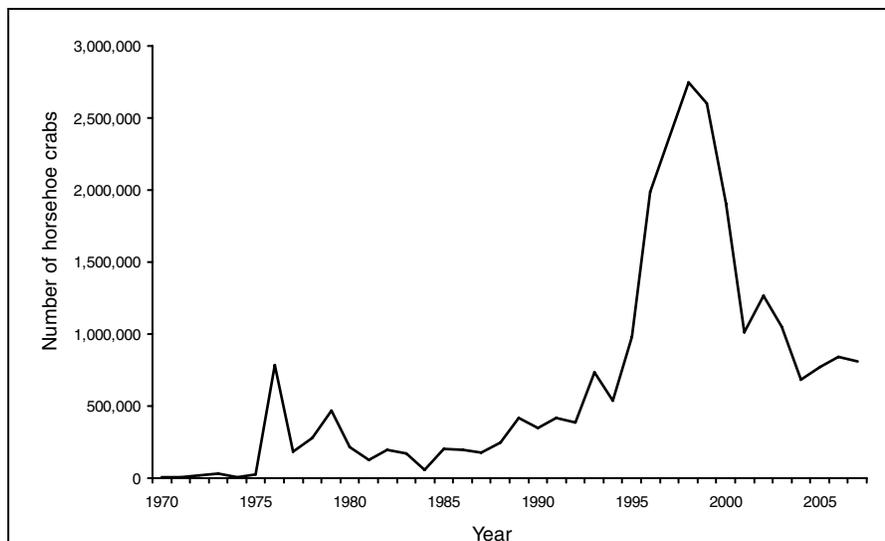
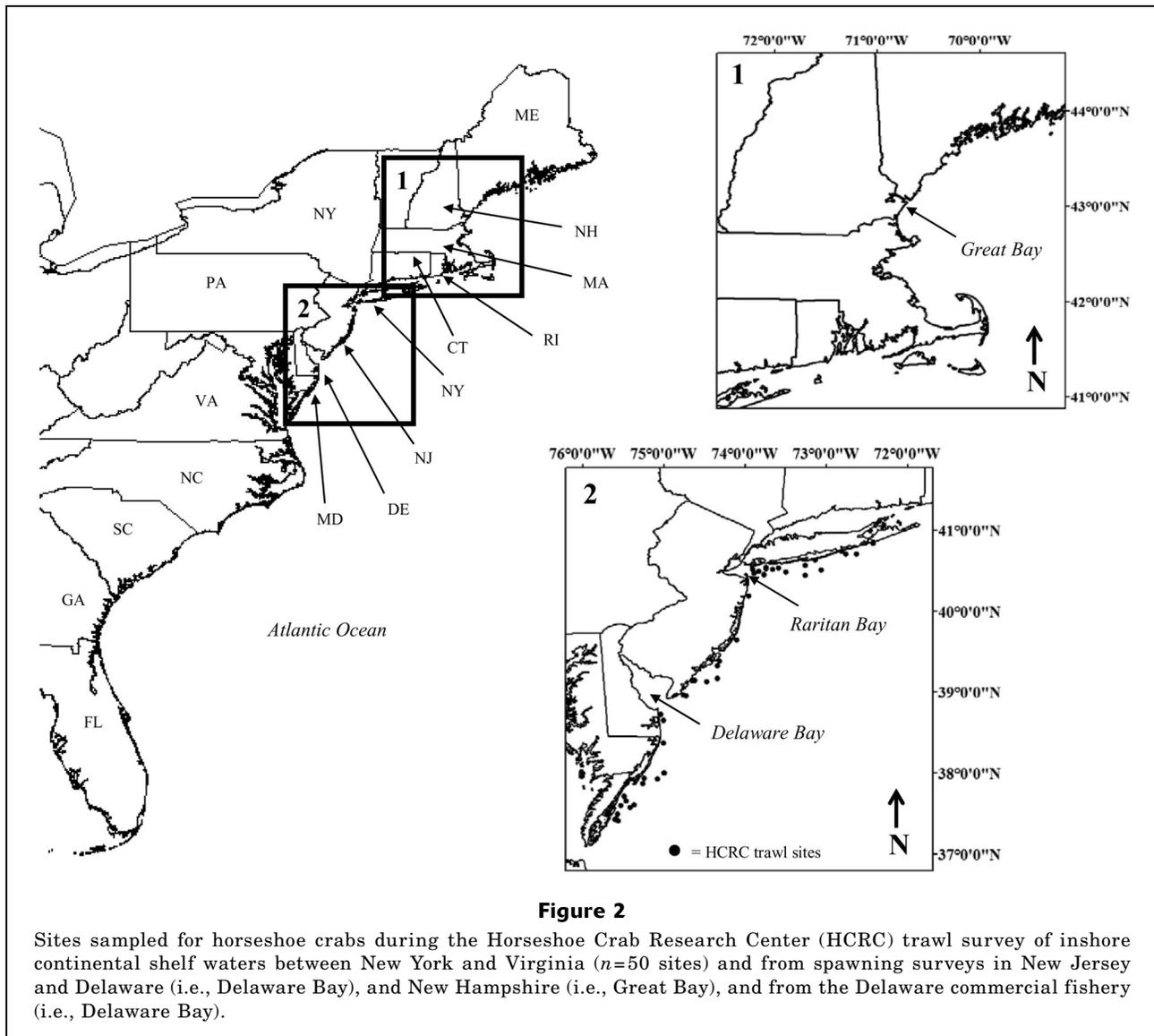


Figure 1

Commercial horseshoe crab (*Limulus polyphemus*) landings between 1970 and 2007. Landings before 1998 were reported in pounds of horseshoe crabs and were converted to numbers of horseshoe crabs using various conversion factors.



crabs. The ground gear on the flounder net was modified with a Texas sweep, which has a chain line instead of a footrope, to effectively sample horseshoe crabs (Hata and Berkson, 2003; Hata and Berkson, 2004). We recorded prosomal width (to the nearest 1 mm), weight (to the nearest 10 g), sex, and maturity stage for all or a subsample of horseshoe crabs at each site. Maturity stage was classified into two groups: immature and mature. Male horseshoe crabs without modified pedipalps (claspers) were considered immature and those with modified pedipalps were considered mature (Hata and Berkson, 2004). Females with mating scars (i.e., indentations and abrasions on the dorsal surface of the opisthosoma resulting from the attached male) were categorized as mature. Maturity stage in newly molted females is not morphologically distinct, therefore some individuals had to be probed with an awl for evidence of eggs and determine the

stage of maturity (Leschen et al., 2006). Females with eggs were categorized as mature (Hata and Berkson, 2004).

Prosomal-width-to-weight relationship

We log-transformed the PW and weight measurements collected during the HCRC trawl survey and used a general linear model (PROC GLM, SAS, vers. 9.1, SAS Inst., Inc., Cary, NC) to test for significant differences in the PW, weight, and PW–weight relationship between sexes and maturity stages. The P -value of each family of comparisons was adjusted using a Bonferroni correction to protect the experimental-wise error rate.

We combined all data (i.e., three spawning surveys, Delaware commercial fishery, HCRC trawl survey) to develop PW–weight regression equations for each group (i.e., mature males, mature females, immature males,

and immature females) of horseshoe crabs using the form

$$\log_e(Wt) = \log_e(PW) \cdot \alpha + \log_e(b), \quad (1)$$

where Wt = weight of a horseshoe crab (kg);

PW = prosomal width (mm);

α = slope; and

b = y-intercept (PROC REG, SAS).

We could not develop equations for each group of horseshoe crabs by state because of the small sample size collected from some states.

Testing current and developing alternative conversion factors

The predictive accuracy of the NOAA Fisheries conversion factor was tested using data collected from four data sets: the three spawning surveys and the Delaware commercial fishery. We calculated total biomass for each sample using the NOAA Fisheries conversion factor and then compared it to the total observed biomass for each sample.

We used various data sets (i.e., three spawning surveys, the Delaware commercial fishery, the HCRC trawl survey, unpublished data) and previously published studies to generate the average PW and weight for male and female horseshoe crabs from each state (Table 1). For some states, the average weight of horseshoe crabs was not available, and therefore we used the PW -weight equations that were derived from this study to estimate the average weight of horseshoe crabs based on an average measured prosomal width. For states where average weight data were available, we compared the observed weight to the estimated weight (i.e., using PW -weight equation) to determine the accuracy of the PW -weight equations.

Results

Prosomal-width-to-weight relationship

The average weight differs between male and female horseshoe crabs. Mature female horseshoe crabs were significantly larger (i.e., prosomal width; $df=1, 346$; $F=1488.03$; $P<0.0001$) and heavier ($df=1, 346$; $F=2245.72$; $P<0.0001$) than mature male horseshoe crabs. The weight of horseshoe crabs was significantly different among sex and maturity stages ($df=7, 924$; $F=6.86$; $P=0.0090$; Table 2). Significant differences did not occur in the PW -weight relationship of mature male and mature female horseshoe crabs ($df=3, 577$; $F=2.19$; $P=0.1396$; Table 2); however, when comparing only horseshoe crabs of overlapping size ranges ($PW=181$ – 292 mm; weight= 0.88 – 3.14 kg), the PW -weight relationship of mature female horseshoe crabs was significantly different than that of mature males ($df=3, 626$; $F=8.21$; $P=0.0043$).

Separate PW -weight equations were developed for all females, mature females, immature females, all males, mature males, and immature males (Table 3). The derived PW -weight equations were used to estimate an average weight of horseshoe crabs from each state based on the observed prosomal width (Table 1). However, we used only the PW -weight equation derived for mature horseshoe crabs (i.e., one for mature males and one for mature females) to estimate weight because the PW -weight relationship was significantly different between sexes of mature horseshoe crabs, and the commercial fishery is directed only at mature horseshoe crabs. The estimated average weight of both male and female horseshoe crabs with the derived PW -weight equations was relatively accurate compared to the observed average weight for each state (Table 1).

Testing current and developing alternative conversion factors

The conversion factor used by NOAA Fisheries (i.e., 1.21 kg/horseshoe crab) consistently overestimated the total weight of horseshoe crabs collected during spawning surveys and from the Delaware commercial fishery (Table 4). For female horseshoe crabs from Mid-Atlantic populations (i.e., Delaware Bay and Raritan Bay), this conversion factor provided a relatively close estimate of total weight. However, when estimating the total weight of male horseshoe crabs, the NOAA Fisheries conversion factor overestimated total weight. The weight of horseshoe crabs from the New England population (i.e., Great Bay) was overestimated to the greatest degree, by more than 70% for both males and females.

The average weight of a horseshoe crab also varies by location. Horseshoe crabs between Rhode Island and South Carolina are larger and heavier than horseshoe crabs from Maine, New Hampshire, Massachusetts, and Florida; and the conversion factors that have been used by most states reflect the differences in size and weight among states (Table 1). For those states where a single conversion factor has been used in the past to estimate the weight for both male and female horseshoe crabs (i.e., Maine, Rhode Island, Virginia, North Carolina, South Carolina, and Florida), the weight of at least one sex, in most cases the weight of female horseshoe crabs (Table 4) has been predicted inaccurately. Most states in the Mid-Atlantic have derived two conversion factors (i.e., one for each sex) that are relatively close to the average weight of mature horseshoe crabs collected within that area (Table 1).

Discussion

Female horseshoe crabs are much larger than male horseshoe crabs; therefore separate conversion factors should be used for each sex. Our results indicate that horseshoe crabs exhibit considerable sexual size dimorphism with mature female horseshoe crabs being significantly larger and heavier than males. Males in any

Table 1

Sample size, mean, and range of the proosomal width (PW) and weight (Wt) of mature horseshoe crabs (*Limulus polyphemus*) sampled along the Atlantic coast of the United States. Samples were collected during the Horseshoe Crab Research Center trawl survey, from the commercial fishery, or during spawning surveys, unless otherwise noted. The conversion factors (CF) that were previously used by each state to convert landing data are also listed (an asterisk indicates areas where the NOAA Fisheries conversion factor is used). The weight of each sample was also estimated (Est. Wt) using the PW-weight equations derived in this study.

State (specific location)	n (PW)	n (Wt)	Mean PW in mm (range)	Previously used CF (kg)	Mean Wt in kg (range)	Est. Wt (kg)
Males						
Maine (Medonak River) ¹	17	—	158 (139–182)	1.21*	—	0.47
Maine (Damariscotta River) ¹	14	—	144 (129–163)	1.21*	—	0.35
Maine (Casco Bay) ¹	4	—	140 (129–146)	1.21*	—	0.33
New Hampshire (Great Bay)	199	199	127 (108–159)	0.25	0.23 (0.14–0.44)	0.24
New Hampshire (Great Bay) ¹	11	—	136 (121–152)	0.25	—	0.30
Massachusetts (Plum Island Sound) ¹	552	—	118 (97–140)	—	—	0.20
Massachusetts (Barnstable Harbor) ¹	32	—	166 (123–212)	—	—	0.54
Massachusetts (Monomoy National Wildlife Refuge, Cape Cod) ²	909	—	188 (135–287)	—	—	0.78
Massachusetts (Pleasant Bay) ¹	288	—	168 (137–222)	—	—	0.56
Massachusetts (Pleasant Bay, Cape Cod) ²	1775	—	179 (120–235)	—	—	0.67
Massachusetts (Nauset Estuary, Cape Cod) ²	433	—	175 (134–249)	—	—	0.63
Massachusetts (Cape Cod Bay, Cape Cod) ²	2942	—	174 (119–250)	—	—	0.62
Rhode Island (Narragansett Bay) ¹	54	—	186 (159–224)	1.87	—	0.76
Connecticut (Milford, New Haven and Norwalk) ³	1760	72	195 (100–300)	—	1.06 (0.6–1.9)	0.87
New York (Inshore continental shelf)	121	121	205 (174–231)	—	0.95 (0.38–1.40)	1.01
New Jersey (Delaware Bay)	211	211	207 (160–254)	1.05	1.12 (0.51–2.04)	1.04
New Jersey (Raritan Bay)	195	195	202 (167–243)	1.05	0.99 (0.51–1.73)	0.97
New Jersey (Raritan Bay) ¹	102	—	186 (159–224)	1.05	—	0.76
New Jersey (Inshore continental shelf)	58	58	210 (177–244)	1.05	1.08 (0.62–1.76)	1.08
Delaware (Delaware Bay) ⁴	87	87	207 (175–245)	1.05	1.03 (0.61–1.53)	1.04
Delaware (Inshore continental shelf)	25	25	205 (176–225)	1.05	0.92 (0.56–1.22)	1.01
Maryland (Chesapeake Bay) ¹	142	—	179 (142–229)	0.96	—	0.67
Maryland (Inshore continental shelf)	57	57	217 (184–239)	0.96	1.14 (0.68–1.88)	1.20
Virginia (Inshore continental shelf)	58	58	207 (172–292)	0.91	1.01 (0.62–3.14)	1.04
Mid-Atlantic (New York to Virginia; Inshore continental shelf)	319	319	209 (172–292)	1.21*	1.02 (0.88–3.94)	1.07
North Carolina (Beaufort Inlet) ¹	13	—	232 (218–251)	1.36	—	1.46
South Carolina (St. Helena Sound) ¹	1	—	240	2.49	—	1.61
Florida (Bald Point and Ochlocknee) ¹	24	—	174 (154–201)	0.45	—	0.62
Florida (Sarasota Bay) ¹	122	—	141 (121–176)	0.45	—	0.33

continued

Table 1 (continued)

State (specific location)	n (PW)	n (Wt)	Mean PW in mm (range)	Previously used CF (kg)	Mean Wt in kg (range)	Est. Wt (kg)
Females						
Maine (Medomak River) ¹	15	—	201 (180–219)	1.21*	—	1.23
Maine (Damariscotta River) ¹	11	—	180 (161–202)	1.21*	—	0.92
Maine (Casco Bay) ¹	5	—	191 (172–208)	1.21*	—	1.07
New Hampshire (Great Bay)	12	12	154 (140–178)	0.80	0.61 (0.33–0.88)	0.61
New Hampshire (Great Bay) ¹	20	—	179 (154–209)	0.80	—	0.90
Massachusetts (Plum Island Sound) ¹	538	—	155 (126–199)	—	—	0.62
Massachusetts (Barnstable Harbor) ¹	13	—	214 (175–238)	—	—	1.45
Massachusetts (Monomoy National Wildlife Refuge, Cape Cod) ²	477	—	242 (186–304)	—	—	2.01
Massachusetts (Pleasant Bay) ¹	115	—	220 (186–272)	—	—	1.56
Massachusetts (Pleasant Bay, Cape Cod) ²	298	—	229 (170–295)	—	—	1.73
Massachusetts (Nauset Estuary, Cape Cod) ²	256	—	234 (185–292)	—	—	1.83
Massachusetts (Cape Cod Bay, Cape Cod) ²	759	—	227 (161–285)	—	—	1.69
Rhode Island (Narragansett Bay) ¹	288	—	240 (201–300)	1.87	—	1.96
Connecticut (Milford, New Haven and Norwalk) ³	1145	71	249 (150–370)	—	2.56 (1.6–3.9)	2.16
New York (Inshore continental shelf)	136	136	262 (219–321)	—	2.53 (1.40–3.94)	2.47
New Jersey (Delaware Bay)	168	168	264 (220–314)	2.32	2.66 (1.02–4.25)	2.53
New Jersey (Raritan Bay)	102	102	254 (207–311)	2.32	2.27 (1.39–3.83)	2.28
New Jersey (Raritan Bay) ¹	56	—	291 (243–351)	2.32	—	3.27
New Jersey (Inshore continental shelf)	41	41	269 (220–304)	2.32	2.66 (1.56–3.84)	2.65
Delaware (Delaware Bay) ⁴	261	261	267 (225–325)	2.32	2.42 (1.48–4.40)	2.60
Delaware (Inshore continental shelf)	3	3	251 (225–272)	2.32	2.23 (1.50–2.64)	2.21
Maryland (Chesapeake Bay) ¹	62	—	291 (243–351)	2.25	—	3.27
Maryland (Inshore continental shelf)	30	30	270 (218–320)	2.25	2.73 (1.46–3.90)	2.68
Virginia (Inshore continental shelf)	40	40	260 (181–306)	0.91	2.35 (0.88–3.82)	2.42
Mid-Atlantic (New York to Virginia; Inshore continental shelf)	259	259	264 (181–321)	1.21*	2.55 (0.38–3.14)	2.53
North Carolina (Beaufort Inlet) ¹	4	—	329 (321–340)	1.36	—	4.52
South Carolina (St. Helena Sound) ¹	3	—	325 (308–335)	2.49	—	4.38
Florida (Bald Point and Ochlocknee) ¹	17	—	231 (208–272)	0.45	—	1.77

¹ Shuster (1979).² James-Pirri et al. (2005).³ J. Mattei and M. Beekey. Unpubl. data. 2006. Sacred Heart University, 5151 Park Ave., Fairfield, CT 06825.⁴ S. Michels. Unpubl. data. 1999, 2003, 2004. Delaware Fish and Wildlife, P.O. Box 330, Little Creek, DE 19961.

Table 2

General linear model F -values and P -values for horseshoe crabs (*Limulus polyphemus*) that were collected during the Horseshoe Crab Research Center trawl survey which sampled inshore continental shelf waters between New York and Virginia. Values are listed for all horseshoe crabs combined, immature and mature females, immature and mature males, mature females and males, and immature females and males. The prosomal-width(PW)-to-weight relationship was analyzed for various combinations of sex and maturity stage (*Mat*). Significant interactions, after Bonferroni adjustment, are indicated by an asterisk.

Variable	All data (df=7, 924; n=925)		Mature females vs. Immature females (df=3, 481; n=482)		Mature males vs. Immature males (df=3, 442; n=443)		Immature females vs. Immature males (df=3, 346; n=347)		Mature females vs. Mature males (df=3, 577; n=578)	
	F	P	F	P	F	P	F	P	F	P
<i>PW</i>	3770.45	<0.0001*	2490.51	<0.0001*	1456.77	<0.0001*	2849.41	<0.0001*	2056.93	<0.0001*
<i>Sex</i>	0.00	0.9866	—	—	—	—	6.17	0.0135*	3.46	0.0635
<i>Mat</i>	0.20	0.6582	1.46	0.2271	5.61	0.0183	—	—	—	—
<i>PW</i> × <i>Sex</i>	1.16	0.2815	—	—	—	—	6.76	0.0097*	2.19	0.1396
<i>PW</i> × <i>Mat</i>	1.59	0.2075	0.98	0.3234	5.51	0.0194	—	—	—	—
<i>Sex</i> × <i>Mat</i>	6.86	0.0090*	—	—	—	—	—	—	—	—
<i>PW</i> × <i>Sex</i> × <i>Mat</i>	6.18	0.0131	—	—	—	—	—	—	—	—

Table 3

The number of individuals sampled (n), coefficient values (a , b), standard errors for coefficients ($SE[a]$, $SE[b]$), and correlation coefficient (r^2) of the relationship between prosomal width and weight for horseshoe crabs (*Limulus polyphemus*), $\log_e(Wt) = \log_e(PW \times a + \log_e(b))$. Samples were collected during the Horseshoe Crab Research Center trawl survey (i.e., inshore continental shelf waters between New York and Virginia), spawning surveys (i.e., New Jersey, Delaware, New Hampshire), and the commercial fishery (i.e., Delaware). All regressions are significant.

	n	a	b	SE(a)	SE(b)	r^2
Female (all)	1025	2.98	-15.71	0.02	0.10	0.96
Females (mature)	802	2.65	-13.85	0.04	0.21	0.86
Females (immature)	223	2.85	-15.10	0.05	0.23	0.95
Males (all)	1055	2.89	-15.39	0.02	0.12	0.94
Males (mature)	931	2.97	-15.80	0.02	0.13	0.94
Males (immature)	124	2.58	-13.81	0.10	0.50	0.85

population average about 80% of the prosomal width of the females (Shuster, 1979) and mature females are significantly heavier than mature males because of their larger size and added weight associated with numerous eggs within their prosomas (Leschen et al., 2006). Therefore, it is inappropriate to use the same conversion factor for both sexes.

Conversion factors should also vary by state, to take into account the larger size and greater weight of horseshoe crabs in Mid-Atlantic states. Horseshoe crabs from the middle Atlantic region are significantly larger than animals from Cape Cod Bay to Maine and those from the Gulf of Mexico (Shuster, 1979). Morphometrics (Shuster, 1979; Riska, 1981), survey data on the distribution of horseshoe crabs along the continental shelf (Botton and Ropes, 1987), and population genetic studies (King et al., 2005) strongly indicate that there are geographically distinct breeding populations throughout

the range. Some intermingling of populations occurs along the middle Atlantic coast, especially from New Jersey to Virginia (Swan, 2005), where much of the trawl-based fishery has been located. Because of this geographic variation, it is inappropriate to use the same conversion factor for horseshoe crabs from all states.

The conversion factor that was used by NOAA Fisheries (i.e., 1.21 kg per horseshoe crab) to estimate reference period landing data does not accurately estimate total biomass. From our results, it seems that reference period landing data were overestimated, especially in cases where the fishery could have been male-biased. The effects of this inaccurate conversion factor could have been further magnified in areas where the average size and weight of horseshoe crabs is much smaller than that for Mid-Atlantic states, notably embayments from the northern (Cape Cod to Maine) and southern (Gulf of Mexico) parts of the distribution range of this

Table 4

The aggregate observed weight and estimated weight using the NOAA Fisheries conversion factor (i.e., 1.21 kg per animal) of horseshoe crabs (*Limulus polyphemus*) collected during spawning surveys. The percent that the NOAA Fisheries conversion factor overestimates weight is also listed.

Location	Sex	Aggregate observed weight (kg)	Aggregate estimated weight (kg)	Percent weight overestimated
New Jersey (Delaware Bay)	Female (n=168)	446	448	0.3
	Male (n=211)	237	563	58
	Total (n=379)	683	1011	32
New Jersey (Raritan Bay)	Female (n=102)	231	272	15
	Male (n=195)	192	521	63
	Total (n=297)	424	793	47
Delaware (Delaware Bay) ¹	Female (n=261)	631	697	9
	Male (n=87)	90	232	61
	Total (n=348)	721	929	22
New Hampshire (Great Bay)	Female (n=12)	7	31	77
	Male (n=119)	28	309	91
	Total (n=131)	35	341	90

¹ S. Michels. Unpubl. data. 1999, 2003, 2004. Delaware Fish and Wildlife, P.O. Box 330, Little Creek, DE 19961.

species. According to our analyses, a New England harvest, composed of mostly male horseshoe crabs, would be the worst-case scenario for overestimating landings data when measured in pounds.

To more accurately estimate reference period landings, biomass should be recalculated using state-specific conversion factors for each sex. However, determining the male-to-female ratios from landing data may be a challenge. Before 1998, participants in the fishery were not required to record the ratio of males to females among landed horseshoe crabs. It has been suggested that eel bait fishermen prefer to harvest females, because of a chemical attractant associated with the eggs (Ferrari and Targett, 2003). In contrast, both male and female horseshoe crabs were used, as available, for the whelk fishery. Unfortunately, no data are available on the percentage of horseshoe crabs landed as bait for eels versus whelks, from which one might be able to deduce the sex ratio in the early commercial catches.

Future estimates of the biomass of harvested horseshoe crabs should incorporate the sex and location of horseshoe crab harvests. Use of geographically-appropriate conversion factors for each sex would provide an accurate estimate of biomass despite the differing regulations among states. Some states have already derived their own sex-specific conversion factors, and most seem to provide an accurate representation of the average weight for male and female horseshoe crabs. States that have used one conversion factor to estimate the weight of both female and male horseshoe crabs (i.e., Maine, Rhode Island, Virginia, South Carolina, and Florida) either underestimate the weight of female horseshoe crabs or overestimate the weight of male

horseshoe crabs. Although state agencies are no longer required to report landings in number and pounds, the conversion factors that have already been derived by state agencies may serve as a useful tool for accurately converting data to be used in prediction models. For states that have not developed accurate conversion factors, the PW-weight equations derived from this study can be used to develop conversion factors based on the average width of male and female horseshoe crabs from that area. Besides providing a more accurate estimate of biomass, use of state-specific and sex-specific conversion factors is feasible for management purposes because states are already required to report the location, sex, and number of horseshoe crabs harvested.

At present, only very limited size and weight data are available for horseshoe crabs from North Carolina through northern Florida. Our PW-weight relationships for both sexes are very robust across a wide range of sizes, but could be further improved by the inclusion of horseshoe crab populations from this part of their range.

Conclusion

It is important to provide accurate biomass estimates of harvest data for future management purposes and, therefore, accurate conversion factors should be developed. From the results of this study, it seems that the most practical approach to estimating landing data is to use state-specific conversion factors, one for females and one for males, based on the average weight of horseshoe crabs from that area. Researchers should continue

to collect data on the average PW of female and male horseshoe crabs to fine tune these conversion factors. The PW-equations derived from this study can be used to estimate weight based on an average prosomal width. In this way, the accuracy of these conversion factors could be improved, thereby providing better data for future management assessments.

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Literature cited

- Berkson, J. and C. N. Shuster.
1999. The horseshoe crab: the battle for a true multiple-use resource. *Fisheries* 24:6–10.
- Botton, M. L., B. A. Harrington, N. Tspoura, and D. Mizrahi.
2003. Synchronies in migration: Shorebirds, horseshoe crabs, and Delaware Bay. *In* The American horseshoe crab (C. N. Shuster Jr., R. B. Barlow, and H. J. Brockmann, eds.), p. 5–32. Harvard Press, Cambridge, MA.
- Botton, M. L., and R. E. Loveland.
1989. Reproductive risk: high mortality associated with spawning by horseshoe crabs (*Limulus polyphemus*) in Delaware Bay, USA. *Mar. Biol.* 101:143–151.
- Botton, M. L., and J. W. Ropes.
1987. Populations of horseshoe crabs, *Limulus polyphemus*, on the northwestern Atlantic continental shelf. *Fish. Bull.* 85:805–812.
- Ferrari, K. M., and N. M. Targett.
2003. Chemical attractants in horseshoe crab, *Limulus polyphemus*, eggs: The potential for an artificial bait. *J. Chem. Ecol.* 29:477–496.
- Haramis, G. M., W. A. Link, P. C. Osenton, D. B. Carter, R. G. Weber, N. A. Clark, M. A. Teece, and D. S. Mizrahi.
2007. Stable isotope and pen feeding trial studies confirm value of horseshoe crab eggs to spring migrant shorebirds in Delaware Bay. *J. Avian Biol.* 37:367–376.
- Hata, D., and J. Berkson.
2003. Abundance of horseshoe crabs (*Limulus polyphemus*) in the Delaware Bay area. *Fish. Bull.* 101:933–938.
2004. Factors affecting horseshoe crab *Limulus polyphemus* trawl survey design. *Trans. Am. Fish. Soc.* 133:292–299.
- Hurton, L., and J. Berkson.
2004. Potential causes of mortality for horseshoe crabs (*Limulus polyphemus*) during the biomedical bleeding process. *Fish. Bull.* 104:293–298.
- James-Pirri, M. J., K. Tuxbury, S. Marino, and S. Koch.
2005. Spawning densities, egg densities, size structure, and movement patterns of spawning horseshoe crabs, *Limulus polyphemus*, within four coastal embayments on Cape Cod, Massachusetts. *Estuaries* 20:296–313.
- Karpanty, S. M., J. D. Fraser, J. Berkson, L. J. Niles, A. Dey, and E. P. Smith.
2006. Horseshoe crab eggs determine red knot distribution in Delaware Bay. *J. Wildl. Manag.* 70:1704–1710.
- King, T. L., M. S. Eackles, A. P. Spidle, and H. J. Brockmann.
2005. Regional differentiation and sex-based dispersal among populations of horseshoe crabs *Limulus polyphemus*. *Trans. Am. Fish. Soc.* 134:441–465.
- Kurz, W., and M. J. James-Pirri.
2002. The impact of biomedical bleeding on horseshoe crab, *Limulus polyphemus*, movement patterns on Cape Cod, Massachusetts. *Mar. Freshw. Behav. Physiol.* 35:261–268.
- Leschen, A. S., S. P. Grady, and I. Valiela.
2006. Fecundity and spawning of the Atlantic horseshoe crab, *Limulus polyphemus*, in Pleasant Bay, Cape Cod. *Mar. Ecol.* 27:54–65.
- Levin, J., H. D. Hochstein, and T. J. Novitsky.
2003. Clotting cells and *Limulus* amoebocyte lysate: an amazing analytical tool. *In* The American horseshoe crab (C. N. Shuster, R. B. Barlow, H. J. Brockmann, eds.), p. 310–340. Harvard Univ. Press, Cambridge, MA.
- Mikkelsen, T.
1988. The secret in the blue blood. Science Press, Beijing, China.
- Novitsky, T. J.
1984. Discovery to commercialization: the blood of the horseshoe crab. *Oceanus* 27:13–18.
- Riska, B.
1981. Morphological variation in the horseshoe crab *Limulus polyphemus*. *Evolution* 35:647–658.
- Rudloe, A.
1983. The effect of heavy bleeding on mortality of the horseshoe crab, *Limulus polyphemus*, in the natural environment. *J. Invertebr. Pathol.* 42:167–176.
- Shuster, C. N. Jr.
1979. Distribution of the American horseshoe “crab,” *Limulus polyphemus* (L.). *In* Biomedical applications of the horseshoe crab (Limulidae) (E. Cohen, ed.), p. 3–26. Alan R. Liss Inc., New York.
- Swan, B. L.
2005. Migrations of adult horseshoe crabs, *Limulus polyphemus*, in the Middle Atlantic Bight: a 17-year tagging study. *Estuaries and Coasts* 28:28–40.
- Tspoura N., and J. Burger.
1999. Shorebird diet during spring migration stopover on Delaware Bay. *Condor* 101:635–644.
- Walls, E. A., and J. Berkson.
2003. Effects of blood extraction on horseshoe crabs (*Limulus polyphemus*). *Fish. Bull.* 101:457–459.