Contributed Paper

A Contemporary, Sex-Limited Change in Body Size of an Estuarine Turtle in Response to Commercial Fishing

MATTHEW E. WOLAK,*‡ GEORGE W. GILCHRIST,† VICTORIA A. RUZICKA,* DANIEL M. NALLY,* AND RANDOLPH M. CHAMBERS*

*W.M. Keck Environmental Field Laboratory, College of William and Mary, Williamsburg, VA 23187, U.S.A.
†Department of Biology, College of William and Mary, Williamsburg, VA 23187, U.S.A.

Abstract: *Juvenile growth rate and adult body size are important components of life-history strategies because of their direct impact on fitness. The diamondback terrapin (*Malaclemys terrapin*) is a sexually dimorphic, long-lived turtle inhabiting brackish waters throughout the Atlantic and Gulf coasts of the United States. In parts of its range, terrapins face anthropogenically imposed mortality: juveniles of both sexes inadvertently enter commercial crab traps and drown. For adult females, the carapace eventually grows large enough that they cannot enter traps, whereas males almost never reach that critical size. We compared age structure, carapace dimensions, growth curves, and indices of sexual dimorphism for a Chesapeake Bay population of terrapins (where mortality of turtles is high due to crab traps) with contemporary terrapins from Long Island Sound and museum specimens from Chesapeake Bay (neither group subject to commercial crab traps). We also calculated the allochronic and synchronic rates of evolutionary change (haldanes) for males and females to measure the rate of trait change in a population or between populations, respectively. We found a dramatic shift to a younger male age structure, a decrease in the length of time to terminal female carapace size, a 15% increase in female carapace width, and an increase in sexual dimorphism in Chesapeake Bay. In a new twist, our results implicate a fishery in the selective increase in size of a reptilian bycatch species. These sex-specific changes in life history and demography have implications for population viability that need to be considered when addressing conservation of this threatened turtle.*

Keywords: anthropogenic selection, haldanes, fisheries, *Malaclemys terrapin*, rapid evolution, sexual dimorphism, size-selective mortality.

Un Cambio Contemporáneo, Limitado por el Sexo, en el Tamaño Corporal de una Tortuga Estuarina en Respuesta a la Pesca Comercial

Resumen: *La tasa de crecimiento de juveniles y el tamaño corporal de adultos son componentes importantes de las estrategias de historia de vida debido a su impacto directo sobre la eficacia biológica. La tortuga* Malaclemys terrapin *es una especie longeva, dimórfica sexualmente, que habita aguas salobres a lo largo de las cosas del Atlántico y Golfo de México de Estados Unidos. En algunas partes de su distribución, las tortugas enfrentan mortalidad de origen antropogénico: juveniles de ambos sexos entran inadvertidamente a trampas para cangrejos y se ahogan. En hembras adultas, el carapacho eventualmente crece lo suficiente y no pueden entrar a las trampas, mientras que los machos casi nunca alcanzan esa talla crítica. Comparamos la estructura de edades, dimensiones del carapacho, curvas de crecimiento e índices de dimorfismo sexual en una población de la Bahía de Chesapeake (donde la mortalidad de tortugas es alta debido a las trampas para cangrejos) con tortugas contemporáneas del Estrecho de Long Island y con especímenes de museo provenientes de la Bahía*

de Chesapeake (ningún grupo sujeto a las trampas comerciales para cangrejos). También calculamos las tasas alocrónicas y sincrónicas de cambio evolutivo (haldanes) para machos y hembras para medir la tasa de cambio en los atributos de una población o entre poblaciones, respectivamente. También encontramos un cambio dramático a una estructura de edades de machos más jóvenes, descenso en el tiempo al tamaño terminal del carapacho de hembras, incremento de 15% en la anchura del carapacho de hembras e incremento en el dimorfismo sexual en la Bahía de Chesapeake. Desde otra perspectiva, nuestros resultados implican a una pesquería en el incremento selectivo del tamaño de una especie de reptil capturada incidentalmente. Estos cambios sexo-específicos en la historia de vida y demografía tienen implicaciones para la viabilidad poblacional que requieren ser considerados al abordar la conservación de esta tortuga amenazada.

Palabras Clave: Dimorfismo sexual, evolución rápida, haldanes, *Malaclemys terrapin*, mortalidad selectiva por talla, pesquerías, selección antropogénica

Introduction

Commercial fisheries exert demographic pressures on target species by selectively harvesting the most marketable age or size classes, generally driving populations toward smaller body size and earlier sexual maturity (Conover & Munch 2002; Lipcius & Stockhausen 2002; Ernande et al. 2004). Nevertheless, discriminating between plastic and evolved shifts in body size is difficult for most wild species (Conover 2000; Fenberg & Roy 2008), although several cases of "contemporary microevolution" (e.g., Grant & Grant 1995; Hendry & Kinnison 1999; Kinnison & Hendry 2001) demonstrate phenotypic and life-history responses to natural selection over relatively few generations. One unintended consequence of the selective harvest is bycatch (i.e., the killing of nontarget species). We argue that bycatch mortality may not be random, such that selection may also be occurring in a bycatch species and have potential consequences for demography and population viability similar in scope to those of the target species.

Body size is a highly heritable fitness character that influences a variety of reproductive fitness components (Roff 1992; Stearns 1992). Male and female body sizes may have different adaptive optima that favor the evolution of sexual size dimorphism (Fairbairn 2007), which can range from subtle to extreme (Owens & Hartley 1998; Blanckenhorn 2005). In such cases, size-selective fisheries can create sex-biased selection that can further shift the sexual dimorphism in the population (Allendorf & Hard 2009).

We documented how fishery-induced selection may affect body size and sexual size dimorphism in a Chesapeake Bay population of diamondback terrapins (*Malaclemys terrapin*). A population model of terrapins from Rhode Island (Mitro 2003) generally supports the results from models of three other turtle species, which indicate that increasing adult mortality (e.g., fisheries-caused mortality) has a detrimental effect on long-term population viability (Crouse et al. 1987; Congdon et al. 1993, 1994). Terrapins, specifically, are extremely susceptible to population declines because of their unique life-history characteristics of delayed sexual maturity, long life span, low reproductive rate, and strong site fidelity (Congdon et al. 1993; Seigel & Gibbons 1995; Tucker et al. 2001). Documented declines in terrapins (Seigel & Gibbons 1995) mirror the more-widespread trend for human-caused population declines in reptiles (Gibbons et al. 2000). Therefore, an important step in terrapin conservation is to elucidate the way in which fishery-induced selection changes a population in order to identify effective management strategies for terrapins.

Terrapins in parts of Chesapeake Bay share their habitat with over a million commercial crab traps that are deployed to harvest blue crabs (*Callinectes sapidus*). Bait inside a completely submerged trap encourages crabs (Lipcius & Stockhausen 2002) and terrapins (e.g., Bishop 1983) to crawl through the trap's narrow openings. Once trapped, the turtles drown. The rate of capture of males and females differs. Female carapaces eventually grow wider than the trap openings; however, the smaller males rarely attain a large enough size to prevent entry (Roosenburg et al. 1997). Thus, terrapin mortality from crab traps has the potential to change terrapin body size and correlated life-history characters (Dorcas et al. 2007).

We hypothesized that size-selective mortality changes the size distribution of terrapins in areas where crab traps are deployed. Specifically, we predicted that females at a contemporary Chesapeake Bay (CCB) site, where crab traps have been deployed for approximately 60 years (10–20 generations), should have a larger terminal carapace width, due primarily to size-selective mortality, than contemporary females from Long Island Sound (LIS), where commercial crabbing has never occurred. We tested the timing of this potential change by comparing contemporary populations with museum specimens from Chesapeake Bay (HCB) collected prior to the deployment of commercial crab traps. Moreover, we also predicted a general increase in female carapace size throughout life, especially among the younger age classes in CCB, relative to the other two samples. Males, on the other hand, could respond in two different ways. First, if female size and male size were genetically correlated, one would expect to see an increase in male size in CCB, relative to the other two samples (Lande 1980), with little shift in sexual size dimorphism. Alternatively, larger males may

experience even higher mortality because smaller individuals have a higher probability of escape from crab traps (Roosenburg et al. 1997); in this case male size may remain unchanged or even be reduced in CCB, resulting in an increase in sexual size dimorphism, relative to the other two samples. We also examined the allometries between carapace width, carapace length, and body mass in these populations.

Methods

Diamondback terrapins are the only aquatic turtle inhabiting estuaries of the Atlantic and Gulf coasts of the United States (Ernst et al. 1994; Gibbons et al. 2001). We sampled terrapins from a Chesapeake Bay (CCB) population during the summers of 2005 and 2006. The population was located around the Goodwin Islands in the York River, Virginia, where commercial crabbing is extensive. We compared this population with terrapins sampled from a contemporary LIS population during the summers of 1997–1999. The LIS population was located near the mouth of the Housatonic River, Connecticut, where commercial crabbing is absent, and represents a genetically distinct population from the CCB population (Hart 2005). Additionally, we measured historical specimens of Chesapeake Bay terrapins (HCB) from the Smithsonian Museum of Natural History Archives. These terrapins originally were collected between 1856 and 1941, corresponding to a time before the widespread use of traps in the commercial blue crab fishery (Van Engel 1962).

We used calipers to measure the maximum straight carapace length and width of individuals. Body mass of the CCB and LIS terrapins was recorded with a hanging spring scale. We estimated terrapin age by counting growth rings on an individual's carapace (each ring represents 1 year) (Dunham & Gibbons 1990; Gibbons et al. 2001; but see Litzgus & Brooks 1998). Sex was determined from the relative location of the cloaca on the tail (Tucker et al. 2001).

Statistical Analyses

All morphological variables were natural log transformed. We used principal components analysis to combine carapace length and width into a single, overall measure of size. We used linear models with sex and population as fixed effects and age as a covariate to examine geographic variation in morphological variables. We made allometric comparisons of carapace length and width and mass with a reduced major axis (RMA) regression and tested for significant slope and intercept differences with 95% confidence intervals (CIs).

We tested for changes in age structure among the populations with analysis of variance, with sex and population as fixed effects, omitting the HCB population because

it represents a composite, both geographically and temporally, of many sampled populations within the Chesapeake Bay region.

To highlight the changes in age-specific size distributions, we fitted a Gompertz function (Wright 1926; Ricklefs 1967) to estimate growth trajectories for comparison among sampling locations. The Gompertz function is

$$Y_{\text{age}} = A + Ce^{-e^{B(\text{age}-M)}}, \qquad (1)$$

where A is minimum size, $C+A$ is maximum size, M is age of maximum growth, B is growth rate, and e is the base of the natural logarithm. We fitted the Gompertz function to the data with nonlinear, least-squares regression. We then plotted the Gompertz functions for the natural log of carapace width for each sex, with a dashed line indicating the 117-mm width of the opening on the traps (Hoyle & Gibbons 2000).

We examined variation in sexual size dimorphism among populations with a sexual dimorphism index (SDI) (Lovich & Gibbons 1992; Fairbairn 2007). This index takes the ratio of the larger sex to the smaller sex and then subtracts one. By convention, the sexual dimorphism index is positive when females are the larger sex. We bootstrapped our estimates of the SDI by randomly pairing females and males (with replacement) of each age group of terrapins and then calculating the SDI for each carapace dimension in the two contemporary populations. The number of pairs within an age group was determined by the minimum count of females or males in that particular group. Then, we calculated the bootstrapped mean, standard error, and 95% CI for each morphological variable from 10,000 resamplings (Huey et al. 2006). The small sample size in each age class of the HCB sample precluded inclusion in the bootstrap. With conservative calculation of the 95% CIs, we assumed that two populations were significantly different when their bootstrapped CIs did not overlap (Huey et al. 2006).

Assuming no change in phenotypic plasticity, we estimated the synchronic rate of evolution (haldanes) of age-specific body size between the CCB and LIS populations, bootstrapping the rates 1000 times to compute confidence intervals (Hendry & Kinnison 1999). We also report the allochronic rates between the HCB sample before crab trapping and the CCB population; however, the small sample size of museum specimens did not allow bootstrapping. In both cases, we assumed a divergence time of 60 years since commercial crabbing began and estimated a generation time of 4 years. Females may not be reproductively mature until 6 to 8 years of age; however, males can probably mate at age 3 to 4 years (Lovich & Gibbons 1990). This assumption produces a minimal estimate of the rate of evolution; a longer generation time means our reported rates are conservative. Therefore, we assumed 15 generations have passed since commercial crabbing began in Chesapeake Bay (assuming

Table 1. The mean (SE) age, carapace length (CL), carapace width (CW), mass, and carapace PC1 scores of Chesapeake Bay (CCB), Long Island Sound (LIS), and historical Chesapeake Bay (HCB) terrapins used in this study.

Sex	Site	Age	CL	CW	Mass	PC1	n
F	CCB	7.4 (0.13)	201.07 (1.012)	151.91 (1.011)	1318.21 (1.038)	0.40 (0.016)	106
	LIS	7.8 (0.23)	172.51 (1.015)	136.03 (1.016)	930.23 (1.045)	0.21 (0.022)	66
	HCB	7.8 (0.40)	167.84 (1.032)	129.63 (1.028)	NA	0.16 (0.041)	21
M	CCB	5.1 (0.08)	130.15 (1.009)	98.52 (1.009)	323.23 (1.025)	−0.21 (0.012)	183
	LIS	6.0 (0.22)	124.35 (1.007)	97.59 (1.008)	349.05 (1.021)	−0.25 (0.010)	77
	HCB	5.3 (0.47)	132.26 (1.033)	100.51 (1.037)	NA	−0.19 (0.048)	10

LIS and CCB were similar in size prior to crabbing, as is supported by the limited HCB samples; Fig. 4). All analyses were performed in the statistical software R.

Results

The age structure of the contemporary Chesapeake Bay and LIS terrapin populations differed significantly because of an interaction between sex and location ($F_{1,428} = 4.68$, $p = 0.031$). No significant difference in female ages of the sampled terrapins was observed between CCB and LIS (Tukey HSD = −0.0566, 95% CI = 0.062 to −0.175); however, males from the two sites had very different age structures (Tukey HSD = −0.188, 95% CI = −0.085 to −0.291).

Female CCB mean carapace length and width appears larger than LIS or HCB (Table 1). The principal component analysis created the variable PC1 (a proxy for overall carapace size), which accounted for 99.3% of the variance. The three-way interaction between age, sex, and population was not a significant effect in the ANOVA for PC1. Because the interaction between sex and location was significant ($F_{2,453} = 10.58$, $p = 0.0000081$), we analyzed each sex separately to test for significant differences among the populations. We could not reject the null hypothesis of equal slopes among populations for either females ($F_{2,187} = 1.25$, $p = 0.288$) or males ($F_{2,264} = 2.92$, $p = 0.055$), so we compared intercepts with an analysis of covariance (Fig. 1). Female carapace size (PC1) differed significantly among sites ($F_{2,189} = 50.18$, $p < 2 \times 10^{-16}$) (Fig. 1a), and the differences between CCB
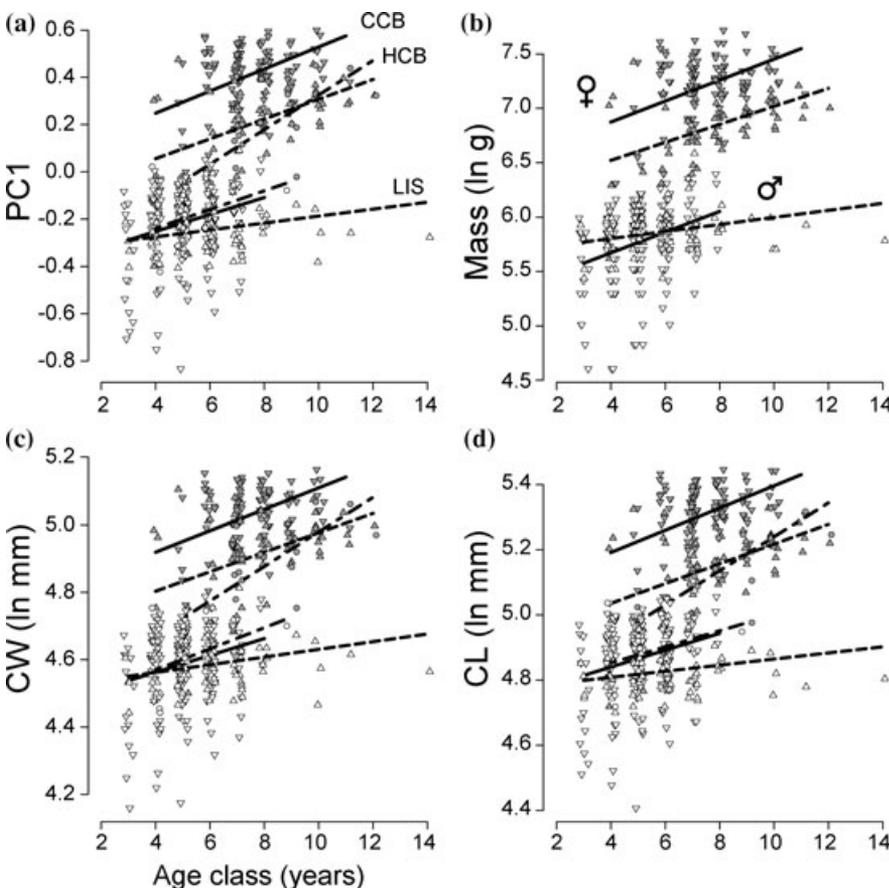

Figure 1. Linear regressions of (a) PC1, (b) mass, (c) carapace width, and (d) carapace length on age of females from contemporary Chesapeake Bay (CCB) (downward-pointing shaded triangles), Long Island Sound (LIS) (upward-pointing, shaded triangles), and historical Chesapeake Bay (HCB) (shaded circles) and males from CCB (downward pointing, open triangles) and LIS (upward pointing, open triangles) (population regression lines: CCB, solid; LIS, dashed; HCB, dot dash).

Table 2. Reduced major axis-regression coefficients of all pairwise combinations of carapace width (CW), carapace length (CL), and mass.*

Pair and sex*	Site*	Int (SE)	95% CI	Slope (SE)	95% CI	R²	df
CW vs. mass							
F	CCB	2.69 (0.069)	2.575, 2.804	0.32 (0.010)	0.309, 0.341	0.973	103
	LIS	2.52 (0.071)	2.399, 2.635	0.35 (0.010)	0.333, 0.368	0.982	64
M	CCB	2.63 (0.063)	2.529, 2.737	0.34 (0.011)	0.321, 0.357	0.940	182
	LIS	2.45 (0.137)	2.217, 2.675	0.36 (0.023)	0.326, 0.404	0.891	75
CL vs. mass							
F	CCB	2.89 (0.058)	2.796, 2.989	0.34 (0.008)	0.322, 0.349	0.982	103
	LIS	2.78 (0.056)	2.682, 2.869	0.35 (0.008)	0.334, 0.361	0.989	64
M	CCB	2.85 (0.066)	2.739, 2.956	0.35 (0.011)	0.331, 0.369	0.937	182
	LIS	2.77 (0.110)	2.591, 2.959	0.35 (0.019)	0.318, 0.381	0.928	75
CW vs. CL							
F	CCB	−0.11 (0.124)	−0.315, 0.095	0.97 (0.023)	0.929, 1.007	0.970	103
	LIS	−0.28 (0.143)	−0.522, −0.044	1.01 (0.028)	0.962, 1.055	0.975	64
	HCB	0.32 (0.280)	−0.163, 0.805	0.89 (0.055)	0.792, 0.981	0.964	19
M	CCB	−0.12 (0.102)	−0.293, 0.044	0.97 (0.021)	0.934, 1.003	0.957	182
	LIS	−0.45 (0.317)	−0.973, 0.081	1.04 (0.066)	0.933, 1.152	0.838	75
	HCB	−0.76 (0.408)	−1.520, −0.003	1.10 (0.084)	0.944, 1.255	0.977	8

**Abbreviations: CL, carapace length; CW, carapace width; F, female; M, male; Int., intercept; CCB, contemporary Chesapeake Bay; LIS, Long Island Sound; HCB, historical Chesapeake Bay.*

and both LIS (Tukey HSD: 0.20, 95% CI = 0.26 to 0.15) and HCB (Tukey HSD: 0.25, 95% CI = 0.34 to 0.17) were large. Nevertheless, the differences between LIS and HCB were insignificant (Tukey HSD: 0.052, 95% CI = 0.142 to −0.037). Male carapace size (PC1) differed among sites to a much lesser degree ($F_{2,266} = 4.26$, $p = 0.015$); the only significant pairwise difference was between CCB and LIS (Tukey HSD: 0.053, 95% CI = 0.099 to 0.006). Similar results held for the individual traits mass, carapace width, and carapace length (Figs. 1b–d).

We examined allometry of carapace size traits and mass for differences among populations sampled. The RMA regressions of all pairwise combinations of the three traits were plotted, with the exception that body mass was not available for the HCB museum samples. Allometry consistent with a more rapid increase in relative size of a trait compared with the other samples would occur if the 95% CIs of slopes did not overlap. Nevertheless, all pairwise comparisons of carapace width, carapace length, and mass scaled isometrically (Table 2).

Carapace width is the shell dimension that potentially limits access to the crab traps. On commercial crab traps, the vertical dimension of the gape in the trap can be expanded dramatically, whereas the horizontal dimension of the gape is structurally much more rigid (R.M. C., personal observation). Females from CCB appeared to attain a larger terminal size earlier than LIS or HCB females (Fig. 2a). This rapid carapace growth rate in CCB females was not observed in males, whose growth rates and terminal size were similar among all three groups (Fig. 2b).
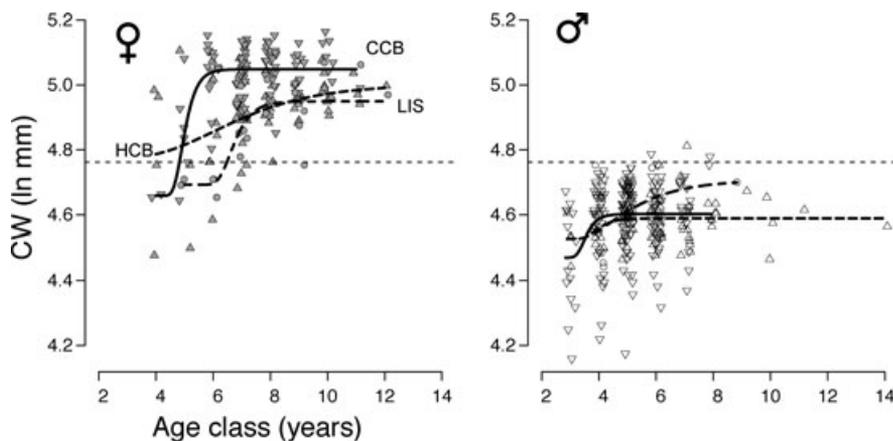

Figure 2. Gompertz growth functions of natural log-transformed carapace widths (CW) for (a) females from Chesapeake Bay (CCB) (downward-pointing shaded triangles), Long Island Sound (LIS) (upward-pointing shaded triangles), and historical Chesapeake Bay (HCB) (shaded circles), and (b) males (open symbols matching symbols from the female samples) (dashed line, natural log-transformed carapace width corresponding to the opening of crab traps [117mm]).
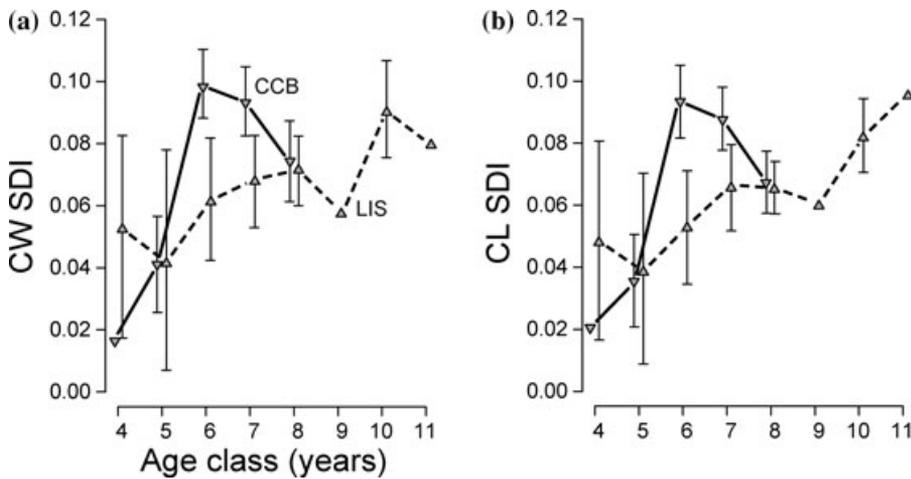
Figure 3. *Sexual size dimorphism index (SDI) of (a) carapace width (CW) and (b) carapace length (CL) across age classes. The downward-pointing shaded triangles and solid line are the CCB SDI, and the upward-pointing shaded triangles and dashed line are LIS SDI (error bars indicate bootstrapped 95% CIs).*

Figure 3 demonstrates substantial divergence in sexual size dimorphism of both carapace length and width between CCB and LIS populations from ages six to seven; the largest divergence was at age six. The mean sexual size dimorphism at ages five and eight were nearly identical in the two populations.

We emphasize that these rates of morphological change should be regarded as minimal rates because females may not reproduce until they are 6–8 years old, so one could argue for a longer generation time, hence fewer generations. The rates of morphological change were relatively stable across age classes. Females exhibited rates of 0.1 to 0.2 haldanes and males exhibited rates of 0.007 to 0.03 haldanes. We did not have enough data to bootstrap the allochronic rates, but observed values generally fell within the range of the synchronic estimates (Fig. 4).

Discussion

Diamondback terrapins in Chesapeake Bay have suffered size-selective mortality because of commercial crab traps that drown these reptiles. We found a dramatic increase in terminal size of CCB females over the last 60 years, compared with females from LIS, which has no commercial crabbing, and historical specimens from Chesapeake Bay collected prior to commercial crabbing. This change is consistent with our hypothesis of fishery-induced
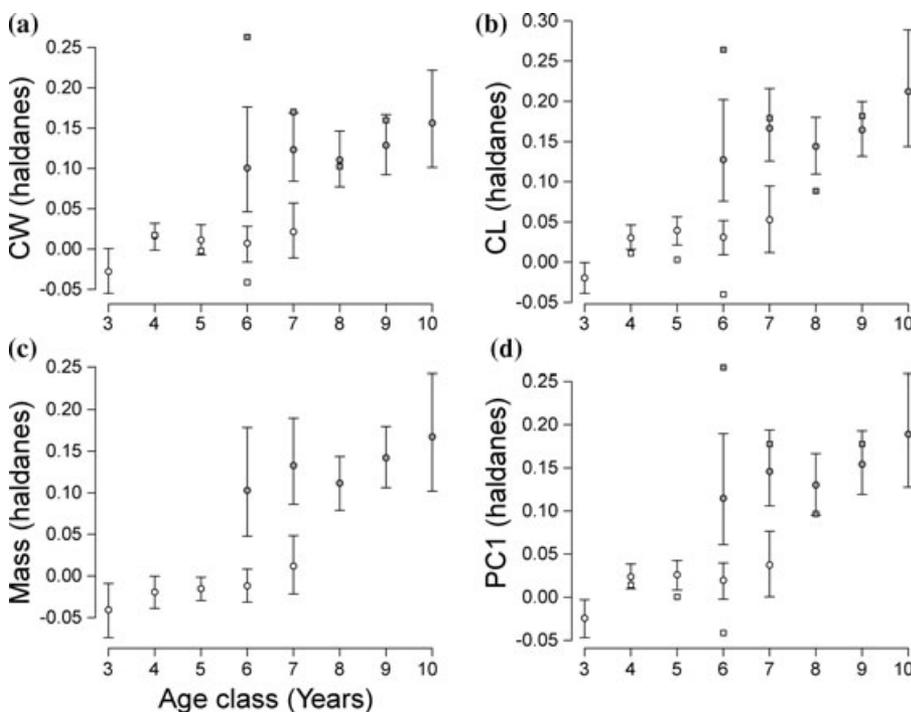

Figure 4. *Female (shaded circles) and male (open circles) synchronic rates of morphological change (haldanes) for (a) carapace width (CW), (b) carapace length (CL), (c) mass, and (d) overall carapace sizes (PC1) (error bars, bootstrapped 95%CIs; allochronic rates, square symbols, shaded for females and unshaded for males).*

size-selective mortality. The shift in female size appears to be driven by an increase in growth rate at ages four—six, which propels female carapace width beyond the dimensions of the opening of crab traps. Maximum growth rate may occur earlier for the CCB population, where immature female terrapins are still small enough to enter and drown in crab traps (e.g., Bishop 1983; Roosenburg et al. 1997; Dorcas et al. 2007). Females that grow fast to a large carapace size would be less likely to drown in a crab trap. One caveat regarding these data is the relative shortage of 4- to 5-year-old females in both CCB and LIS, which may contribute to the rapid growth rates suggested by the Gompertz equation. Males, on the other hand, virtually never outgrow the opening. Moreover, the age structure and sex ratio of the CCB populations differs from that of LIS, which suggests larger demographic changes may be taking place (Dorcas et al. 2007). Other researchers have estimated mortality from crab traps at 10–78%, with peak capture rates of females at ages four–six and males at five–six (Roosenburg et al. 1997; Dorcas et al. 2007), which suggests strong selection on carapace growth rates imposed by mortality from traps.

Interestingly, body mass, carapace width, and carapace length appear to be isometric in CCB compared with LIS (Table 2). This suggests that selection on one trait has resulted in a correlated response in the other traits (Lande & Arnold 1983). In sexually dimorphic species, larger female size is often hypothesized to have evolved in response to selection for increased fecundity (Preziosi & Fairbairn 1992). Terrapins in another tributary of Chesapeake Bay do show a significant, but weak, correlation between body size and clutch size (Roosenburg & Dunham 1997); however, the range of clutch size and mass at any one site is very large. Fecundity selection, however, does not appear to be driving the increase in size. A nesting study conducted on the CCB population (V. A. R., unpublished data) showed mean clutch size at CCB was no different than expected, given the geographic variation of other diamondback terrapin nesting studies (e.g., Seigel 1980; Goodwin 1994; Giambanco 2002).

Alternatively, increased mortality imposed by crab traps could decrease population size in CCB, making more food available per individual and thereby allowing a plastic increase in growth rate to a larger terminal body size (Reznick et al. 2001; Walsh & Reznick 2008). Higher resource levels should benefit both sexes; therefore, we expected a substantial increase of body size in CCB males and females. This was not observed (Fig. 2). Additionally, another turtle species (*Emydura macquarii*) shows no significant resource limitation on growth rate in populations with higher densities (Spencer et al. 2006). Further, the allometric regressions (Table 2) indicated that for a given carapace size CCB females were the same weight as LIS females. If release from competition were a factor, CCB females would have been heavier for a given

carapace size, as was found in green turtles (*Chelonia mydas*; Bjorndal et al. 2000). Therefore, we do not believe an increase in per capita resources is responsible for the increase in female CCB carapace size. Results of a recent survey of Emydid turtles showed that eight of 11 species exhibited larger size with latitude and eight of nine species exhibited smaller size with temperature, consistent with Bergmann's rule applied to ectotherms (Ashton & Feldman 2003). Counter to this pattern, the observed larger size of female terrapins in the CCB relative to terrapins from the higher latitude and cooler temperature of LIS is further evidence of the strength of the selection pressure imposed by crab traps.

The CCB and LIS populations showed similar female age structure, so the observed female size difference cannot be due to different age distributions among the populations. Male age structure, on the other hand, differed significantly between CCB and LIS. No males more than 8 years of age were found in CCB; however, many older males were found in LIS. Our results suggest that older males are rare in CCB because they rarely outgrow the opening of crab traps (Fig. 2) and are therefore susceptible to intense fishery-induced mortality throughout their lives. Adult survival of most turtles is generally high for both sexes (Iverson 1991). Other studies of diamondback terrapin populations not exposed to crab traps routinely show males more than 10 years of age (Roosenburg et al. 1997; Tucker et al. 2001).

The small difference among body size of males from the three samples is somewhat surprising. Terrapins have temperature-dependent sex determination and no sex chromosomes, so clearly both sexes must share genes affecting body size. We wrongly hypothesized that this genetic correlation would produce a parallel increase in male and female size in CCB. The limited response of males suggests some selective factor may oppose immediate increases in body size. We propose that no direct or correlated selection on the few largest adult males can overcome the advantage of small juvenile size and subsequently carry male carapace size beyond the threshold for trap exclusion (Fig. 2). The large increase in female size plus the small change in male size implies that sexual size dimorphism is increasing in CCB terrapins, a species that already exhibits the greatest sexual size dimorphism of any turtle species in North America (Carr 1952). The mean sexual size dimorphism in CCB and LIS is similar in all age classes, except for years six and seven, where CCB females are dramatically larger.

We cannot determine from these data if the increased growth rate and larger terminal body size in CCB is a plastic change or an evolutionary shift. In the 60 years since commercial crabbing began, carapace size has increased about 15% in females more than 5 years of age. A truly plastic change of this magnitude is unlikely; how could the presence of crab traps induce more-rapid growth to a large size in females, but not males? Alternatively, the size

range observed today may simply represent the survivors from an unchanged distribution of genotypes within the population (selection but no evolution), implying a heritability of body size close to zero. Only one study has estimated turtle body size variability and, not surprisingly, found it strongly dependent on environment. Janzen (1993) studied snapping turtles (*Chelydra serpentina*) and estimated $h^2 = 0.72$ (SE 0.34) in a wet environment, but found no heritable variation in a stressful dry environment. If we assumed body size were heritable and the shift in phenotypes were an evolutionary change, the rate of evolution in haldanes (Fig. 4), the mean trait change per generation in standard deviations, would be among the fastest observed (Hendry & Kinnison 1999; Kinnison & Hendry 2001). Females appear to have evolved a larger carapace at a minimum rate of 0.1–0.2 haldanes, whereas the rate of evolution for males is over an order of magnitude smaller. Both synchronic (assuming LIS and CCB were similar in size prior to crabbing, as is supported by the limited HCB samples) and allochronic rates were similar. Our study represents only the second evaluation in reptiles of either evolutionary rates (e.g., Losos et al. 1997) or human-induced phenotypic change (e.g., Sasaki et al. 2009)

Although the results from most studies of size-selective mortality show that larger individuals are favored in nature, the effect of this selection on mean fitness and population viability is less clear (Conover & Munch 2002; Ernande et al. 2004; Dorcas et al. 2007). Investment in rapid growth rate and large terminal size may affect aging and longevity (Jonsson et al. 1992), energy storage (Forsman & Lindell 1991), and resistance to pathogens (Smoker 1986). Additionally, life-history theory (Roff 1992; Stearns 1992) predicts the increase in juvenile growth rate and terminal size should be balanced by some negative trait(s), such as a delay in reproductive maturity or a reduction in fecundity. For example, females selected for rapid somatic growth to escape mortality from crab traps might delay sexual maturity (Roosenburg 1991) or have smaller clutches, which would reduce population growth rate and increase vulnerability to stochastic events (Sogard 1997). Population viability may be limited by the high site fidelity and low dispersal rates of terrapins (Gibbons et al. 2001; Tucker et al. 2001). Further compounding the negative effects of low dispersal on population viability, Hart (2005) found males (the sex most susceptible to drowning in crab traps) are responsible for a greater proportion of dispersal.

Combined with other threats, including loss of nesting habitat and increased nest predation (Dorcas et al. 2007), ongoing crabbing pressure in coastal wetland environments will continue to put this declining terrapin population (M.E. W., unpublished data) and others at risk. An effective diamondback terrapin management policy would incorporate the use of bycatch reduction devices (BRDs).

An effective BRD that narrows the opening to crab traps also reduces terrapin mortality from crab traps, without adversely affecting crab capture rates (Roosenburg 2004). Because the terrapin is listed as near threatened by the International Union for Conservation of Nature (Butler et al. 2006), coastal management of both terrapin populations and blue crab fisheries are needed to ensure the survival and coexistence of these species into the future.
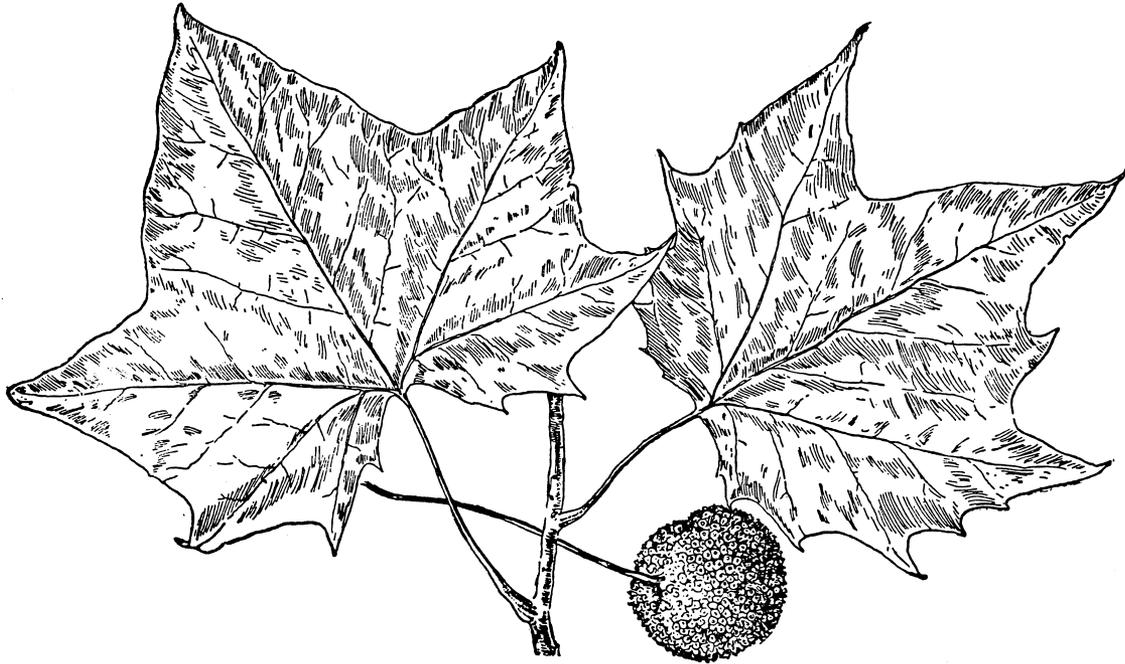
Acknowledgments

Literature Cited

Allendorf, F. W., and J. J. Hard. 2009. Human-induced evolution caused by unnatural selection through harvest of wild animals. Proceedings of the National Academy of Sciences **106:**9987–9994.

Ashton, K. G., and C. R. Feldman. 2003. Bergmann's rule in nonavian reptiles: turtles follow it, lizards and snakes reverse it. Evolution **57:**1151–1163.

Bishop, J. M. 1983. Incidental capture of diamondback terrapin by crab pots. Estuaries **6:**426–430.

Bjorndal, K. A., A. B. Bolten, and M. Y. Chaloupka. 2000. Green turtle somatic growth model: evidence for density dependence. Ecological Applications **10:**269–282.

Blanckenhorn, W. U. 2005. Behavioral causes and consequences of sexual size dimorphism. Ethology **111:**977–1016.

Butler, J. A., R. A. Seigel, and B. K. Mealey. 2006. *Malaclemys terrapin* – diamondback terrapin. Pages 279–295 in P. Meylan, editor. Biology and conservation of Florida turtles. Chelonian Research Monographs. Chelonian Research Foundation, Lunenburg Massachusetts.

Carr, A. 1952. Handbook of turtles. The turtles of the United States, Canada, and Baja California. Cornell University Press, Ithaca, New York.

Congdon, J. D., A. E. Dunham, and R. C. V. L. Sels. 1993. Delayed sexual maturity and demographics of Blanding's turtles (*Emydoidea blandingii*): implications for conservation and management of long-lived organisms. Conservation Biology **7:**826–833.

Congdon, J. D., A. E. Dunham, and R. C. V. L. Sels. 1994. Demographics of common snapping turtles (*Chelydra serpentina*): implications for conservation and management of long-lived organisms. American Zoologist **34:**397–408.

Conover, D. O. 2000. Darwinian fishery science. Marine Ecology Progress Series **208:**303–307.

Conover, D. O., and S. B. Munch. 2002. Sustaining fisheries yields over evolutionary time scales. Science **297:**94–96.

Crouse, D. T., L. B. Crowder, and H. Caswell. 1987. A stage-based population model for loggerhead sea turtles and implications for conservation. Ecology **68:**1412–1423.

Dorcas, M. E., J. D. Wilson, and J. W. Gibbons. 2007. Crab trapping causes population decline and demographic changes in diamondback terrapins over two decades. Biological Conservation **137:**334–340.

Dunham, A. E., and J. W. Gibbons. 1990. Pages 135–145 in J. W. Gibbons, editor. Life history and ecology of the slider turtle. Smithsonian Institution Press, Washington, D.C.

Ernande, B., U. Dieckmann, and M. Heino. 2004. Adaptive changes in harvested populations: plasticity and evolution of age and size at maturation. Proceedings of the Royal Society of London B **271:**415–423.

Ernst, C. H., J. E. Lovich, and R. W. Barbour 1994. Turtles of the United States and Canada. Smithsonian Institution Press, Washington, D.C.

Fairbairn, D. J. 2007. Introduction: the enigma of sexual size dimorphism. Pages 1–15 in D. J. Fairbairn, W. U. Blanckenhorn, and T. Székely, editors. Sex, size, and gender roles: evolutionary studies of sexual size dimorphism. Oxford University Press, New York.

Fenberg, P. B., and K. Roy. 2008. Ecological and evolutionary consequences of size-selective harvesting: how much do we know? Molecular Ecology **17:**209–220.

Forsman, A., and L. E. Lindell. 1991. Trade-off between growth and energy storage in male *Vipera berus*, under different prey densities. Functional Ecology **5:**717–723.

Giambanco, M. R. 2002. Comparison of viability rates, hatchling survivorship, and sex ratios of laboratory- and field- incubated nests of the estuarine, emydid turtle *Malaclemys terrapin*. Hofstra University, New York.

Gibbons, J. W., J. E. Lovich, A. D. Tucker, N. N. FitzSimmons, and J. L. Greene. 2001. Demographic and ecological factors affecting conservation and management of the diamondback terrapin (*Malaclemys terrapin*) in South Carolina. Chelonian Conservation and Biology **4:**66–74.

Gibbons, J. W., et al. 2000. The global decline of reptiles, Déjà vu amphibians. BioScience **50:**653–666.

Goodwin, C. C. 1994. Aspects of nesting ecology of the diamondback terrapin (*Malaclemys terrapin*) in Rhode Island. University of Rhode Island, Kingston.

Grant, P. R., and B. R. Grant. 1995. Predicting microevolutionary responses to directional selection on heritable variation. Evolution **49:**241–251.

Hart, K. M. 2005. Population biology of diamondback terrapins (*Malaclemys terrapin*): defining and reducing threats across their geographic range. Duke University, Durham, North Carolina.

Hendry, A. P., and M. T. Kinnison. 1999. Perspective: the pace of modern life: measuring rates of contemporary microevolution. Evolution **53:**1637–1653.

Huey, R. B., B. Moreteau, J.-C. Moreteau, P. Gibert, G. W. Gilchrist, A. R. Ives, T. Garland Jr., and J. R. David. 2006. Sexual size dimorphism in a *Drosophila* clade, the *D. obscura* group. Zoology **109:**318–330.

Iverson, J. B. 1991. Patterns of survivorship in turtles (order Testudines). Canadian Journal of Zoology **69:**385–389.

Janzen, F. J. 1993. An experimental analysis of natural selection on body size of hatchling turtles. Ecology **74:**332–341.

Jonsson, B., J. H. L'Abee-Lund, T. G. Heggberget, A. J. Jensen, B. J. Johnsen, T. F. Naesje, and L. M. Saettem. 1992. Longevity, body size, and growth in anadromous brown trout (*Salmo trutta*). Canadian Journal of Fisheries and Aquatic Sciences **48:**1838–1845.

Kinnison, M. T., and P. Hendry. 2001. The pace of modern life II: from rates of contemporary microevolution to pattern and process. Genetica **112–113:**145–164.

Lande, R. 1980. Sexual dimorphism, sexual selection, and adaptation in polygenic characters. Evolution **34:**292–305.

Lande, R., and S. J. Arnold. 1983. The measurement of selection on correlated characters. Evolution **37:**1210–1226.

Lipcius, R. N., and W. T. Stockhausen. 2002. Concurrent decline of the spawning stock, recruitment, larval abundance, and size of the blue crab *Callinectes sapidus* in Chesapeake Bay. Marine Ecology Progress Series **226:**45–61.

Litzgus, J. D., and R. J. Brooks. 1998. Testing the validity of counts of plastral scute rings in spotted turtles, *Clemmys guttata*. Copeia **1998:**222–225.

Losos, J. B., K. I. Warheitt, and T. W. Schoener. 1997. Adaptive differentiation following experimental island colonization in Anolis lizards. Nature **387:**70–73.

Lovich, J. E., and J. W. Gibbons. 1990. Age at maturity influences adult sex ratio in the turtle *Malaclemys terrapin*. Oikos **59:**126–134.

Lovich, J. E., and J. W. Gibbons. 1992. A review of techniques for quantifying sexual size dimorphism. Growth Development and Aging **56:**269–281.

Mitro, M. G. 2003. Demography and viability analyses of a diamondback terrapin population. Canadian Journal of Zoology **81:**716–726.

Owens, I. P. F., and I. R. Hartley. 1998. Sexual dimorphism in birds: why are there so many different forms of dimorphism? Proceedings of the Royal Society of London: Biological Sciences **265:**397–407.

Preziosi, R. F., and D. J. Fairbairn. 1992. Genetic population structure and levels of gene flow in the stream dwelling waterstrider, *Aquarius* (= Gerris) *remigis* (Hemiptera: Gerridae). Evolution **46:**430–444.

Reznick, D., M. J. Butler IV, and H. Rodd. 2001. Life-history evolution in guppies. VII. The comparative ecology of high- and low-predation environments. The American Naturalist **157:**126–140.

Ricklefs, R. E. 1967. A graphical method of fitting equations to growth curves. Ecology **48:**978–983.

Roff, D. A. 1992. The evolution of life histories. Chapman and Hall, New York.

Roosenburg, W. M. 1991. The diamondback terrapin: population dynamics, habitat requirements, and opportunities for conservation. Pages 227–234 in New perspectives in the Chesapeake system: a research and management partnership. Proceedings of a Conference. Publication 137. Chesapeake Research Consortium, Solomons, Maryland.

Roosenburg, W. M. 2004. The impact of crab pot fisheries on terrapin (*Malaclemys terrapin*) populations: where are we and where do we need to go? Pages 23–30 in C. Swarth, W. M. Roosenburg, E. Kiviat, editors. Conservation and ecology of turtles of the Mid-Atlantic region: a symposium. Biblomania, Salt Lake City, Utah.

Roosenburg, W. M., W. Cresko, M. Modesitte, and M. B. Robbins. 1997. Diamondback terrapin (*Malaclemys terrapin*) mortality in crab pots. Conservation Biology **5:**1166–1172.

Roosenburg, W. M., and A. E. Dunham. 1997. Allocation of reproductive output: egg- and clutch-size variation in the diamondback terrapin. Copeia **1997:**290–297.

Sasaki, K., S. F. Fox, and D. Duvall. 2009. Rapid evolution in the wild: changes in body size, life-history traits, and behavior in hunted populations of the Japanese mamushi snake. Conservation Biology **23:**93–102.

Seigel, R. A. 1980. Nesting habits of diamondback terrapins (*Malaclemys terrapin*) on the Atlantic coast of Florida. Transactions of the Kansas Academy of Science **83:**239–246.

Seigel, R. A., and J. W. Gibbons. 1995. Workshop on the ecology, status, and management of the diamondback terrapin (*Malaclemys terrapin*), Savannah River Ecology Laboratory, 2 August 1994: final results and recommendations. Chelonian Conservation and Biology **1:**240–243.

Smoker, W. W. 1986. Variability of embryo development rate, fry growth, and disease susceptibility in hatchery stocks of chum salmon. Aquaculture **57:**9–226.

Sogard, S. M. 1997. Size-selective mortality in the juvenile stage of teleost fishes: a review. Bulletin of Marine Science **60:**1129–1157.

Spencer, R. J., F. J. Janzen, and M. B. Thompson. 2006. Counterintuitive density-dependent growth in a long-lived vertebrate after removal of nest predators. Ecology **87**:3109–3118.

Stearns, S. C. 1992. The evolution of life histories. Oxford University Press, Oxford.

Tucker, A. D., J. W. Gibbons, and J. L. Greene. 2001. Estimates of adult survival and migration for diamondback terrapins: conservation insight from local extirpation within a metapopulation. Canadian Journal of Zoology **79**:2199–2209.

Van Engel, W. A. 1962. The blue crab and its fishery in Chesapeake Bay. Part 2. Types of gear for hard crab fishing. Commercial Fisheries Review **24**:1–10.

Walsh, M. R., and D. N. Reznick. 2008. Interactions between the direct and indirect effects of predators determine life history evolution in a killifish. Proceedings of the National Academy of Sciences **105**:594–599.

Wright, S. 1926. Review. Journal of the American Statistical Association **21**:493–497.