Morphometrics and estimates of force generation by the chelae of a North American population of the invasive green crab, Carcinus maenas (L.)

S.C. Mitchell, S.M. Kennedy, P.J. Williams, and M.E. DeMont

Abstract: The European green crab, Carcinus maenas, is an invasive species in eastern North America and has the potential to significantly impact wild and aquaculture shellfish in the southern Gulf of St. Lawrence, Canada. To examine potential predation effects on local shellfish and assess the appropriateness of extrapolating results from studies conducted elsewhere, the morphometry of chelae from a recently established population of C. maenas in Nova Scotia was examined for comparison with the presumed founding (European) population, and forces generated by the chelae over a range of crab sizes were estimated. The Nova Scotia population was found to be morphologically very similar to European populations with respect to chela structure. Force generation by the chelae was found to scale with isometry in the female crab and with positive allometry in the male. Estimated forces compare well with previously reported forces, and force generation is calculated to increase in a nonlinear manner proceeding from the chela tips proximally toward the fulcrum. The calculated forces generated by the chelae are clearly sufficient for outright crushing of some shells (e.g., Mya arenaria), even for small crabs, but appear to be too low for crushing those of other molluscs. There is a complex interplay between gape and maximum force along the length of the dactyl that allows great variability in force application, and thus also in the size of prey consumed and prey-handling behaviour. We suggest that for such a lever system, the gape angle of the chelae, which does not change with crab size, is optimal with respect to the resultant force generated.

Résumé : Le crabe vert, Carcinus maenas, est une espèce envahissante de l’est de l’Amérique du Nord qui a le potentiel de causer un impact important sur les cultures de mollusques et de crustacés dans le secteur sud du Golfe St-Laurent. Dans le but de déterminer localement les effets d’une prédation éventuelle sur les mollusques et les crustacés et pour évaluer la pertinence d’extrapoler les résultats de recherches faites à d’autres endroits, nous avons examiné la morphométrie des pinces du crabe vert chez une population établie depuis peu (en Nouvelle-Écosse) par comparaison à la population présumée fondatrice (européenne) et évalué les forces générées par les pinces dans l’étendue des tailles des crabes. La structure des pinces chez la population de la Nouvelle-Écosse est très semblable morphologiquement à ce qu’on retrouve chez la population européenne. La force générée par les pinces est proportionnelle à l’isométrie chez les femelles et à l’allométrie positive chez les mâles. L’estimation des forces générées a donné des résultats qui se comparent à ceux obtenus au cours de travaux antérieurs et le calcul de cette génération de forces révèle que les forces augmentent de façon non linéaire de l’extrémité des pinces en direction proximale vers le fulcrum. Les forces calculées sont amplement suffisantes pour écaser les coquilles de certains animaux (e.g., Mya arenaria), même chez les petits crabes, mais elles ne sont pas suffisantes pour écaser les coquilles d’autres mollusques. Il se produit une interaction complexe entre l’ouverture de la pince et la force maximale qui s’exerce le long du doigt, ce qui confère au système une grande flexibilité dans l’application des forces, et par ce fait même, une variabilité importante de la taille des proies et des comportements de prédation. Nous croyons que l’angle d’ouverture de la pince, qui ne change pas avec la taille des crabes, est optimal, compte tenu de la force résultante dans un tel système de levier.

[Traduit par la Rédaction]

Introduction

The European green crab, Carcinus maenas, has proved to be a very successful invader outside its natural range on the coasts of Eastern Europe (Jamieson et al. 1998). Following accidental introduction (via ballast water, seaweed packing for shellfish, etc.), the green crab has undergone impressive population growth and range expansion in South Africa (Le Roux et al. 1990), Australia (Jamieson et al. 1998), and on both the west (Cohen et al. 1995) and east (Glude 1955) coasts of North America. Attributes that contribute to its success as an invasive species include a very high reproductive output, a planktonic larval phase, tolerance of wide salinity and temperature ranges (Crothers 1968), and the
ability to thrive in densities of several individuals per square metre (Young et al. 1999). Green crabs became established in the Cape Cod area on the Atlantic coast of North America during the mid-1800s (Glude 1955). This initial population then expanded its range northward, and reached the mouth of the Bay of Fundy in the early 1950s (Glude 1955; MacPhail et al. 1955; Elner 1981). Expansion then continued during the next 30 years both into the Bay of Fundy and in a northeasterly direction along the southern coast of Nova Scotia, in the latter case possibly slowed somewhat by the relatively small number of estuaries and cool water in summer along that shore. It appears that by the early 1990s, green crabs were established in the southern Gulf of St. Lawrence (Gillis et al. 2000). The Gulf, with its relatively high summer temperatures and numerous estuaries and bays, could be considered optimum habitat for green crabs. Evidence of this may be seen in Antigonish Harbour, where green crabs have achieved densities greater than 1/m² in less than 15 years since their establishment (Campbell 2001). Many studies have examined the ecological impact of invasive green crab populations on pre-invasion flora and fauna (Cohen et al. 1995). Green crabs are very aggressive omnivores (LeCalvez 1987), and in gut-content studies, representatives of many groups, including bivalves (Cohen et al. 1995), gastropods (Hughes and Elner 1979; Hadlock 1980), annelids (Gee et al. 1985), crustaceans (Ropes 1968), and even algae (Elner 1981) have been found. Green crabs tend to have the greatest impact on bivalves (Elner 1981; Scherer and Reise 1981), and have been associated with collapses of softshell clam (Mya arenaria) populations in New England (Glude 1955) and severe reductions of the clams Nutricula tantilla and Nutricula confusa on the west coast of North America (Grosholz et al. 2000). In addition to impacting single taxa, the green crab has also been implicated in influencing the distribution and morphology of their prey (Hughes and Elner 1979; Brandwood 1985; Gee et al. 1985; Preston et al. 1996) and altering prey community structure (Ebeling et al. 1964; Scherer and Reise 1981; Schratzberger and Warwick 1999; Grosholz et al. 2000).

In terms of morphology, the green crab is heterochelous, with a larger, more robust crusher chela (usually the right chela) and a smaller, pincer-type cutter chela (Elner 1980; Lee and Seed 1992). These crabs exhibit sexual dimorphism, with males possessing larger chelae than females; in the males the chelae may comprise 20% of body mass, while in females they represent less than 15% (Lee and Seed 1992). The chelae have many roles, including feeding, mate acquisition, defence, and agonistic interactions (Stein 1976; Juanes and Smith 1995; Sneddon et al. 1997; Mariappan et al. 2000). The green crab exhibits two different colour forms, red and green, which exhibit physiological and ecological differences. The two forms are capable of generating different maximal forces with their chelae (Kaiser et al. 1990). Despite their relatively small size (maximum carapace width approximately 95 mm; Grosholz et al. 2000), green crabs use their chelae very effectively to open and consume bivalves, and in the case of M. arenaria, have even been shown to consume clams with lengths approaching the crab’s carapace width (MacPhail et al. 1955). Optimal prey size increases with predator size (Elner 1980). Green crabs use their cutter to hold and manipulate shellfish while attempting to crush them with the crusher (Elner and Hughes 1978). If repeated attempts to crush the whole shell are not successful, green crabs may eventually gain access to the organism by using the tips of the chelae to chip at the thinner margin of the shell. The latter, slower method allows green crabs to open bivalves with very thick shells, such as quahogs (Mercenaria mercenaria) and oysters (Crassostrea virginica).

Despite the behavioural plasticity shown, prey-size selection is thought to be largely governed by chela size and morphology (Lee and Seed 1992; Freire et al. 1996), though other physical factors (e.g., moult, tooth wear, microfractures, etc.) also likely contribute to prey selection. Yamada and Boulding (1998) classify crabs with slender claws, fine denticles, and a mechanical advantage less than 0.3 as generalists feeding on a wide variety of prey, and those with at least one powerful, molariform chela and a mechanical advantage greater than 0.3 as specialists preying on hard-shelled organisms. However, the difficulty with such a classification is that the chela may be used behaviourally to alter the mechanics of occlusion by altering the position of an object within the gape, and hence the mechanical advantage and occlusive surfaces, exerted by the claw. This behavioural variability allows for a wide variety of forces to be exerted and thus makes a wide range of potential prey available for handling/consumption.

Crab chelae are known to grow allometrically (e.g., Abbe-Kalb and Warner 1989; Lee and Seed 1992; Mariappan et al. 2000, and others). This type of growth is commonly described using a power curve, \( y = ax^b \), which may be linearized as \( y = b \log x + \log a \) and its original form is equivalent to the traditional ordinary least squares (OLS) equation when \( b = 1.0 \) and \( a = \) slope of the best fit line. In allometric analysis the data are log-transformed to normalize the distribution and stabilize the variance of the \( y \) variate (LaBarbera 1989). However, such transformation may affect the underlying error structure of the data (Myers 1990), thereby potentially violating the assumptions of traditional OLS regression. Even if this is not the case during the transformation, the general lack of knowledge of error structure in most analyses, and the fact that the \( x \) variate is not known or is measured without error, imply that OLS assumptions may not be met in this type of research. Therefore, the alternative method, reduced major axis (RMA) was used (for a discussion of RMA see McArdle 1988).

Given their penchant for shellfish and their ability to thrive at high densities, the invasive green crabs pose a considerable threat to both wild and aquaculture shellfish in the southern Gulf of St. Lawrence. In terms of both predicting impacts on a regional basis and planning or designing efforts to prevent or minimize this impact (e.g., determining if there is a size at which cultured bivalves are no longer vulnerable to crab predation), a detailed understanding of the biomechanics and force generation of the chelae over a range of crab sizes is essential. The research described below was undertaken 2E. Campbell. 2001. The ecology of the green crab, Carcinus maenas, and its invasion in the southern Gulf of Saint Lawrence. B.Sc. (Hons.) thesis, Department of Biology, St. Francis Xavier University, Antigonish, N.S.
with two principal goals: (1) to assess the morphometry of a recently established population of green crabs for comparison with a presumed founding population, and (2) to estimate and model force generation by the green crab relative to its ability to prey on hard-shelled organisms. Each of these components has significance in the estimation of impacts of the continual invasion of this crab species into new environments.

**Materials and methods**

**Morphometrics**

We examined 56 green crabs from two capture locations in Nova Scotia, Canada: Antigonish Harbour (45°40′N, 61°55′W; 9 crabs were sampled in November 2000 as a preliminary/feasibility study) and Pomquet Harbour (45°38′N, 61°48′W; 47 crabs were sampled in May–July 2001). Animals were selected to span as large a size range as possible, with relatively equal size intervals. These green crabs (28 females, carapace width (CW) 21.8–63.1 mm, mass 4.4–61.4 g; 28 males, CW 27.2–78.3 mm, mass 14.2–149.8 g) were killed by raising the water temperature to 40°C, in accordance with the Canadian Council on Animal Care protocol, and CW (mm) and mass (g) were measured. CW was determined as the distance across the carapace measured in the gap immediately behind the first anterolateral spine. This differs slightly from other studies, but was used here to prevent false measurements in the case of broken spines. To calibrate this measure against standard carapace width, a regression of the more usual carapace measure from spine tip to spine tip against this measure between the indents behind the spines was conducted and indicated that the tip-to-tip carapace measure (y) is a function of the smaller measure (x) as $y = 1.068x + 0.271$ ($r^2 = 0.996, n = 20$, range 28.3–68.9 mm CW). Thus, our measure is approximately 7% less than the tip-to-tip measure. Linear measurements were made using vernier calipers (±0.05 mm) and mass was measured using a Mettler PJ3600 balance (±0.01 g). Both chelae were cut out. Paper images and reference areas were weighed using a Mettler AE100 analytical balance (±0.0001 g). The surface area of the apodeme ($SA_{apodeme}$, mm$^2$) was calculated as

$$SA_{apodeme} = (SA_r / M_r) \times M_{apodeme}$$

where $SA_r$ is the surface of the reference area (291.039 mm$^2$), $M_r$ is the mass (g) of the reference area, and $M_{apodeme}$ is the mass (g) of the paper apodeme.

Rates of increase in chela height, $L_1$, $L_2$, maximum gape, and surface area of the apodemes over the size range of sampled animals were examined using allometric techniques. Data were log (base 10)-transformed and plotted using OLS regression (Microsoft Excel 97). The slope estimates from the OLS ($b_{OLS}$) were recalculated to provide RMA estimates ($b_{RMA}$) (from LaBarbera 1989):

$$b_{RMA} = b_{OLS}/r^2$$

where $r^2$ is the coefficient of determination. If $r^2$ was less than 0.8, RMA procedures were not conducted, as this would likely lead to falsely, and grossly, inflating the slope parameter. Confidence intervals for the slope were calculated as follows (from McArdle 1988):

$$95\% CI = b_{RMA} \times [(B + 1)^{0.5} \pm (B)^{0.5}]$$

where $B = (r^2 \times (1 - r^2))(n - 2)$, $t$ being Student’s $t$ for $n - 2$ degrees of freedom. The relationships of gape angle and mechanical advantage (the ratio of $L_1$ to $L_2$) to body size were examined using the untransformed data. Hypothesis tests of the slope and elevation parameters were conducted using OLS techniques on both the OLS and RMA regressions. The $y$ intercept was not tested, as it is inappropriate based on these regressions (Zar 1999). Instead, the elevation of the best fit line was tested. This is equivalent to comparing the “centre points” of the lines, and thus is a test of the elevation of the midpoint of one line with respect to the other(s). Where appropriate, parametric tests were conducted on mean values, consisting of single-factor analysis of variance (ANOVA) followed by Tukey’s honestly significant difference (HSD) multiple comparison. All testing and analysis was conducted at $\alpha = 0.05$.

**Force production**

The force ($F_1$ from Fig. 1) exerted by the muscle apodeme complex in a pinnated system may be estimated as follows (from Alexander 1969):

$$F_1 = (A \times \sin 2\theta)\sigma$$

where $A$ is the muscle cross-sectional area (represented here by apodeme surface area), $\theta$ is the muscle-fibre pinnation angle (multiplied by 2 because both surfaces have muscle attachment in a bipinnate muscle system such as the crab chela), and $\sigma$ is muscle stress (force per unit cross-sectional area). The apodeme surface area for a given crab size is calculated from the regression equations of apodeme surface area on body size determined here. The muscle-fibre pinnation angle for each crusher and cutter varies throughout the closing process. Elner (1978) provides $\theta$ values for three positions along the apodeme when the claw is opened and closed. For this analysis, the pinnation angle at each point during closing (i.e., percentage of maximum gape) was interpolated from Elner’s values at fully open and fully closed.

We anticipate that the greatest error in estimates of $F_1$ will arise from the selection of a muscle-stress value ($\sigma$) and so the rationale behind it is presented in some detail here. We

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selected the values of 67 N·cm⁻² for the crusher and 47 N·cm⁻² for the cutter as representative; these values are from Warner et al. (1982). Our use of a published mean value of muscle stress to calculate chela forces, rather than direct measurements, is based upon a three-point rationale: (1) Direct measurements are of limited value when trying to generalize (which is the goal of the model), owing to variability in the behaviour of individual crabs. Crab chela forces measured will be dependent upon the strategy the crab selects to crack the prey shell (i.e., chipping versus repeated loading versus outright crushing, and grasping location within the chela; see Discussion). Therefore, direct measurements, while necessary in describing specific actions or forces generated by a crab of a given size have limited applications for generalization. Indeed, the great variance associated with these estimates by Warner et al. (1982; SE = ±58 and ±41 N·cm⁻² for the crusher and cutter, respectively) indicates the great variability exhibited by a relatively small number of crabs (n = 18) within a small size range (50–70 mm CW). (2) Previous work in which green crab chela forces have been measured have utilized relatively large crabs (e.g., 50–70 mm CW; Elner 1978; Warner et al. 1982; Kaiser et al. 1990). Our interest in extending estimates of force generation to much smaller animals (i.e., <60 mm CW) creates technical difficulties in accurately measuring these forces. These difficulties are not insurmountable, but deriving reliable estimates from such small animals is challenging. (3) The error in our estimate of muscle-stress will only act to scale the force estimates; the general trends and relationships described will be maintained. We believe that though we do not yet have directly measured estimates of force, the physical principles outlined here allow us to estimate the forces exerted by these smaller crabs.

The force calculation in eq. 4 estimates the force applied by the apodeme to the dactyl (F₁ in Fig. 1); it does not account for the lever component of the system. To account for this, by assuming the pivot point is frictionless and knowing that F₁ × L₁ = F₂ × L₂ it is possible to calculate F₂, the force at the chela tip (Fig. 1) as

\[ F₂ = F₁(L₁/L₂) \]

where L₁, L₂, and F₁ are as previously defined.

Several of the parameters of the model have been measured and these measurements involve inherent variance as well as measurement error. The propagation of these errors through successive calculations to provide final error estimates on calculated forces was done using the following equation (modified from Bevington 1969):

\[ \hat{\varepsilon} = (F₂ × [\frac{\text{var}(\sigma)}{\sigma^2} + \text{var}(\text{MA})/\text{MA}^2] + \text{var}(\theta)/\theta^2 + \text{var}(\text{SA}_{\text{apodeme}})/\text{SA}_{\text{apodeme}}^2)^{1/2} \]

where \( \hat{\varepsilon} \) is the error associated with the estimate of \( F₂ \), var() is the variance associated with the parameter in parentheses, and MA is the mechanical advantage.

To estimate forces generated within the gape along the length of the dactyl, the mechanical advantage was calculated at 1-cm increments along the dactyl, proceeding from a point equivalent in length to \( L₁ \) (i.e., when the mechanical

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Fig. 1. Chelae of green crabs (Carcinus maenas), illustrating morphometric measurements and dimensions for force calculations. F, fulcrum of the joint; CH, chela height; GM, maximum gape; AC, closer apodeme; F₁ and F₂ are forces and L₁ and L₂ are distances from the fulcrum to the site of force generation/application. See the text for details. Chelae are from male crabs of 59 mm carapace width.
Advantage is equal to 1.0) to the chela tip. The force at each increment was calculated by multiplying $F_1$ by this location-dependent mechanical advantage. This force along the dactyl was then plotted against proportion of dactyl length throughout the range where the mechanical advantage is less than 1.0 (i.e., $L_1 < L_2$).

**Results**

**Morphometrics**

Green crab body mass increased with carapace width as $3.359 \times 10^{-4} \times CW^{2.947} \pm 0.183 (n = 39, r^2 = 0.966)$ and thus is isometric (i.e., isometric exponent = 3.0) with the linear measure of carapace size. When the mass versus CW data were plotted, the data for males and females were intermixed, so males and females were treated together. Calculation of relative chela size (RCS) as chela height / CW indicated that as a proportion of CW, chela height was greater for males than for females, and greater for the crusher than for the cutter (Table 1; $p < 0.001$ for all comparisons; Tukey’s HSD). The slopes of the allometric regressions of chela height versus CW are similar within sexes but greater for males than for females (Table 2). The elevation of the line indicates within-sex size differences. Because of differences in mean size of crabs between the sexes (44.7 ± 10.7 mm (mean ± SD) for females; 56.9 ± 13.5 mm for males; $t$ test, $p < 0.001$), comparison of line elevations between the sexes is not possible, as the mean elevation in the two sexes occurs at different values of CW. Chela height in females grows approximately isometrically (i.e., $b_{iso} = 1.0$), while in males it scales with positive allometry ($b > 1.0$). Therefore, for this population of green crabs, the height of the corresponding chelae of the female increases with carapace size at a lower rate than in the male. Within a sex, cutter height is less than crusher height, though the rates of increase with CW are equal for the two chelae.

A significant relationship of mechanical advantage with carapace size could not be established ($p > 0.40, r^2 < 0.05$), indicating that during the growth of the crab and the chela the mechanical advantage remains approximately constant. This is explained by the growth of $L_1$ being similar to that of $L_2$ (Table 3), and so the mechanical advantage remains the same over the size range examined here. The components of mechanical advantage, $L_1$ and $L_2$, scale with isometry ($b_{iso} = 1.0$) or less than isometry for the female crabs and with positive allometry in the male crabs. Comparisons of the mean mechanical advantage are shown in Table 1.

Maximum chela gape as a function of body size increases at similar rates for both the cutter and crusher within each sex (Table 4). The elevation of the line, reflecting the maximum gape measurement of a crab of mean size, showed that the crusher has a larger maximum gape than the cutter. Like chela height and $L_1$ and $L_2$, maximum gape also scales with positive allometry in the males; the females appear to exhibit negative allometry. The gape angle of the chelae shows statistically significant negative relationships (untransformed data, $p = 0.009–0.028$) with body size for all chelae. However, only 18–25% of the variation is explained by these regression equations, and thus the functional significance of these relationships is questionable. The mean gape angle of the chelae (Table 5) indicates that the male crusher has a smaller maximum gape angle than the male cutter or the female cutter and crusher ($p < 0.005$; Tukey’s HSD).

The regression of apodeme surface area on CW for this population of green crabs indicates that the apodemes of all chelae scale the same with body size (Table 6; $b_{OLS} = 1.94–2.64$; $r^2 = 0.607–0.874$; $b_{common} = 2.23$). Based on the 95% confidence interval, these slopes are not different from isometry ($b_{iso} = 2.0$). A comparison of elevations indicates that although all apodemes scale equally with body size, there are significant differences in apodeme size between chelae (cutter females < crusher females; cutter males < crusher males).

**Force generation**

Because muscle force scales with the square of a linear measure ($L^2$; Katz and Gosline 1993), isometry predicts that $F_1$ is proportional to $L^2$. The mechanical advantage, under isometry, is a linear measure divided by a second linear measure ($L_1/L_1 = L^0$) and thus the multiplication of force and mechanical advantage ($L^2 \times L^0$) yields an isometric condition of $L^3$ for force exerted by these crab chelae as a function of linear dimension. The force generated by the male crusher and cutter appears to scale with positive allometry (i.e., isometry = 2.0), while for the female the allometry is negative or isometric. Statistical testing could not be done, as these were calculated curves rather than distributions of measurements. Estimated forces at the dactyl tips are presented in Fig. 2 and equations for the calculated curves in Table 7. There are considerable differences in force generated by the two chelae with increasing size and between the sexes. The fit to previously published direct measurements (Fig. 3) is encouraging in that the estimates are in the range of most of the estimates of force generated by these chelae of green crabs.

In a lever system such as the crab chela, the force exerted at the tip of the dactyl is at the lower end of that which may be exerted. Figure 4 illustrates this using a 58 mm CW male crab and shows a nonlinear increase approaching the fulcrum. The applied force may be doubled between the tips of the chela and a point 50% along the dactyl, from which point the increase in applied force becomes rapidly greater.

**Discussion**

**Morphometrics**

The RCS found in the Nova Scotia population agrees well with values for Lee and Seed’s (1992) North Wales crabs, which had crusher ratios of 0.285 for males and 0.225 for females. Work by Kaiser et al. (1990) on crabs from that area indicates that there is no significant difference in RCS between red and green forms of green crabs. Chela height increases with body size at a lower rate for females than for males; this difference between the sexes has been reported previously for green crabs in North Wales (Elner 1980; Lee and Seed 1992). Elner (1980) reports slope values for the regression using untransformed chela height on CW of 0.23 for females and suboptimal males and 0.48 for optimal males (classification as suboptimal and optimal is based on foraging efficiency). Lee and Seed (1992) found allometric slopes of chela height versus CW of 1.287 for male crabs and 1.055 for females.
Table 1. Relative chela size and mechanical advantage for the crusher and cutter chelae of green crabs, *Carcinus maenas*, of both sexes in Nova Scotia.

<table>
<thead>
<tr>
<th></th>
<th>Relative chela size</th>
<th>Mechanical advantage</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Mean</td>
<td>SD</td>
</tr>
<tr>
<td>Females</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Crusher</td>
<td>0.221</td>
<td>0.015</td>
</tr>
<tr>
<td>Cutter</td>
<td>0.201</td>
<td>0.015</td>
</tr>
<tr>
<td>Males</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Crusher</td>
<td>0.275</td>
<td>0.046</td>
</tr>
<tr>
<td>Cutter</td>
<td>0.232</td>
<td>0.026</td>
</tr>
</tbody>
</table>

* Equality of slopes Cutter female < crusher female, cutter male < crusher male
* Equality of elevations Cutter female < cutter male, crusher female > crusher male

Table 2. Allometric regressions of chela height versus carapace width for the crusher and cutter of green crabs of both sexes.

<table>
<thead>
<tr>
<th>Regression</th>
<th>$b_{OLS}$ 95% CI</th>
<th>$r^2$</th>
<th>$b_{RMA}$</th>
<th>$b_{RMA}$ 95% CI</th>
<th>$p^*$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Females</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Crusher</td>
<td>$Y = 1.042X - 0.725$</td>
<td>0.937–1.148</td>
<td>27</td>
<td>0.940</td>
<td>1.108</td>
</tr>
<tr>
<td>Cutter</td>
<td>$Y = 0.954X - 0.623$</td>
<td>0.844–1.065</td>
<td>26</td>
<td>0.927</td>
<td>1.029</td>
</tr>
<tr>
<td>Males</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Crusher</td>
<td>$Y = 1.417X - 1.291$</td>
<td>1.242–1.593</td>
<td>26</td>
<td>0.917</td>
<td>1.545</td>
</tr>
<tr>
<td>Cutter</td>
<td>$Y = 1.323X - 1.202$</td>
<td>1.209–1.438</td>
<td>27</td>
<td>0.956</td>
<td>1.384</td>
</tr>
</tbody>
</table>

*Values indicate significant departures of reduced major axis (RMA) slope from isometry (isometric exponent = 1.0). OLS is ordinary least squares.

Table 3. Allometric regressions of $L_1$ and $L_2$ versus carapace width for crushers and cutters of green crabs of both sexes.

<table>
<thead>
<tr>
<th>Regression</th>
<th>$b_{OLS}$ 95% CI</th>
<th>$r^2$</th>
<th>$b_{RMA}$</th>
<th>$b_{RMA}$ 95% CI</th>
<th>$p^*$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Females</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Crusher (L1)</td>
<td>$Y = 0.790X - 0.770$</td>
<td>0.579–1.00</td>
<td>28</td>
<td>0.685</td>
<td>—</td>
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<tr>
<td>Crusher (L2)</td>
<td>$Y = 0.876X - 0.368$</td>
<td>0.729–1.02</td>
<td>28</td>
<td>0.847</td>
<td>1.034</td>
</tr>
<tr>
<td>Cutter (L1)</td>
<td>$Y = 0.728X - 0.724$</td>
<td>0.478–0.979</td>
<td>25</td>
<td>0.594</td>
<td>—</td>
</tr>
<tr>
<td>Cutter (L2)</td>
<td>$Y = 0.824X - 0.298$</td>
<td>0.667–0.981</td>
<td>24</td>
<td>0.829</td>
<td>0.994</td>
</tr>
<tr>
<td>Males</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Crusher (L1)</td>
<td>$Y = 1.381X - 1.667$</td>
<td>1.195–1.567</td>
<td>28</td>
<td>0.896</td>
<td>1.541</td>
</tr>
<tr>
<td>Crusher (L2)</td>
<td>$Y = 1.248X - 0.945$</td>
<td>1.123–1.373</td>
<td>28</td>
<td>0.940</td>
<td>1.328</td>
</tr>
<tr>
<td>Cutter (L1)</td>
<td>$Y = 1.166X - 1.393$</td>
<td>1.018–1.313</td>
<td>28</td>
<td>0.907</td>
<td>1.285</td>
</tr>
<tr>
<td>Cutter (L2)</td>
<td>$Y = 1.231X - 0.922$</td>
<td>1.126–1.335</td>
<td>28</td>
<td>0.956</td>
<td>1.287</td>
</tr>
</tbody>
</table>

*Values indicate significant departures of RMA slope from isometry (isometric exponent = 1.0). Some RMA slopes were not calculated, as $r^2 < 0.8$.

for females. For crabs off the Isle of Cumbrae, Scotland, Abby-Kalio and Warner (1989) found allometric slopes of 1.347 (crusher) and 1.380 (cutter) for “right-handed” (crusher on the right) males and 0.857 and 0.941 for crusher and cutter, respectively, for “left-handed” males. The results of all of these previous studies agree well with ours, the allometric slopes of Lee and Seed (1992) and the right-handed crabs (79% of the population) of Abby-Kalio and Warner (1989) fall within the confidence intervals of the (OLS) slopes presented here. An analysis of untransformed chela height on CW for these Nova Scotia crabs (OLS to be comparable with Elner’s (1980) results) indicates slopes of 0.237 ± 0.026 for the female’s crusher and 0.391 ± 0.064 for the male’s crusher; these compare well with Elner’s (1980) results (we did not discriminate optimal and suboptimal males). Thus, the Nova Scotia green crab populations appear to have similar chela-height characteristics as the eastern Atlantic (North Wales and Scotland) population reported by the previous authors. This similarity in size relationships, despite the use of different methodologies of measuring CW, suggests that the

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underlying relationships are likely robust in that different measurement methodologies result in similar relationships.

In contrast to this geographic intraspecies similarity, the untransformed slope estimates of chela height on CW for the green crab are lower than those reported for four other crab species (0.37–0.74 for *Hemigrapsus nudus*, *Lophopanopeus bellus*, *Cancer oregonensis*, and *Cancer productus*) by Yamada and Boulding (1998). When evaluated relative to other crab species, the positively allometric growth of male green crabs and isometric growth of females is not unusual. The blue crab, *Callinectes sapidus*, shows the same dimorphism in chela height (Seed and Hughes 1997), and Mariappan et al. (2000) list six other decapod species (including the two portunids *Aranaeus cribarius* and *Liocarcinus depurator*) with positive allometric patterns for males and isometric or negative allometric patterns for females. The RMA slope for the crusher of
female green crabs in this study was found to be weakly statistically different from isometry; however, as Clayton (1990) points out, the uncritical use of allometry and acceptance of statistical tests may be misleading. We feel that the weak significance for this chela is likely an artifact rather than representing a biological process.

Mechanical advantage of the chelae has been reported for two European green crab populations: in the Menai Straits in Wales (Lee and Seed 1992) and off the Isle of Cumbrae in Scotland (Abby-Kalio and Warner 1989). Crabs from these locations had very similar mechanical advantage to crabs from Nova Scotia (female crusher, range 0.282–0.290; female cutter, 0.251–0.267; male crusher, 0.326–0.358; male cutter, 0.262–0.266).

The mechanical advantage of the chelae did not appear to change appreciably with growth in green crabs in our study. This is in agreement with Warner and Jones (1976), Seed and Hughes (1995), and Rebach and Wowor (1997). However, Abby-Kalio and Warner (1989) found that mechanical advantage does vary with size for green crabs. The results reported by the latter authors ($r^2$ values for mechanical advantage on CW of less than 0.1 for the male crusher and cutter; $n = 157$; range 55–95 mm CW) suggest that their relationship may be statistically significant, but of question-

Table 7. Force (N) as function of carapace width for crushers and cutters of male and female green crabs of both sexes (see Fig. 2).

<table>
<thead>
<tr>
<th></th>
<th>Female Crusher</th>
<th>Female Cutter</th>
<th>Male Crusher</th>
<th>Male Cutter</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>$Y = 8.65 \times 10^{-3}CW^{1.94}$</td>
<td>$Y = 7.26 \times 10^{-3}CW^{1.74}$</td>
<td>$Y = 1.97 \times 10^{-3}CW^{2.46}$</td>
<td>$Y = 3.07 \times 10^{-4}CW^{2.64}$</td>
</tr>
</tbody>
</table>

Fig. 2. Force generated at the tips of the chelae (●, crusher; ◊, cutter) of male (a) and female (b) green crabs as a function of carapace width. Broken lines indicate propagated errors (see eq. 6).
able practical utility. There may be variability in the allometry of mechanical advantage of chelae between the Scottish population and the Canadian one, or (more likely) the allometric analysis may be highly sensitive to sample size and variability of measurements between observers (see Clayton 1990). Where differences in mechanical advantage with size have been detected in crabs, they have been attributed to a relative increase in the distance from the fulcrum to the apodeme insertion ($L_1$) and a relative decrease in distance from the fulcrum to the dactyl tips ($L_2$) (Lee and Seed 1992; Taylor 2001). Because a crab can modify the mechanical advantage of the lever system depending upon where in the chela gape the item is grasped, there is likely little selective pressure on the animal to increase the mechanical advantage at the chela tips. With increasing muscle volume in the chela, the absolute force generated increases ($F_1$ in Fig. 1) and thus the absolute force at the chela tips also increases though the mechanical advantage remains the same. The similarity in the mechanical advantage of the cutter between the sexes probably reflects its common use by both

Fig. 3. Calculated force generated at the tip of the chela (male crusher) over a range of carapace widths, with accompanying validation from the literature.

Fig. 4. Calculated force generated along the length of the dactyl for the crusher of a male crab of 58 mm carapace width. Note the end at ~0.25, where the mechanical advantage is equal to 1.0.
sexes. This chela is unlikely to be used to maximize force production (for which the crusher is used) or to play as large a role in intraspecific interactions as the crusher (for example, see Stein 1976; Sneddon et al. 1997; Mariappan et al. 2000) and thus the two sexes may converge on the same mechanical advantage, since the needs of the cutter (object/food manipulation and holding; Elner 1978) are the same for the two sexes.

Gape angle does not change with body size, and this combined with a constant mechanical advantage suggests that the basic mechanics of the chela do not change appreciably during growth. Larger animals do not produce a larger gape angle, though they take larger prey than smaller animals (Elner 1980; though see also Juanes 1992; Seed and Hughes 1995). An increase in gape angle may be expected, as that would allow the placement of a larger prey item closer to the fulcrum, thus increasing the mechanical advantage and therefore the force delivered. However, as \( L_1 \) and \( L_2 \) increase with growth, the maximum gape for a given gape angle increases and so an object of a given size may be moved closer to the fulcrum. For example, a 30 mm CW male crab could fit a 6.3 mm long shell in the maximum gape of its crusher (calculated from Table 4), where the mechanical advantage is approximately 0.33, while for a 60 mm CW crab, a shell of the same size would fit approximately 45% of the distance from the fulcrum to the tip, where the mechanical advantage would be on the order of 0.75 (see also Fig. 4 and Preston et al. 1996). In addition, increasing the gape angle above 60° may produce force vectors exerted on a rounded prey item (e.g., gastropod or bivalve shell) that act to push the item out of the chela. At a gape angle of 60°, the \( x \) component of the vector is 0.866 (i.e., \( \cos 60° \)) and \( y \) component is only 0.5 (i.e., \( \sin 60° \)). Therefore, despite the chela denticles there is a large outwardly directed force, and this may be expected to increase with gape angle. A gape angle of 60° may be the optimum above which prey items are pushed out of the chela rather than compressed. Of further note is that the generally lesser gape angle of the male crusher is consistent with the latter suggestion, as the male crusher is larger and prey size is related to crab size (see Fig. 3 in Elner 1980), so the male may take larger prey. Larger prey may be expected to require a greater compressive component (Elner 1978; Preston et al. 1996) than smaller prey, and thus the male crusher need not open as wide as the others, as this would increase the force in the \( x \) component, or outward direction, the opposite of what is required. In addition, Scherer and Reise (1981) and Ropes (1968) report that males, at least at some sites, take a larger proportion of hard-shelled prey than females, who preferentially take annelids. This observation is likely related to the limitation of forces generated by the smaller chela of the female.

Male crabs have a larger maximum gape than females and the increase in this with body size is also greater for the males than for the females. This difference does not appear to be due to differences in gape angle, which are quite similar between chelae, but is due to an increase in the size of the chela (chela heights \( L_1 \) and \( L_2 \)). Yamada and Boulding (1998) conducted a similar analysis of gape width on body size for three crab species (\( H. nudus \), \( L. bellus \), and \( C. orege- nensis \)) and found untransformed regression slopes of 0.36–0.95 when mid-dactyl gape was regressed against body mass. We conducted a similar untransformed (OLS) regression analysis for comparison, using body mass in place of CW, and found slopes of 0.175 ± 0.02 (mean ± SE) for the female cutter, 0.209 ± 0.02 for the female crusher, 0.275 ± 0.02 for the male cutter, and 0.329 ± 0.03 for the male crusher. The scaling of maximum gape with body mass is thus less for the green crab than for the other three species. Of interest is that \( H. nudus \) showed the lowest slope value (i.e., most similar to the green crab) and Yamada and Boulding (1998) classified \( H. nudus \) as an omnivore, while the other two specialize on hard-shelled prey. Therefore, for the green crab, also a generalist, the relationship of gape with body size is more similar to the generalist \( H. nudus \) than to the predators that specialize on hard-shelled prey.

Within each sex, the surface area of the closer apodemes differ between the cutter and crusher. Despite this absolute size difference, the rates of increase in apodeme surface area during the growth of the crab are similar, and isometric, for the two chelae. Similar isometric apodeme growth has been reported for the male rock crab, Cancer irroratus (Block and Rebach 1998). Lee (1993) reported only the untransformed regression of apodeme area as a function of CW (sexes combined) for crabs in Wales; slopes were 2.7 for the crusher apodeme and 1.8 for the cutter. We reanalyzed our apodeme data to match that study and found untransformed (OLS) slopes of 1.33 ± 0.13 (mean ± SE) for the female cutter, 2.20 ± 0.19 for the female crusher, 3.31 ± 0.70 for the male cutter, and 4.81 ± 0.88 for the male crusher. Our results suggest that there is considerable variability between the sexes that was masked in Lee’s (1993) paper because the sexes were combined.

Considerable work has been done on the allometry of the apodeme area as it relates to chela height (Elner and Campbell 1981; Blundon 1988; Kaiser et al. 1990; Block and Rebach 1998; Taylor 2001), and Lee (1993) points out that the regression of apodeme area on chela height is stronger than when it is regressed on CW. However, in applied fisheries management, CW is the more commonly measured dimension and so we were interested in the relationships between chela morphometrics and body size. We accept that the derived regressions \( (r^2 = 0.61–0.87; \text{Table 6}) \) are not as statistically robust as if we had used chela height \( (r^2 \text{ values from previously cited studies are above } 0.64–0.96) \), but we believe that the derived relationships and force modelling based on them are applicable to a larger body of measured crab populations by relating to CW rather than chela height.

The preceding morphometric analysis showed that despite great geographic distances, chelal dimensions and mechanics are very similar between the populations on either side of the Atlantic Ocean. This implies that biomechanical characteristics found for one population will be largely applicable to the other. As the green crab continues to invade new habitat (e.g., Cohen et al. 1995; Grosholz and Ruiz 1995; Grosholz et al. 2000), confirmation of the homogeneity of structures will gain in importance as increasing numbers of investigators examine these animals in an increasing diversity of environments.

**Force generation**

Forces generated by the chelae of the male green crab scale with body size with an exponent greater than 2.4,
while for the female it is less than 2.0. Levinton and Judge (1993) provide a scaling exponent (1.76) for the fiddler crab (Uca pugnax) which is very similar to that which we found for the cutter of the female green crab. In contrast to these derived power curves for the green crab, the forces generated by the American lobster (Homarus americanus) and C. irroratus are reported to scale linearly with body size (Elner and Campbell 1981; Block and Rebach 1998). Taylor (2000, 2001) states that maximum claw biting force is negatively allometric with claw size. This observation may be consistent with our findings provided that claw size (= chela height) is sufficiently positively allometric with body size to exceed the negative allometric decline of force with claw size. If so, force may still show a positively allometric relationship with body size.

Predicted forces at the chela tips agree quite well with previously measured forces generated by the green crab. In addition to the forces illustrated in Fig. 3, Brandwood (1985) reports forces of between 0 and 80 N exerted by the green crab on the gastropod Littorina rudis. The three extreme points shown in Fig. 3 of Preston et al. (1996), ~160 N, are unusually high, as Elner (1978) reports a maximum force of approximately 90 N for a 72 mm CW crab, and Kaiser et al. (1990) report a maximum of 112 N for crabs between approximately 40 and 90 mm CW. Thus, while they cannot be considered outliers, they likely represent extreme crushing force generation rather than normal events.

The forces generated by these crab chelae are formidable for such small animals; however, are they sufficient to crack or crush their prey? Preston et al. (1996) provide data that the gastropod Callistoma sp. can withstand 450–500 N at its lips and around 700 N when outright crushing of the shell is attempted. Brandwood (1985) reports forces of between 20 and 300 N when L. rudis shells are broken. Boulding and LaBarbera (1986) demonstrated that 200–400 N was sufficient to break large bivalves (Prototheca staminea), provided they were repetitively loaded a large number of times. Blundon and Kennedy (1982) provide considerably lower estimates of shell strength (less than 90 N to break the bivalves Malinia lateralis, Macoma balistica, M. arenaria, Mytilopsis leucophaeta, Macoma michelli, and Ischadium recurvum less than 50 mm in length). These low shell-strength estimates for M. arenaria are significant, as predation on this bivalve by green crabs is of concern for commercial harvesting, and Fig. 2 suggests that both male and female crabs at the lower range of our measured sizes may exert forces sufficient to break M. arenaria shells (2–59 N for M. arenaria <50 mm in length, according to Blundon and Kennedy 1982). Escaping predation by increasing size, according to our calculations of crab chelal force, is not likely to occur at less than 50 mm length for bivalves in the Nova Scotia area, based on Campbell’s (2001)² finding of a maximum of 80 mm CW for the green crab (which would be capable of exerting a force of approximately 95 N, sufficient to break shells 50 mm long; Fig. 2). MacPhail et al. (1955) found that green crabs will successfully prey on M. arenaria as long as the crab is wide, while Eheling et al. (1964) found that Mytilus edulis over 45 mm in length (requiring crushing loads in excess of 200 N; Elner 1978) were immune to predation by crabs up to 57 mm CW, showing a size-related ability to escape from predation for some taxa.

Behavioural alternatives to outright crushing by green crabs include a chipping action at the shell edges (Ropes 1968; Scherer and Reise 1981), insertion of the chela into gastropod shells and removal of the animal without damaging the shell (Crothers 1968; Rangeley and Thomas 1987), and manipulating bivalve shells within the crusher to apply repeated crushing forces in attempts to find/generate cracks and weak areas (Elner 1978; Boulding and LaBarbera 1986). Based on the preceding suggestion of force vectors, it is likely that large shells may not simply be too tough to be crushed, but rather the resultant force vector may not be sufficient to crush the shell, owing to lack of space in the chela gape. Thus, a larger shell, if selected for only by green crab predation, may not have to be all that much stronger than a smaller shell, as the crab cannot fit a larger shell as deeply into its chela gape. Instead, on the larger prey item it must use the chela tips, which produce a relatively low force. Obviously, a complex interplay of prey-shell strength and size, crab handling ability (i.e., chela gape), and crab behaviour in determines the effectiveness of predation.

Error in the estimation of all parameters has been included within the force model. However, muscle stress is not a static parameter like apodeme area and the linear measures L₁ and L₂. Muscle stress may vary according to the motivational state of the animal, and the modelled stress values can represent only mean values. Warner et al. (1982) used two different nerve-stimulation strategies to cause chelal contraction — exposure to either a high potassium concentration or a caffeine solution — and found very similar mean stress values of 66–67 N·cm⁻² for the crusier and 42–47 N·cm⁻² for the cutter. Abby-Kalio and Warner (1984) found comparable stress values (60–78 N·cm⁻² for the crusier and 44–54 N·cm⁻² for the cutter). Muscle stress is treated as a single unvarying value, yet it is reasonable to presume that it will vary in time as the chela is being closed and may vary along the length of the apodeme. It may further be expected to be affected by the health of the animal and the moult stage. A further complication with the muscle-stress estimate is that muscle stress may decline as a function of animal size (Elner and Campbell 1981; Blundon 1988; Taylor 2001). However, this has not yet been documented for the green crab, and Taylor (2001) found that the decline with size was not consistent between genera (Menippe, Homarus, Cancer) and warns against extrapolation outside those taxa for which it is demonstrated. Therefore, while these force estimates produced by the model are reasonable, it is important to recognize that they are based in part on an “artificial” muscle-stress value. Intriguing future work would include analyzing and modelling the time course of these muscle-stress values during crabs’ crushing behaviour.

Another issue surrounding the use of the muscle stress is the circularity of the reference. The common method (e.g., Elner and Campbell 1981; Warner et al. 1982; Abby-Kalio and Warner 1984) of estimating muscle stress is to externally measure the chela force exerted and then rearrange eq. 4 to isolate and solve for σ. Our use of this stress value to estimate forces means that the force estimate is dependent upon these other force measurements used to derive σ. That is, we are merely calculating what others have measured directly. The advantage of our approach is that we have extended others’ findings to other crab sizes (i.e., smaller crabs,
for which it is very difficult to accurately measure forces), making it feasible to estimate the forces generated by crabs of sizes not yet measured.

The present study has presented evidence for two aspects of the biology and ecology of the green crab. Firstly, despite large geographical separation, the morphometrics of the recently arrived green crabs in eastern Canadian waters are very similar to those of the (presumed) founding population in western European waters. This similarity may be due to either insufficient time for morphological changes to have occurred, or to the fact that the crabs are operating within the same niche from which they came, and so do not require significant adaptation to the local environment. At present there are insufficient morphometric studies from a wide variety of geographic locations to allow comparisons. As the green crab continues its invasion of the east and west coasts of North America, comparative morphometrics can be expected to yield valuable results. The second aspect of the ecology of the green crab is that we now have quantitative estimates of maximal chelal forces over a “continuous” range of sizes rather than for only a few discrete (and arbitrary) sizes. This should allow greater accuracy in predicting predation ability and prey selection by these animals. The presented model allows predictions of prey selection or crushing ability based on crab size to be tested; combined with future field and laboratory behavioural investigations, it should lead to a greater understanding of the role of the green crab in nearshore environments.

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