

Spatial scaling from latitudinal gradients: growth rates in the American lobster *Homarus americanus*

Jamie L. D. Raper^{1,*}, David C. Schneider²

¹Department of Biology, Memorial University of Newfoundland, St. John's, Newfoundland A1B 3X9, Canada

²Department of Ocean Sciences, Memorial University of Newfoundland, St. John's, Newfoundland A1C 5S7, Canada

ABSTRACT: Estimates of vital rates, at appropriate spatial scales, are essential for stock assessment and sustainable management of exploited populations. Substantial research efforts are often required to estimate vital rates, with results of unknown applicability to other locations or larger areas within the species range. We investigated whether a rate variable, growth, can be estimated across the entire range of a species. We used data from the commercial range of the American lobster *Homarus americanus* to develop a model to calculate von Bertalanffy growth parameters at any location in that range. Fixing the maximum size parameter (L_{∞}) to a biologically reasonable value resulted in more realistic estimates of growth than estimating this parameter from data at any one location. The growth parameter k decreased with latitude at a rate of 0.51 % per year per degree of latitude for males and 0.40 % for females. The von Bertalanffy parameters apply to individual growth; the bias in using these parameters to estimate population growth was minor. The underlying mechanism for the latitude model was investigated by GIS mapping of candidate environmental factors: depth, temperature, and salinity. Multiple regression analysis showed a significant positive relationship between the growth parameter k and temperature. Growth rates of American lobster can now be estimated on a site-specific basis without having to undertake resource-intensive tag-recapture field studies or adopting an estimate from a distant location. Similar approaches with other vital rates allow calculations at any spatial scale, from local scales to those of populations and ecosystems.

KEY WORDS: Growth modeling · American lobster · von Bertalanffy · Tag-recapture

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INTRODUCTION

A fundamental problem in ecology is that patterns and processes at one spatial or temporal scale do not necessarily translate to other spatial and temporal scales (Levin 1992, Schneider 2009). When examining vital rates in a population, we are often interested in values at the scale of an ecosystem or species range, yet observations are confined by logistics to local areas. These localized measurements do not necessarily apply at the larger scale of management areas, stocks, or populations.

Measurements of vital rates, such as recruitment, mortality, and somatic growth, are necessary for the management and conservation of economically im-

portant marine species. Estimates of growth are required to establish a minimum legal size for harvesting based on maximum yield (Wilder 1953), optimum yield (Walters 1969), or egg-per-recruit models (FRCC 1995). Growth information has been used to develop bioeconomic models for management (Comeau & LeBreton 2010) and to compare stocks (Cooper & Uzmann 1971). Growth rates are necessary when evaluating restoration efforts in response to sudden population declines (French McCay et al. 2003) as well as enhancement measures (Chandrapavan et al. 2010). Growth parameters are also used to calculate yields and exploitation rates (Fogarty 1995). Growth rates can be used as a baseline to monitor changes over time. Models that allow estimates to be calcu-

*Email: jamie.raper@mun.ca

lated at any location and any spatial scale within a species range allow best use of local data within the range of a species (Currie & Schneider 2011).

Growth rates in marine species vary geographically. This variation can be due to average annual temperature or latitude (Jensen et al. 2000), habitat area (Durham et al. 2005), density (Steneck 2006), or the duration of the growing season (Durham et al. 2005, Houston & Belk 2006). Photoperiod, food availability, and salinity can also influence growth, depending on life stage (Templeman 1936a). Growth in marine crustaceans notably depends on temperature via increased molt frequency (Aiken & Waddy 1986) and duration of the molting season above a critical temperature (Aiken 1980).

The American lobster *Homarus americanus* occupies a latitudinal range that exposes it to temperatures ranging from subarctic waters of northern Newfoundland to warm temperate waters of North Carolina (Pezzack 1992). Lobsters range from shallow coastal waters to offshore locations up to 700 m deep (Cooper & Uzman 1971). The range of this species encompasses the strongest latitudinal gradient in ocean temperatures in the world (Springer 2011), 0 to 7°C in winter and 10 to 24°C in summer (Parr 1933). Lobster growth rates within this range vary substantially, with a north to south trend (Russell 1980) that is consistent with what is known about the effect of temperature on growth in this species.

This geographic trend in growth, together with the known physiological effects of temperature on growth in lobsters, suggests that a general growth model could be developed, allowing site-specific estimation of growth parameters based on latitude. A model of growth as a function of latitude (and hence temperature) would reduce the cost for resource-intensive tag-recapture studies, which are otherwise necessary for site-specific calculations in the context of resource management, conservation, or effects of global warming. A further advantage is that growth parameters at any site of interest would not need to be estimated from a site with data chosen by some arbitrary criterion, whether proximity, similar water depth, or whatever environmental data happen to be available. A general model would also allow mean growth rates to be estimated at any spatial scale, to address questions at the appropriate spatial scale for stock assessment (e.g. Springer 2011), environmental monitoring, evaluating conservation measures, or projecting effects of climate change.

The ecological literature is replete with models to calculate growth from size-at-age data (Quinn & Deriso 1999), but few of these can be modified for use

with tag-recapture data. We chose the von Bertalanffy growth model because it is widely used and its parameters are biologically interpretable, the result of the difference between anabolic and catabolic reactions within an individual. It also has a form that can be used for tag-recapture data without knowledge of age. This model has the additional advantage that it is well studied, with known biases and corrections (Sainsbury 1980, Maller & DeBoer 1988). The von Bertalanffy model produces curves that closely resemble (1) curves based on indeterminate growth with an increase of energy allocated to reproduction with age (Kozłowski 1996) and (2) stepwise growth increments based on crustacean molt intervals (Caddy 2003).

The von Bertalanffy growth function has been used to estimate lobster growth rates in >15 studies within the geographic range of the commercial lobster fishery, which extends from Newfoundland (Ennis et al. 1982, 1986, 1989) to the Bay of Fundy (Campbell 1983), Maine (Krouse 1977), and Massachusetts (Fair 1976). The major impediment to developing a general growth model in this species is the absence of a reliable method of determining age in the wild. All hard tissues are shed and replaced through regular ecdysis, leaving no record of age in the body. Measuring lipofuscin, or 'age pigments', found in the brain tissue of crustaceans is a possible solution, but this method cannot be applied to large sample sizes because lobsters have to be sacrificed for the pigments to be quantified, and the pigment accumulation is affected by environmental conditions, so the method must be calibrated separately for each location (Wahle et al. 1996). Because size-at-age cannot be directly measured, we rely on tag-recapture studies to determine growth parameters for lobster. Several procedures exist to estimate von Bertalanffy growth parameters from tag-recapture data. These are known to produce disparate (sometimes biologically unreasonable) parameter estimates, and thus, in the present study, we evaluated alternative procedures using data from throughout the commercial range. We further anchored the study with data from field studies at the northern end of the range. The von Bertalanffy growth parameters were estimated from data at each site, and the relationship between growth rate and latitude was then determined and used to develop an equation that estimates the growth rate for *Homarus americanus* anywhere within the commercial range. We then used a geographic information system (GIS) to investigate the relation between growth rate and a variety of oceanographic factors (depth, temperature, salinity) likely to affect growth rates.

MATERIALS AND METHODS

Field tagging

Tag-recapture studies were carried out in 2 sites in Newfoundland (Fig. 1). The sites were chosen to represent the latitudinal range of the coastline: Port-aux-Basques (47.57° N, 59.14° W) at the southern tip of the west coast and Port-au-Choix (50.72° N, 57.33° W) close to the northern boundary of the American lobster's range.

Lobsters were captured by professional fishermen using commercial lobster traps. Each lobster was tagged with a polyethylene streamer tag bearing a unique ID number. These tags are inserted through the dorsal musculature between the carapace and abdomen and are usually retained through the molt. The carapace length (CL) was measured from the posterior edge of the eye socket to the edge of the carapace, parallel to the dorsal midline, to the nearest mm with vernier calipers. The size ranges of lobsters tagged were 57 to 122.5 mm (males) and 61 to 129 mm (females) in Port-aux-Basques and 66.5 to 134.5 mm (males) and 66 to 151 mm (females) in Port-au-Choix. Lobsters were released as close to their capture site as possible shortly after tagging.

Tagging was first conducted during September and October of 2009, beginning late in September to target post-molt lobsters. Because lobsters would

then experience substantial removal during the spring fishing season before their next molting period, there was concern that the recapture rate would be low at the time of the fall molt in 2010. To improve the sample size for recaptures, an additional tagging session was conducted from May to June 2010 during the commercial fishing season. Lobsters that did not meet the size requirements for landing were tagged, as well as ovigerous and v-notched females, which cannot be harvested. Recaptures were conducted from September to October 2010.

Historical tagging data

In addition to the field efforts from this project, all of the available historical tagging data sets (51) were compiled from various locations throughout the species' range. Any tag-recapture study carried out over at least 1 molting season with records of CL was included. The data sets from Newfoundland were error checked by personnel at Fisheries and Oceans Canada (DFO), St. John's. Other data sets were also from government agencies, and so we assumed the data met similar standards of quality assurance and quality control. Tagging data sets collected are summarized in Table 1. The locations of all tagging sites are shown in Fig. 1.

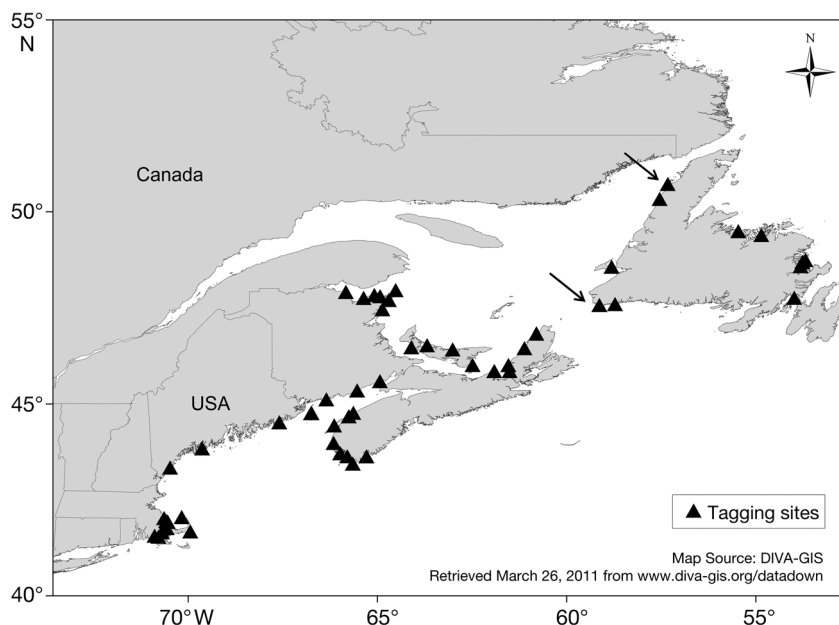


Fig. 1. *Homarus americanus*. Tagging locations in the northwest Atlantic. Arrows indicate field sites in Newfoundland: Port-aux-Basques (47.57° N, 59.14° W) and Port-au-Choix (50.72° N, 57.33° W)

GIS analysis

Bathymetry data were obtained from the General Bathymetric Chart of the Oceans (BODC 2010) as a 30 arc-second grid. Temperature (Locarnini et al. 2010) and salinity (Antonov et al. 2010) data were obtained from the World Ocean Atlas as ¼ degree annual means and were available for multiple depths at each sample point. ArcGIS® was used for all spatial analyses. All layers were projected with the North America Albers Equal Area projection. Tagging sites were reported as a single latitude/longitude coordinate usually corresponding to the harbor out of which the study was based. A 15 km buffer zone was delineated around each tagging site to account for the area covered by a typical tagging study as well as

Table 1. *Homarus americanus*. Historical tagging data compiled for growth analysis. DFO: Fisheries and Oceans Canada; MADMF: Massachusetts Division of Marine Fisheries; NL: New Foundland; NB: New Brunswick; NS: Nova Scotia; PE: Prince Edward Island; ME: Maine; MA: Massachusetts

Region	Site	Dates	Records of growth (n)	Size range (carapace length, mm)	Source
Newfoundland	Arnolds Cove, NL	1970–1989	205	42–125	R. Collins & G. Ennis, DFO
	Bellburns, NL	1976–1981	300	62–127	R. Collins & G. Ennis, DFO
	Boswarlos, NL	1974–1981	92	69–132	R. Collins & G. Ennis, DFO
	Comfort Cove, NL	1971–1975	176	46–105	R. Collins & G. Ennis, DFO
	Duck Islands, NL	1997–2008	284	69–135	J. Janes, DFO Oceans
	Leading Tickles, NL	2004–2006	103	68–132	J. Janes, DFO Oceans
	Round Island, NL	1997–2008	275	54–139	J. Janes, DFO Oceans
	Shag Rocks, NL	1976–1984	1034	69–144	R. Collins, DFO
	St Chads, NL	1968–1976	157	49–145	R. Collins, DFO
Gulf of St. Lawrence	Anse-Bleu, NB	1994–1997	55	54–89	M. Comeau, DFO
	Ballantynes Cove, NS	1986–1987	124	54–130	M. Comeau, DFO
	Baxters Cove, NS	2000–2001	3	71–102	M. Comeau, DFO
	Beach Point, PE	1982–1983	51	61–120	M. Comeau, DFO
	Belledune, NB	1980–1983	563	52–138	M. Comeau, DFO
	Caraquet, NB	1993–1999	343	53–133	M. Comeau, DFO
	Egmont Bay, PE	1982–1983	248	48–97	M. Comeau, DFO
	Le Goulet, NB	1996–1998	7	59–98	M. Comeau, DFO
	Malpeque, PE	1989–1990	401	50–101	M. Comeau, DFO
	Margaree, NS	1984–1993	375	53–117	M. Comeau, DFO
	Miscou, NB	1994–1998	73	54–117	M. Comeau, DFO
	Pleasant Bay, NS	1988–1993	262	54–128	M. Comeau, DFO
	Port Hood, NS	1988–1993	867	54–143	M. Comeau, DFO
	Stonehaven, NB	1994–2000	52	53–111	M. Comeau, DFO
	Tracadie Bay, PE	1984–1985	11	56–111	M. Comeau, DFO
	Val Comeau, NB	1984–1987	9	88–112	M. Comeau, DFO
Bay of Fundy	Alma, NB	1979–1986	251	66–187	P. Lawton, DFO
	Chance Harbour, NB	1979–1986	793	61–186	P. Lawton, DFO
	Clarks Harbour, NS	1979–1982	16	79–122	P. Lawton, DFO
	Delaps Cove, NS	1979–1983	17	106–158	P. Lawton, DFO
	Flagg Cove, NB	1990–1993	6	81–128	P. Lawton, DFO
	Little River, NS	1986–1988	6	21–149	P. Lawton, DFO
	Lower Wedgeport, NS	1983–1986	29	95–152	P. Lawton, DFO
	Lower West Pubnico, NS	1984–1987	5	36–80	P. Lawton, DFO
	McNutt Island, NS	1982–1987	72	21–149	P. Lawton, DFO
	North Head, NB	1977–1988	739	60–198	P. Lawton, DFO
	Port Maitland, NS	1978–1987	84	67–127	P. Lawton, DFO
	St Martins, NB	1979–1994	133	63–182	P. Lawton, DFO
		Victoria Beach, NS	1993–1995	9	78–128
Maine	Boothbay Harbor, ME	1975–1976	25	81–102	Krouse (1977)
	Jonesport, ME	1975–1976	23	81–113	Krouse (1977)
	Kennebunkport, ME	1975–1977	10	81–102	Krouse (1977)
Cape Cod	Canal, MA	1979–1981	9	68–90	R. Glenn, MADMF
	Chatham, MA	1984–1989	3	91–129	R. Glenn, MADMF
	Cole's Hole, MA	1971–1974	15	77–103	R. Glenn, MADMF
	Manomet, MA	1970–1977	240	64–95	R. Glenn, MADMF
	Provincetown, MA	1969–1972	14	55–162	R. Glenn, MADMF
	Rocky Point, MA	1971–1977	154	64–107	R. Glenn, MADMF
		White Horse, MA	1973–1977	111	52–99
Buzzards Bay	Lower Buzzards Bay, MA	1971–1972	7	70–105	R. Glenn, MADMF
	North Ledge, MA	1969–1972	103	70–101	R. Glenn, MADMF
	Upper Buzzards Bay, MA	1982–1984	24	67–92	R. Glenn, MADMF

localized lobster movement. A polygon vector layer of world exclusive economic zones (VLIZ 2011) was applied as a mask over the buffer zones so that land values would not be sampled. The masked buffer zones were used to clip data from the interpolated raster layers for bathymetry, temperature, and salinity. Mean temperature and salinity were calculated at the depth level that most closely corresponded to the average depth at each site.

Quantitative analysis

Separate analyses were carried out for males and females. Only lobsters that exhibited an increase in CL > 3 mm were considered for analysis. This was to exclude lobsters that did not molt between captures, assuming a 3 mm measurement error based on lengths recorded from lobsters that were captured multiple times during a single tagging period.

The von Bertalanffy growth function (vBGF) with 2 parameters, the growth coefficient k (growth rate, yr⁻¹) and asymptotic length L_∞ (maximum size), was estimated for males and females at each site using non-linear least squares analysis on 2 versions of the Fabens tag-recapture equation. The first version (Fabens 1965) gives the change in CL (ΔL) as a function of the initial length (L_1) and time at large (Δt).

$$\Delta L = (L_\infty - L_1)(1 - e^{-k\Delta t}) \quad (1)$$

The second version is a modification by Quinn & Deriso (1999), which reorganizes the equation in terms of post-molt length (L_2).

$$L_2 = L_\infty(1 - e^{-k\Delta t}) + L_1e^{-k\Delta t} \quad (2)$$

Residual vs. fit plots were examined to determine which model was most appropriate with respect to homoscedasticity of errors. Nonlinear least squares was carried out on Eq. (2) for each site. This resulted in unrealistic parameter estimates at many sites, likely due to the known problem of small numbers of larger individuals at some sites. The problem was resolved by revising Eq. (2) to a model with a single free parameter k , with L_∞ fixed at a constant value, a modification that is consistent with the biological interpretation of L_∞ . Three different methods were used to fix L_∞ at a reasonable value: (1) L_∞ for each location was fixed at the maximum CL recorded in that data set, (2) L_∞ was determined for each location from a regression of the maximum CLs and latitude (Lat), weighted by sample size ($L_\infty = 1.54\text{Lat} + 49.415$ for males and $L_\infty = 1.18\text{Lat} + 66.6$ for females), and (3) L_∞ was fixed across all locations, using the value of

the largest CL recorded for American lobster in the primary literature, $L_\infty = 326$ mm (Wolff 1978). The results were evaluated with respect to several criteria: biologically reasonable values of k and L_∞ , homogeneous scatter in residual vs. fit plots, and minimum standard errors of estimates of k .

Estimates of von Bertalanffy growth rates were regressed against latitude. To determine if sample size had any potential biasing effect on the parameter estimates, sample size was plotted against maximum CL, k , and latitude. The bias due to failure to weight the means appropriately was evaluated by comparing the unweighted estimates to estimates weighted by sample size or weighted by the inverse of the variance (Draper & Smith 1988). A general equation for estimating k from latitude was then developed for males and females.

Validation of the estimated size-at-age

To assess the latitude-based k estimates, we used them to predict ages at a location not used in developing the growth model. In the Magdalen Islands (47.47° N, 61.76° W), Gendron & Sainte-Marie (2006) determined mean length-at-age for American lobster at ages 0 to 3 yr. They also estimate age at the minimum legal size (83 mm). Estimates of age can be calculated by rearranging Eq. (1) as follows:

$$\Delta t = -\frac{1}{k} \ln \left[\frac{(L_\infty - L_2)}{(L_\infty - L_1)} \right] \quad (3)$$

If we take L_1 to be the CL at the first instar (4.7 mm) and assume that the first instar has an age of zero, then Δt becomes t , the age at which a lobster with growth rate k has a CL of L_2 :

$$t = -\frac{1}{k} \ln \left[\frac{(L_\infty - L_2)}{(L_\infty - L_1)} \right] \quad (4)$$

Latitude-based estimates of k at the Magdalen Islands were combined with mean CLs from Gendron & Sainte-Marie's (2006) Table 5 to estimate age via Eq. (4). Age was also estimated at the minimum legal size of 83 mm to compare with their estimated age of 7 to 8 yr.

The bias in size-at-age estimates associated with using k to calculate average somatic growth in the population (Sainsbury 1980) was calculated for males and females from ages 1 to 30 yr (Raper 2012). The relationship between this bias and latitude was determined through examination of the plotted data and through nonlinear least squares analysis to estimate coefficients.

To examine the relationship between growth rate and environmental factors, multiple regression was performed with k as the response variable. The explanatory variables were Lat, depth (D), temperature (Temp), and salinity (Sal). Adjusted (Type III) SS was used for tests. β_0 is the intercept, β_{Lat} , β_D , β_{Temp} , and β_{Sal} are regression coefficients and res is the error. The full model was as follows:

$$k = \beta_0 + \beta_{\text{Lat}} \cdot \text{Lat} + \beta_D \cdot D + \beta_{\text{Temp}} \cdot \text{Temp} + \beta_{\text{Sal}} \cdot \text{Sal} + \text{res} \quad (5)$$

Once the explanatory variables were examined for correlation, latitude was eliminated as an independent factor because of high correlation with temperature. The reduced model was as follows:

$$k = \beta_0 + \beta_D \cdot D + \beta_{\text{Temp}} \cdot \text{Temp} + \beta_{\text{Sal}} \cdot \text{Sal} + \text{res} \quad (6)$$

Regression estimates were carried out using a nonlinear fitting routine, assuming a normal error. Heteroscedasticity was evaluated from residual plots. The criterion for statistical significance was set at 5%.

RESULTS

Newfoundland field tagging

Despite a substantial field effort (57 person days at sea), recapture numbers were low. In Port-au-Choix, 62 of the 1518 tagged lobsters were recaptured the following year. In Port-aux-Basques, 50 of the 1252 tagged lobsters were recaptured. These recaptures resulted in 20 records of growth for Port-au-Choix and 36 records of growth from Port-aux-Basques.

vBGF: 2-parameter estimation

Upon examination of the residual versus fit plots for both Eqs. (1) & (2), it was determined that the model with L_2 as the dependent variable (Eq. 2) was most appropriate for this situation. Heteroscedasticity was eliminated or reduced in the majority of sites using Eq. (2), less so with Eq. (1). The error associated with post-molt length (L_2) was close to constant, while the error associated with the growth increment increased with increasing initial length (L_1) and Δt .

The nonlinear least squares fitting algorithm failed to converge on a parameter estimate for several sites despite numerous adjustments of the parameter starting values. For the locations that did produce estimates, the parameter values for both k and L_∞ were inconsistent and unrealistic in some cases, with large

standard errors. Values for k ranged from -0.182 to 17.1 for males and from -0.242 to 100 for females. Several of the growth rates were negative or had standard errors that exceeded the estimate. Results for k and L_∞ are summarized in Table 2, which shows that fits were often poor when L_∞ was estimated at each site.

vBGF: 1-parameter estimation

Fixing L_∞ and estimating only k by least squares analysis produced more consistent k values, free of negative estimates of growth rates or failure to converge. The results are shown in Fig. 2. $L_\infty = 326$ mm produced the smallest range of k values and was chosen for the subsequent growth model. The relation of maximum recorded CL at each site to latitude was not significant for males ($F_{1,47} = 1.08$, $p = 0.303$) or females ($F_{1,50} = 0.4451$, $p = 0.508$), nor was L_∞ estimated by the initial analysis related to latitude for males ($F_{1,30} = 1.43$, $p = 0.242$) or females ($F_{1,37} = 3.09$, $p = 0.0870$). In the absence of evidence for latitudinal gradient in maximum size, L_∞ was kept fixed at 326 mm across all sites.

Latitude-based growth model

No statistical relationship was found between sample size and maximum CL, k , or latitude. k , estimated with a fixed L_∞ , decreased with increasing latitude.

The unweighted regressions between k and latitude produced the following estimates, where \hat{k} is the estimate of the parameter k :

$$\hat{k} = -0.0036\text{Lat} + 0.213 \quad r^2 = 0.26, p < 0.0001 \quad (7)$$

for males, and for females

$$\hat{k} = -0.0027\text{Lat} + 0.165 \quad r^2 = 0.20, p = 0.001 \quad (8)$$

Regressions of k on latitude weighted by sample size resulted in higher estimates of the latitudinal gradient with improvement in r^2 (Fig. 3):

$$\hat{k} = -0.0051\text{Lat} + 0.283 \quad r^2 = 0.45, p < 0.0001 \quad (9)$$

for males, and for females

$$\hat{k} = -0.0040\text{Lat} + 0.224 \quad r^2 = 0.54, p < 0.0001 \quad (10)$$

Regressions of k on latitude weighted by the inverse of the variance produced estimates of the gradient (on the order of -0.03% per year per degree of latitude) that were similar to the unweighted estimate, with no improvement in r^2 compared to sample size-weighted estimates:

Table 2. *Homarus americanus*. Estimates of growth parameters for male and female American lobsters. k : von Bertalanffy growth constant; L_{∞} : maximum asymptotic length; -: situations in which non-linear least squares analysis failed to converge on parameter estimates. nd: no data

Location	Latitude (° N)	Males				Females			
		k (yr ⁻¹)	SE	L_{∞} (mm)	SE	k (yr ⁻¹)	SE	L_{∞} (mm)	SE
Lower Buzzards Bay	41.54	-	-	-	-	-0.242	0.399	30.3	89.7
North Ledge	41.57	-	-	-	-	100	60.9	88.43	0.483
Upper Buzzards Bay	41.66	1.05	1.15	105	22.9	24.8	14.4	84.7	0.861
Chatham	41.68	nd	nd	nd	nd	-0.222	0.394	78.9	24.8
Canal	41.77	nd	nd	nd	nd	6.25	4.73	88.1	1.22
Manomet	41.93	17.1	4.27	89	0.439	12.3	2.15	88.3	0.312
White Horse	41.93	-	-	-	-	-	-	-	-
Rocky Point	41.95	5.04	0.74	90.1	0.587	5.39	1.11	88.7	0.704
Cole's Hole	42.03	2.87	2.86	92.3	3.68	5.59	2.74	89.8	0.888
Provincetown	42.05	0.0465	0.243	345	1375	0.18	0.193	203	70.5
Kennebunkport	43.34	3.87	1.09	96.1	1.46	-	-	-	-
Clark's Harbour	43.45	3.15	4.07	110	6	1.36	0.535	114	4.17
McNutt Island	43.64	-0.182	0.0441	-4.39	11.1	-	-	-	-
Lower West Pubnico	43.64	-	-	-	-	nd	nd	nd	nd
Lower Wedgeport	43.72	-	-	-	-	0.983	0.88	126	8.63
Boothbay Harbor	43.85	0.0833	0.311	221	467	0.461	0.864	111	22.4
Port Maitland	43.98	0.251	0.0457	143	7.75	0.396	0.0775	121	5.33
Little River	44.44	-	-	-	-	-	-	-	-
Jonesport	44.52	4.22	2.34	103	4.18	6.11	4.39	99.7	2.5
Victoria Beach	44.68	-	-	-	-	-	-	-	-
Flagg Cove	44.76	nd	nd	nd	nd	-	-	-	-
North Head	44.76	0.0411	0.0194	406	126	0.0934	0.0113	212	9.72
Delaps Cove	44.77	-	-	-	-	0.126	0.152	209	121
Chance Harbour	45.12	0.0847	0.0144	291	29.1	0.2	0.0138	167	4.27
St Martins	45.35	0.149	0.0485	232	33.1	0.268	0.0457	160	7.1
Alma	45.60	0.081	0.0192	284	36.4	0.158	0.0247	175	8.26
Ballantynes Cove	45.86	-	-	-	-	-	-	-	-
Baxter's Cove	45.86	-	-	-	-	nd	nd	nd	nd
Port Hood	46.01	0.131	0.0282	151	17.2	-	-	-	-
Beach Point	46.02	-	-	-	-	0.22	0.0787	134	16.7
Tracadie Bay	46.42	-	-	-	-	-	-	-	-
Margaree	46.45	0.268	0.0583	109	8.29	0.03	0.0262	386	274
Egmont Bay	46.48	0.103	0.126	194	153	0.0466	0.105	338	613
Malpeque	46.53	-	-	-	-	0.0239	0.0282	459	462
Pleasant Bay	46.83	-	-	-	-	-	-	-	-
Val Comeau	47.46	-	-	-	-	-	-	-	-
Port-aux-Basques	47.57	0.0397	0.117	503	1198	1.48	0.417	105	2.93
Shag Rocks	47.60	0.181	0.0202	141	3.9	0.168	0.0172	132	2.16
Le Goulet	47.70	-	-	-	-	nd	nd	nd	nd
Stonehaven	47.76	0.0498	0.0313	207	81.5	0.133	0.0776	114	26.6
Arnolds Cove	47.76	0.112	0.045	184	41.2	0.228	0.0298	120	5.01
Caraquet	47.80	0.147	0.0223	133	9.02	0.233	0.0322	106	4.56
Anse-Bleu	47.83	0.0398	0.0839	257	394	0.0841	0.0468	137	38.3
Belledune	47.91	0.0965	0.0167	193	18.4	0.194	0.027	119	6.02
Miscou	47.96	-	-	-	-	0.215	0.0993	108	16.2
Boswarlos	48.57	0.141	0.0859	168	45.1	0.089	0.0531	187	56.4
Round Island	48.58	0.0721	0.0238	190	29.6	0.0352	0.0127	238	51.4
St Chad's	48.69	0.164	0.0298	122	6.77	0.111	0.0245	136	12.2
Duck Islands	48.74	0.0629	0.0204	204	31.9	0.0328	0.0184	267	94.8
Comfort Cove	49.39	0.541	0.149	98.9	4.95	0.424	0.0901	101	4.23
Leading Ticks	49.50	0.0658	0.047	226	96.4	0.175	0.0738	133	15.9
Bellburns	50.34	-	-	-	-	0.145	0.0331	120	8.27
Port-au-Choix	50.72	0.1	0.273	216	350	0.151	0.311	155	132

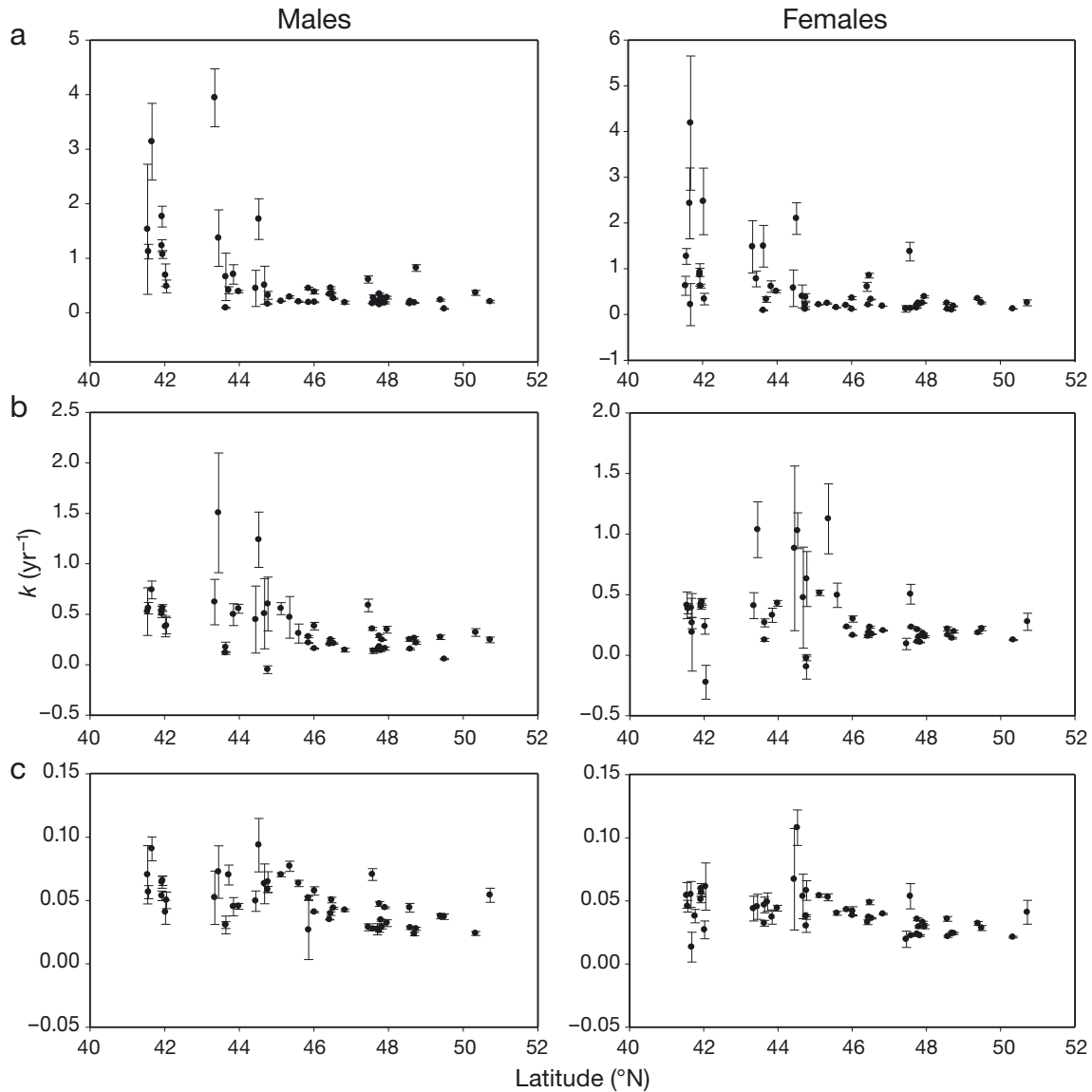


Fig. 2. *Homarus americanus*. Growth parameter k for male and female lobsters estimated by fixing L_{∞} at (a) the maximum carapace length recorded at each location, (b) a value generated by a regression of the largest carapace length recorded and latitude, and (c) the largest carapace length recorded (326 mm) across all sites. See Table 2 for definitions

$$\hat{k} = -0.0031\text{Lat} + 0.177 \quad r^2 = 0.21, p = 0.0008 \quad (11)$$

for males, and for females

$$\hat{k} = -0.0040\text{Lat} + 0.224 \quad r^2 = 0.54, p < 0.0001 \quad (12)$$

Validation of the estimated size-at-age

The latitude model produced accurate estimates of age at a location not used to estimate the model parameters. Estimates of k for the Magdalen Islands location were obtained from Eqs. (9) & (10) ($k = 0.0409$ for males and $k = 0.0341$ for females). Age estimates from Eq. (4) using mean CLs for ages 1, 2,

and 3 yr for L_2 were 1.14, 1.93, 2.92 yr respectively for males and 1.36, 2.32, and 3.50 yr respectively for females. At the minimum legal size ($L_2 = 83$ mm), age estimates from the latitude-based estimate of k were 6.83 yr for males and 8.19 yr for females, closely matching those given by Gendron & Sainte-Marie (2006) (7 to 8 yr).

Bias in estimation of population growth rate

The bias in length estimations (Sainsbury 1980) for male and female lobsters was calculated at ages 8 and 25 yr, using the growth rates from the single-

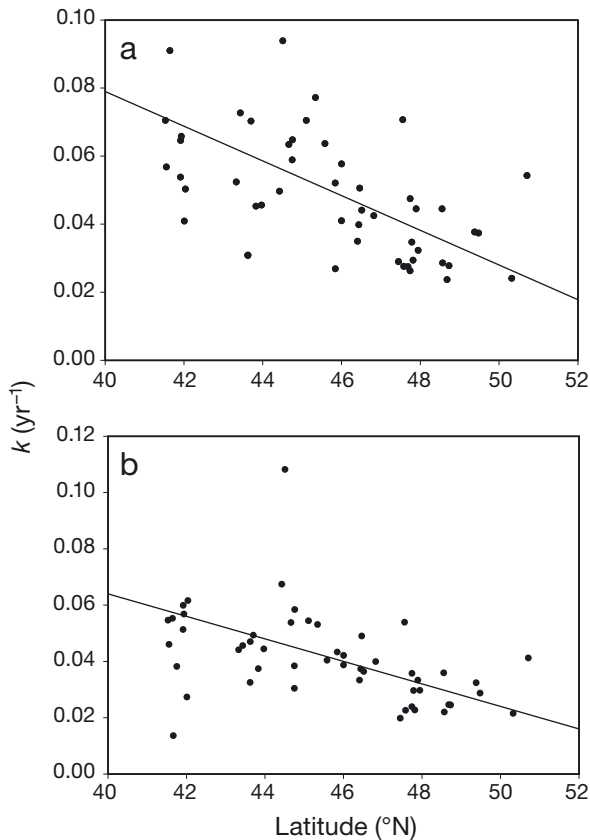


Fig. 3. *Homarus americanus*. Relationship of von Bertalanffy growth parameter k and latitude for (a) male and (b) female American lobsters, with regression lines weighted by sample size

parameter estimation method (Raper 2012). Average bias for male lobsters was approximately 3% at age 8 and 6% at age 25. For females, the average bias was 4% at age 8 and 8% at age 25. Fig. 4 shows the relationship between the bias and latitude for male and female lobsters at ages 8 and 25. In all 4 cases, there was a significant decrease in bias with increasing latitude: males age 8 ($F_{1,48} = 9.44$, $p = 0.0035$), males age 25 ($F_{1,48} = 5.16$, $p = 0.028$), females age 8 ($F_{1,49} = 9.93$, $p = 0.0028$), and females age 25 ($F_{1,49} = 10.45$, $p = 0.0022$).

The bias-corrected estimate of k was determined by the product of the estimate of k as a function of latitude (weighted by the sample size) and the estimate of bias as a function of latitude and age. The magnitude of the bias was linearly related to latitude, but the slope and intercept of this relationship depended on age in a nonlinear fashion that was well described by fitting a quadratic term, A^2 . The slopes and intercepts of the regression of bias on latitude were determined for lobsters ages 1 to 30 yr, and non-linear least squares analysis was performed to determine

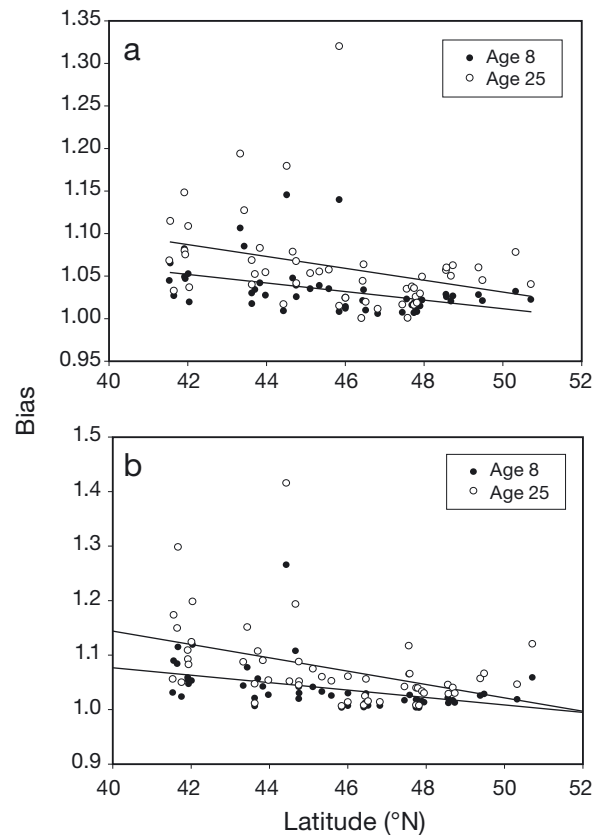


Fig. 4. *Homarus americanus*. Relationship between bias in length-at-age estimates and latitude for (a) male and (b) female lobsters ages 8 and 25 yr

the parameters of the quadratics. The result was the following equations to calculate bias-corrected values of k from both latitude Lat and age A :

$$k' = (-0.0051\text{Lat} + 0.283)[(-0.0077A^2 + 0.033A + 1.0) - (1.5 \times 10^{-5}A^2 - 0.0063A - 0.00072)\text{Lat}] \quad (13)$$

for males, and for females

$$k' = (-0.0040\text{Lat} + 0.224)[(-0.0014A^2 + 0.056A + 0.99) - (2.8 \times 10^{-5}A^2 - 0.0011A + 0.00016)\text{Lat}] \quad (14)$$

Effect of environmental factors on growth rates

Eq. (5) (full model) produced a significant positive relationship between k and temperature in male lobsters ($F_{1,45} = 5.30$, $p = 0.026$), controlling for the remaining variables. No relationship was found between k and latitude, salinity, or depth when controlling for the remaining variables. In females, no significant relationships were found between k and

Table 3. Correlation coefficients (r) with associated p -values between latitude, depth, temperature, and salinity variables. *Significant at $p < 0.05$

	Latitude	Depth	Temp.	Salinity
Latitude	1.0			
Depth	0.51 ($p = 0.002$)*	1.0		
Temp.	-0.87 ($p < 0.0001$)*	-0.63 ($p < 0.0001$)*	1.0	
Salinity	0.13 ($p = 0.38$)	0.56 ($p = 0.002$)*	0.12 ($p = 0.42$)	1.00

latitude, depth, temperature, or salinity after controlling for the remaining variables. Correlations among explanatory variables were substantial (Table 3). When the strong correlation between temperature and latitude was eliminated by removing latitude Eq. (6) (reduced model), temperature emerged as significant, controlling for salinity and depth. The partial regression coefficients were $0.0036 \text{ yr}^{-1} \text{ }^{\circ}\text{C}^{-1}$ ($F_{1,46} = 14.48$, $p < 0.001$) for males and $0.0022 \text{ yr}^{-1} \text{ }^{\circ}\text{C}^{-1}$ ($F_{1,47} = 5.96$, $p < 0.018$) for females. The effect of salinity, controlling for temperature and depth, was significant for males ($F_{1,46} = 5.71$, $p = 0.021$) but not for females ($F_{1,47} = 2.12$, $p = 0.152$). The effect of depth, controlling for salinity and temperature, was not significant for males ($F_{1,46} = 0.00$, $p = 0.971$) or females ($F_{1,47} = 0.14$, $p = 0.715$).

DISCUSSION

The most reliable and biologically reasonable estimates of von Bertalanffy growth rates in lobster came from a 1-parameter model in which the maximum asymptotic size was fixed at a constant value across locations. These estimates of the growth parameter, k , showed a negative relationship with latitude for both male and female lobsters. The bias in using the individually based model to estimate growth rates in a population was minor. Von Bertalanffy growth rates for American lobster can now be estimated from latitude at any location within the current commercial range.

Our model was restricted to the commercial range by lack of data from the southern part of the range. Published estimates of k exist from as far south as Virginia (Russell 1980), but the data upon which these estimates were based could not be located, despite substantial effort. Published estimates of k south of Massachusetts were based on estimation procedures that we found to be unreliable for lobster, especially when L_{∞} is estimated from within a single data set. Our experience demonstrates the need for archiving data sets such as those compiled here.

The tag-recapture study in Newfoundland was carried out over a single year and is therefore subject to error due to unusual conditions. The same is true for 8 of the 51 sites used in the present study. This limitation, and others that attend single season studies, hold throughout the range. We demonstrate a latitudinal trend despite the variation introduced by

this and other sources of uncontrollable variation.

None of the factors latitude, depth, temperature, and salinity had a significant effect on female lobster growth rates when accounting for the other variables (full model, Eq. 5), but temperature had an effect on growth rates for males. When latitude was removed from the model as an explanatory variable (Eq. 6), growth rate was dependent on temperature for both males and females. Because latitude and temperature were highly correlated ($r = -0.87$), there is little room for temperature to emerge as significant after controlling for latitude.

One-parameter vs. 2-parameter growth models

The 1-parameter model (L_{∞} fixed across locations) produced more consistent k values than the 2-parameter model, with no convergence errors. In our study, L_{∞} was fixed at 326 mm, the largest CL recorded (Wolff 1978), with no evidence of latitudinal gradient in maximum size in the 25 values listed by Wolff (1978). It is reasonable to assume that American lobsters from any location are capable of reaching the same maximum size. This is more realistic than estimating L_{∞} from trap data since the largest lobsters may not fit into commercial lobster traps and are unlikely to be represented in the tagging data. Lobsters are heavily exploited (FRCC 2007), which removes individuals from the population before they can reach their maximum size. Population density also affects the size of lobsters found in any given area (Steneck 2006), resulting in poor estimates due to the rarity of large lobsters in dense areas.

CLs as reported by Wolff (1978) were measured from the tip of the rostrum to the edge of the carapace, which results in larger CL values than the conventional method of measuring from the eye socket. A conversion factor of 0.757 was provided by an anonymous reviewer, which brings the maximum CL down to 247 mm. Reducing L_{∞} from 326 to 247 mm reduced the estimate of k by a value of 0.2% for 84 mm CL lobsters and by 0.3% for 120 mm CL lobsters where ΔL

was 4 mm. The reduction in the estimate of k was just over 1% for an unusually large ΔL of 20 mm. We concluded that variations in L_{∞} , whether due to differences in measurement methods, latitude, or sexual dimorphism, have little effect on the estimated k values provided ΔL is small relative to L_{∞} .

Latitudinal gradient in growth rates

The von Bertalanffy growth parameter k decreased with increasing latitude in both male and female lobsters, a result consistent with the biology of this species. Temperature has been shown to have a substantial effect on lobster growth, and latitude and temperature were highly correlated within the latitudinal range of this species. As expected, growth rates were higher in the warmer waters of the southern part of the species' range and decreased along a gradient from south to north. Here, using the regression equations weighted by sample size, growth rates decreased by ~0.5 and 0.4% per year for each degree of latitude for males and females, respectively. At the scale of the commercial range, there was a significant relation between growth rate and GIS-estimated water temperature, controlling for depth and salinity. This result, together with the known relation between growth rate and temperature in this species (Aiken & Waddy 1986), indicates that temperature is largely responsible for the observed latitudinal gradient in growth rate.

Residual effects of salinity on growth rates were detected for males, but the absence of a relation between growth rate and salinity for female lobsters is consistent with other studies (Aiken & Waddy 1986), which found that salinity does not affect physiology below a threshold rarely reached in the benthic environment. However, there are other factors that may play a part in growth rates, such as primary production and habitat type (Aiken 1980). Our estimates (from Eqs. 9 & 10) are free of inconsistencies in estimation procedure, allowing the relation of growth rates to these and other environmental factors to be investigated in future studies.

Another consideration when interpreting the observed gradient in k is that size-at-maturity also depends on temperature while having an inverse effect on growth rates. Once lobsters, especially females, reach maturity, they allocate more resources to reproduction rather than growth, and so the growth rate slows. This may explain why the relationship between latitude and growth rate is stronger for males than females. Since lobsters reach maturity faster in

warmer waters, the slowing of growth occurs at a smaller size and younger age (Ennis et al. 1986, Templeman 1936b). This is a possible reason why the latitudinal differences in k were not more pronounced.

The latitudinal growth model performed well when k was used to estimate age from the mean CL of lobsters in the Magdalen islands. Age estimates produced using k from the latitudinal model and CLs from lobsters ages 1, 2, and 3 yr (Gendron & Sainte-Marie 2006) were better for males (1.14, 1.93, and 2.92 yr) than for females (1.36, 2.32, and 3.50 yr). This is likely because the k values used were determined from a model developed with primarily adult lobster growth data, with different parameters for males and females. In the data reported from the Magdalen islands, the average CLs were given for males and females combined. As noted above, growth in females is more likely to differ from that of males after the onset of maturity, while juvenile growth patterns are similar between the sexes (Campbell 1983).

The bias in growth estimates (Sainsbury 1980) caused by the von Bertalanffy model failing to account for individual variability in growth parameters was minor, on the order of $\leq 8\%$. The magnitude of the bias remains within 1 SE of the estimates of k . However, since the estimate of bias is not constant across latitudes, the bias-corrected equations (Eqs. 13 & 14) were estimated.

These models will be useful for management of the American lobster fishery in North America because growth parameters can now be estimated without arbitrarily choosing growth parameter estimates from one area to apply to a new location. It will also reduce the need for new tag-recapture studies, which are time- and resource-intensive. The cost of such programs is especially high when recapture rates are low, as found in the 2 field studies in Newfoundland, where only 4% of tagged lobsters were recaptured, and only half of those showed growth during the field study. Because the relation between growth rate and latitude was linear, growth can be estimated at any spatial scale, from that of a single site to that of an entire region. For a region, the average growth rate in that region will be that calculated at the latitudinal midpoint.

The problem of scale in ecology (Levin 1992, Schneider 2009) is that estimates of vital rates are often needed at the scale of a population or ecosystem, that logistics constrain measurement to limited areas, and that small-scale measurements do not necessarily scale to that of a population or ecosystem. Several heuristic solutions have been proposed, often based on summation over available data or calibra-

tion against some extensively measured variable (Rastetter et al. 1992, Wiens et al. 1993). One problem attending calibration against a measured variable is the error associated with that variable, if it is large relative to the parameter of interest. We used latitude, which is measured with little error and which was expected to have a strong relation to growth via the known effects of temperature on growth. Currie & Schneider (2011) showed that another biologically important parameter, fecundity, can be estimated from latitude at any point within the species' range of *Homarus americanus*. We extend their result by showing that a time-specific rate (somatic growth) can be estimated at any point and at any spatial scale within the species range of *H. americanus*. A logical extension would be to develop similar models for vital rates such as recruitment or mortality.

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