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Is size at sex transition an indicator of growth or abundance in pandalid shrimp?

P.A. Koeller*, M. Covey, M. King

Department of Fisheries and Oceans, Invertebrate Fisheries Division, Bedford Institute of Oceanography,
P.O. Box 1006, Dartmouth, NS, Canada B2Y 4A2

Abstract

Growth and sexual development of northern shrimp *Pandalus borealis* was determined on the Scotian Shelf during two periods, one of low and one of high population abundance, using deviation and modal analysis. Growth rates were higher during the period of low abundance, probably due to density dependent effects and higher temperatures. Faster growth during the first period was associated with a smaller size at transition (L_t) from male to female and a smaller maximum size (L_{max}), while slower growth during the later period was associated with a larger L_t and L_{max} (and older age). Results are consistent with the theory of invariance in the ratio of pandalid L_t/L_{max} and its implications, i.e. that growth can be determined from measurements of L_t or L_{max} alone. L_t was not a good indicator of short-term changes in population abundance; consequently L_t or L_{max} should be used as measure of growth, not abundance. The theoretical and practical implications of the results are discussed. In particular, it is suggested that decreased fecundity resulting from an increased growth rate and decreased L_t and L_{max} is responsible for the negative lagged relationships between temperatures and abundance in stocks at the southern limit of their distribution. It is also suggested that measurements of L_t and/or L_{max} could be used in quantitative assessment models and to develop harvest limit reference points.

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1. Introduction

Pandalus borealis, the northern pink shrimp, is a protandric hermaphrodite shrimp with a circumpolar distribution in the northern hemisphere. Growth and sexual development of *P. borealis* are of both practical and theoretical interest and are among the most studied aspects in the life history of decapod crustaceans. Management of the large commercial fisheries for northern shrimp in the North Atlantic requires information on growth to validate population at age and

year-class strength estimates usually determined from modal analysis of length frequency data (Frechette and Parsons, 1983). Growth characteristics have also been used to define management units (e.g. Aschan, 2000). On the theoretical side, pandalid shrimp have been used as models in studies of the selective advantages of protandry and the regulation of sex ratios in organisms. The most influential of these in terms of practical application in northern shrimp fisheries management is the sex allocation theory (Charnov, 1982), which predicts that pandalids decrease the size at sex transition (L_t) during periods of low female abundance to compensate for decreased reproductive capacity. This was apparently substantiated by field observations (Charnov and Anderson, 1989) and as a

* Corresponding author. Tel.: +1-902-426-5379;
fax: +1-902-426-1862.
E-mail address: koellerp@mar.dfo-mpo.gc.ca (P.A. Koeller).

result decreases in L_t are often viewed as signs of population decline in stock assessments (e.g. Armstrong et al., 1999). However, Koeller et al. (2000a) showed that increases in L_t also occur at low stock size.

Charnov and Skúladóttir (2000) used field observations from the Icelandic shrimp stocks to show that L_t and the maximum size individuals attained in the population (L_{\max}) were directly related and predicted that their ratio is approximately constant (invariant) for all *P. borealis* stocks. This finding has potential practical applications in stock assessments, because it implies that pandalid growth rates can be determined from simple measurements of L_t or L_{\max} alone. The difficulty in determining age and growth of shrimp and other crustaceans has greatly restricted the use of population models for these species.

In terms of practical applications, the findings on sex allocation (Charnov and Anderson, 1989) and life

history invariants (Charnov and Skúladóttir, 2000) are ambiguous; the first implies that size at transition can be used to determine changes in stock status (abundance of females), whereas the latter implies that it is a measure of individual growth rate. In this paper, the relationship between sexual development and growth rate of *P. borealis* on the Scotian Shelf is explored during two periods when the population abundance was significantly different. The question of whether L_t is an indicator of growth or population size is answered and the practical and theoretical implications of the results are discussed.

2. Methods and materials

Shrimp surveys were conducted on the eastern Scotian Shelf shrimp “holes” (Fig. 1) by the research

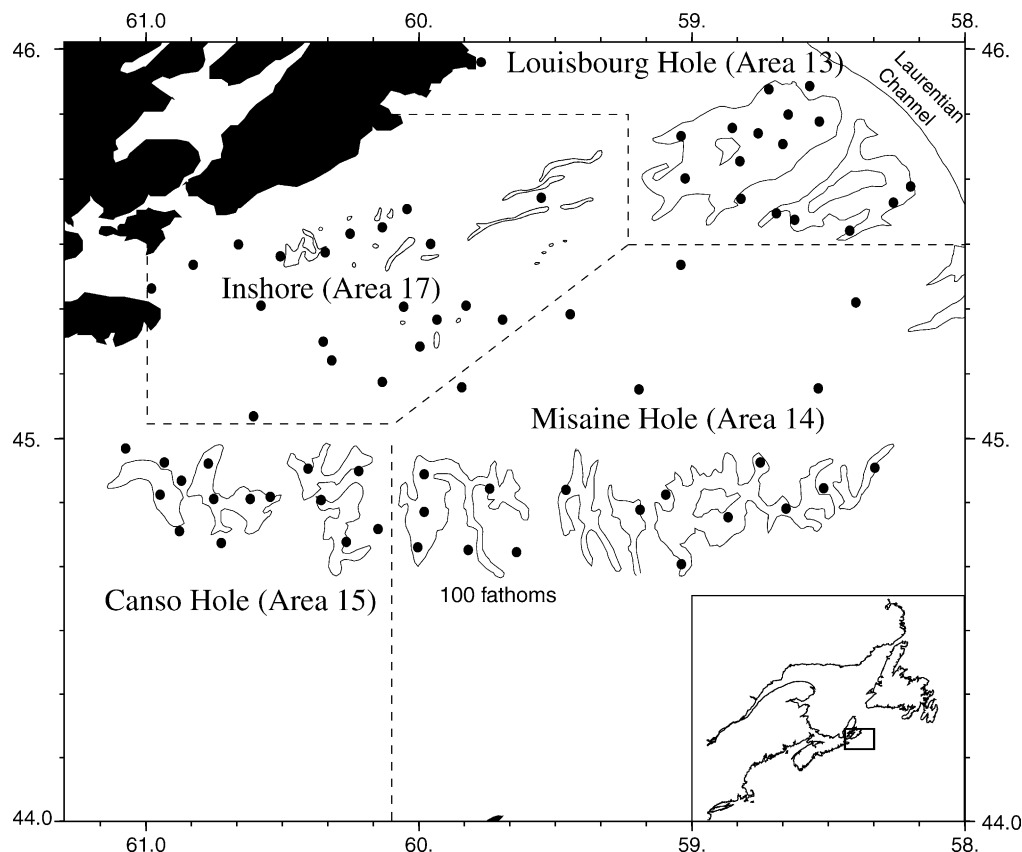


Fig. 1. The eastern Scotian Shelf, showing the shrimp holes and the boundaries of the subareas identified in the text. Coverage was similar for both survey series discussed in the text and only station locations for the June 2000 survey are shown.

vessel “E. E. Prince” of the Department of Fisheries and Oceans, Canada (DFO) in spring (end April–early May) and autumn (October–November) of 1982–1988 inclusive, and in early June 1995–2000 by commercial shrimp trawlers during DFO–industry co-operative surveys. For all surveys, at least forty-five 30 min trawl sets were conducted during daylight hours, allocated approximately equally among the main shrimp “holes” (Louisbourg Misaine and Canso, subsequently called Areas 13, 14 and 15). In 1995–2000 additional coverage (approx. 15 sets annually) was obtained for the newly discovered inshore shrimp grounds (subsequently called Area 17). Stations were allocated randomly within each of the four areas except in Area 14, where the same stations were always fished due to difficulties finding trawlable bottom. RV E.E. Prince used the same trawl (Yankee 36 shrimp trawl, 40 mm codend mesh) throughout its series, whereas three different commercial vessel/trawl combinations were used during 1995, 1996 and 1997–2000, requiring comparative fishing experiments in 1996 and 1997 to allow comparisons across the series in terms of catch rates and size selectivities (Koeller et al., 1996, 1997). Since there were no comparative fishing data between vessels and gears used in 1982–1988 and 1995–2000, catches were adjusted by the differences in wingspread of the trawls used during the two periods. The same codend mesh size (40 mm) was used for both series, and selectivities were assumed to be reasonably similar. Long-term shrimp abundance trends spanning these two periods were also determined from commercial shrimp trawler catch and effort information available from logbooks (Koeller et al., 1997).

At each survey station, approximately 500 shrimp were randomly collected from various locations in the receiving bin and frozen for determinations of carapace length and sexual development stage. Carapace lengths were measured to the nearest 0.1 mm. Length frequencies were smoothed with a 0.9 mm running average, i.e. $(n_1 + n_2 \dots n_9)/9$. Shrimp were identified according to the methods of Allen (1959) and McCrary (1971) as immature, male, transitional, primiparous (females that have never spawned) or multiparous (females that have spawned at least once), with transitional and primiparous representing the new females of that year. Transitionals were absent or rare in autumn surveys because all or almost all had completed sex

change; consequently, only spring surveys were used in analyses requiring summarized data on transitionals. Since transitionals were identified, it was possible to determine actual mean sizes at transition, L_t , rather than L_{50} , the size at which 50% of the shrimp are female. Standardized shrimp catches from each set were calculated from the total weight caught and the area swept by the trawl. Swept area was calculated from the distance traveled during the tow and the wingspread of the trawl determined from trawl design specifications (1982–1988) or actual measurements during the set using a SCANMAR net measuring device (1995–1997).

Two independent methods were used to determine differences in growth between the two time periods: (a) the identification and separation of modes using the method of MacDonald and Pitcher (1979), and (b) a variation of deviation analysis, as described by Skúladóttir (1981). The latter requires the presence of a strong year class throughout a sampling period that spans all ages of that year class and so can be used to determine growth of only such strong year classes. Consequently, a separate deviation analysis was conducted for each area to obtain replicate growth data (one estimate for length-at-age of the strongest year class in each time period and area). Length deviations for each survey were calculated as the difference between the estimated population number of shrimp at each length and the average number of shrimp at that length for the entire survey series:

$$D_{l,t} = N_{l,t} - \frac{\sum N_{l,t}}{t_s} \quad (1)$$

where $D_{l,t}$ is the deviation at length l and time t , $N_{l,t}$ the stratified estimate of shrimp numbers at length l and time t and t_s the number of sampling times. Annual mean lengths of the strong year classes were calculated as the mean of their positive deviations.

The unbiased but approximate growth rates obtained from deviation analysis were used to assign year classes to modes for modal analysis, which can be used to determine growth for all identifiable modes and year classes. Modal analysis is limited by the difficulties in identifying older year classes in the length frequency as modes blend due to decreased growth rates. Identification of sexual stages can sometimes be used to help separate these blended modes into at least 2-year classes (Frechette and Parsons, 1983). Examination showed that, on the Scotian Shelf, tran-

sitionals and primiparous females together constituted a separate year class within the blended last mode of the length frequency (see Section 3). Multiparous females were assumed to be the oldest year class in the length frequency, unless additional modes were distinguishable.

Modal analysis was conducted for Area 13 only. Although the same modes were generally seen in all areas, this area tended to have the clearest and the most consistent separation of modes, possibly due to its physical isolation and geographical location “upstream” relative to the prevailing ocean currents, which would tend to minimize immigration from other areas and “blending” of modes. This analysis therefore resulted in one estimate of length-at-age for each identifiable mode during each of the survey years.

Modal analysis was conducted with the MIX 3.1aa software (Ichthus Data Systems 1994). The smoothed length frequencies were grouped into 3 mm bins before analysis. This resulted in a number of length bins that was close to the maximum allowed by the program (80). Normal distributions were assumed in all cases. Analysis began by entering the estimated number of modes and their means, including those determined by sexual staging, from visual inspection of the length frequency. Proportions and sigmas of all components were initially set to 1 and the proportions for each component estimated using the initial means and sigmas. Estimates of component means, proportions and sigmas and their standard errors were then estimated using the quasi-Newtonian algorithm option without constraints. In most cases, good fits were obtained at this point and no further analysis was conducted. Constraints were applied when the chi-square fit between the actual and expected distribution was poor, or the program failed to find a solution. In these cases, a constraint on the proportion of the last one or two components, based on the relative proportion of the transitional/primiparous versus multiparous shrimp in the sample, was usually sufficient to provide a satisfactory fit. Constraints on means were not used.

The von Bertalanffy growth coefficients were calculated from a variation of the original suggested by Charnov and Skúladóttir (2000), i.e.:

$$L_t = L_{\max}(1 - e^{-k \cdot t}) \quad (2)$$

Since L_t , L_{\max} and the age at transition, t , are known the growth coefficient can be calculated as

$$k = \ln \frac{1 - L_t/L_{\max}}{t} \quad (3)$$

3. Results

Deviation analysis identified a strong year class in each series that was prominent throughout the sampling period (Fig. 2a and b). These were identified as the 1980 and 1994 year classes based on juvenile trawl survey results conducted in February 1999–2001 (Koeller et al., 2001), which showed that 1-year old shrimp are about 8–10 mm in length. This first mode was usually rare in standard survey trawl samples (<25 specimens per survey), although the 1994 year class was clearly identifiable as 1-year old shrimp in 1995 (Fig. 2b). The 2-year classes identified by deviation analysis were prominent in all areas during both series and allowed calculation of their mean positive deviations by area (Fig. 3a and b). Growth was similar in all areas; however, there was more variation during the later period, probably because deviations were calculated from the average of only 6 surveys (June) as compared to 14 (spring and fall) for the earlier period. Growth based on deviation analysis was not significantly different between time periods based on individual area lengths at age (two factor ANOVA, $P = 0.16$); however, von Bertalanffy growth curves fitted to the deviations of all areas combined (Fig. 3c) indicated marginally slower growth from 1995 to 2000.

The results of the modal analysis are illustrated in Fig. 4 for the first year of each time series (1982 and 1994). Transitionals or primiparous females were never present during the fall 1982–1988 surveys (fall data not shown) because all shrimp in these stages had completed sex change and extruded their eggs by October–November. Primiparous females were also absent from spring surveys in this series (Fig. 4a), probably due to the earlier sampling time (by about 1 month) relative to the 1995–2000 series (Fig. 4b). Apparently no shrimp had completed transition in late April to early May 1982–1988, but 1 month later in 1995–2000 many, but not all, had. Transitionals and primiparous females were always common during the June 1995–2000 series and together were considered as a single, distinct year class because these

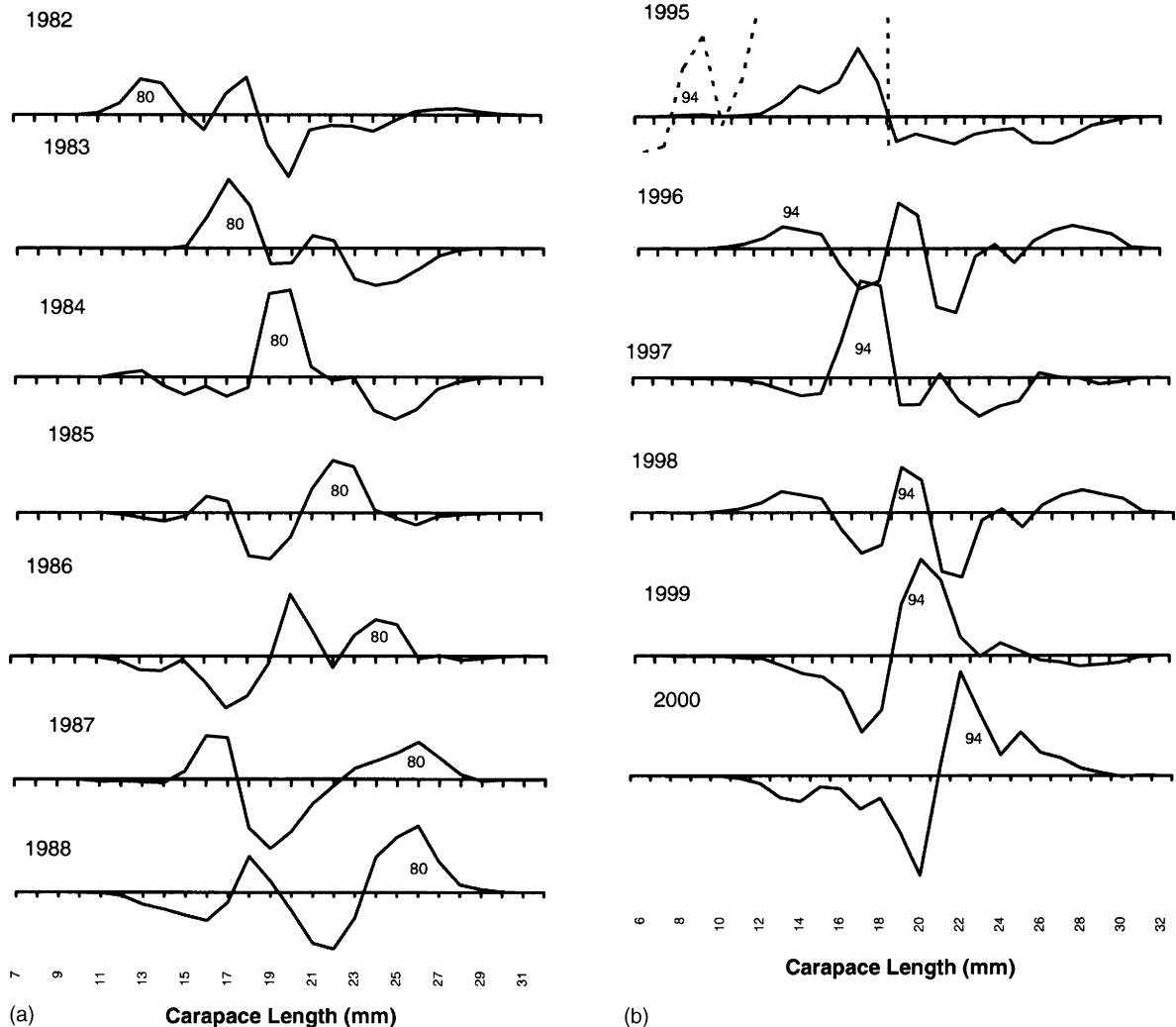


Fig. 2. Results of deviation analysis (all areas combined) identifying the 2-year classes that were used to determine growth during the two time periods including (a) 1980; (b) 1994. The dotted line in the graph for 1995 gives the same data on an expanded scale to accentuate the mode of 1-year-old shrimp. Note that for clarity only the spring survey is given in (a) although both spring and fall surveys were used to determine the mean positive deviations shown in Fig. 3.

stages combined were relatively normally distributed and comprised a distinct mode within the “blended” larger modes. In 1982, transitionals constituted a distinct mode and made up most of the 1978 year class. Since there were no transitionals in the fall 1982 survey, this year class changed sex in 1982 at age four (Fig. 4a). In 1995, transitionals were clearly at least 5 years old, 1 year older than in 1982 (Fig. 4b). However, sigmas for the third mode during the 1995–2000 series were always significantly higher than for other modes,

indicating the presence of a “blended” mode. Reruns with an additional mode always resulted in a better fit; consequently age at transition was set at 6 years during the later period. Table 1 gives the age for the main life history events, including sex change, in Area 13.

Table 2 gives the annual mean carapace lengths for each identified year class from modal analysis of length frequencies from Area 13, and Fig. 5 shows the von Bertalanffy growth curves fitted to the mean carapace length-at-age across year classes during the

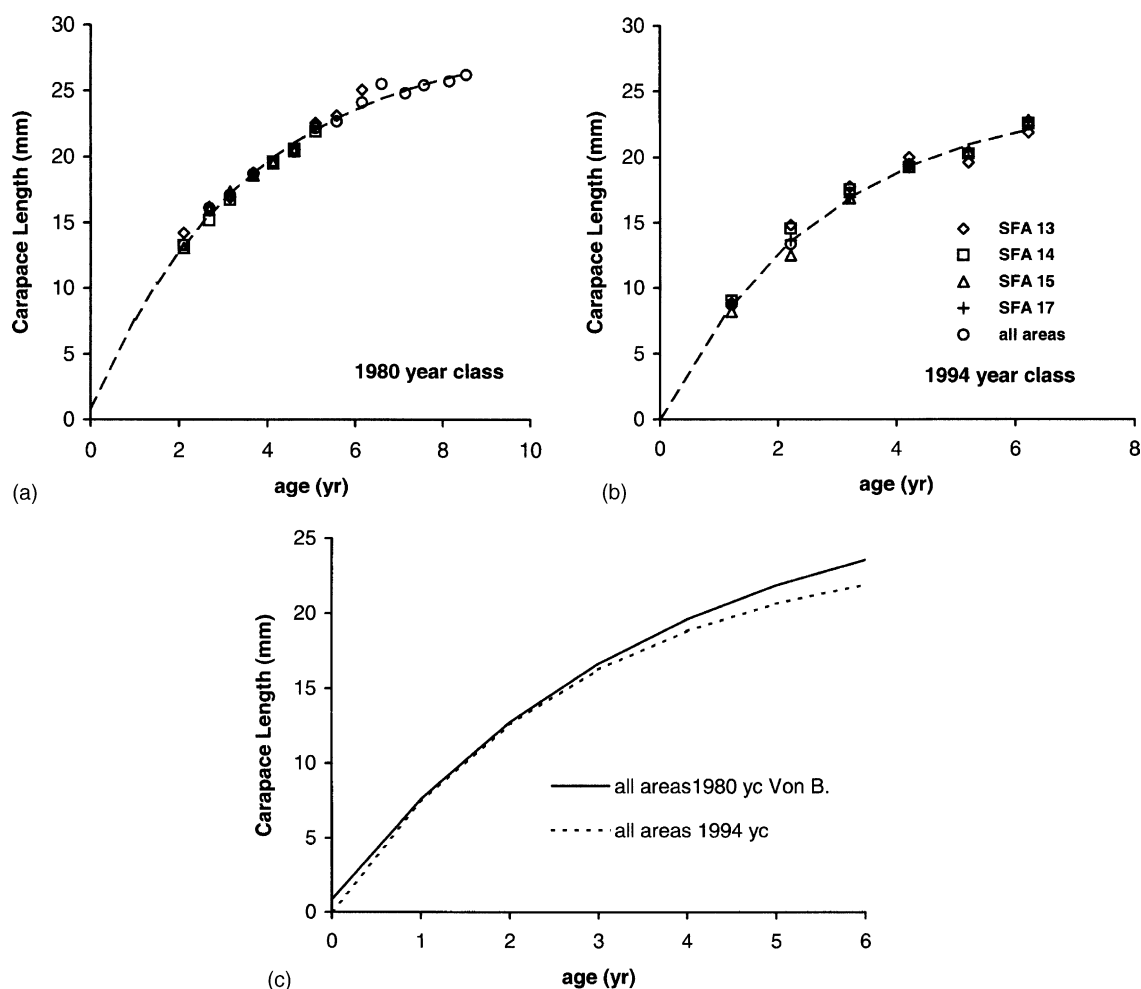


Fig. 3. The means of the positive deviations for the (a) 1980 and (b) 1994 year classes. The von Bertalanffy growth function was fitted to the data for all areas combined and the resulting curves are given on the same chart in (c).

two periods. As with deviation analysis, growth was slower during the later period, although the difference was more pronounced and statistically significant for the results obtained by modal analysis (two factor ANOVA, $*P < 0.05$). Average L_t and L_{max} are also shown for the two periods in Fig. 5. L_t and L_{max} were significantly lower during the period of faster growth.

Fig. 6 shows the relationship between L_t and L_{max} , including overall annual means for the entire survey area as a time series (Fig. 6a) and a linear regression (Fig. 6b). The ratios of L_t/L_{max} were very similar between time periods. They were also remarkably close to those obtained by Charnov and Skúladóttir (2000)

for the Icelandic stock, i.e. 0.9 versus 0.8, despite the different methods used in determining size at transition (i.e. L_t versus L_{50}). Regressions of L_t and L_{max} for individual sets gave virtually identical slopes of 0.8 for the two time periods (Fig. 6c), the same as the Icelandic stocks. Annual growth increments and von Bertalanffy coefficients calculated from the summarized L_t and L_{max} data and the age at transition (Tables 1 and 3) agree with results from deviation and modal analysis and indicate that growth was slower during the 1995–2000 time period.

Two independent estimators (i.e. commercial and shrimp survey catch/hour) during and between the two

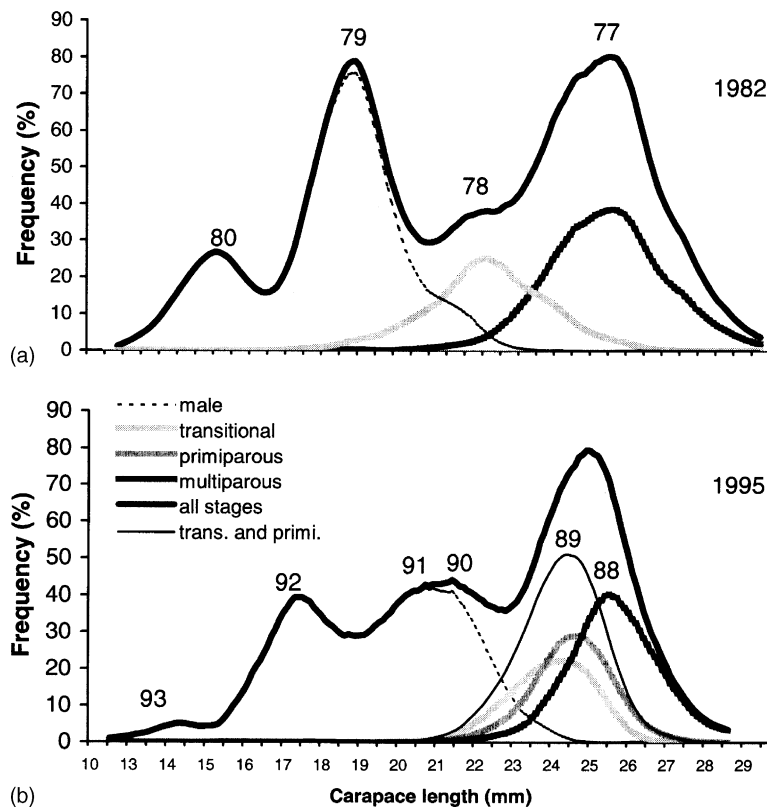


Fig. 4. Length frequencies for the spring 1982 and June 1995 surveys. Also shown are the frequencies for the sexual development stages including males, shrimp that were actively changing to females (transitional), shrimp that were identified as females and would spawn for the first time that year (primiparous), all shrimp that will spawn for the first time that year constituting transitionals and primiparous shrimp (trans. and primi.) and shrimp that had spawned during previous years (multiparous).

Table 1

Age in years at significant life history events for *P. borealis* on the Scotian Shelf, including when year classes started to change sex, when most shrimp spent their last year as males, first year as females (completed sex change), and second year as females (multiparous) in SFA 13, as determined from sexual staging exemplified in Fig. 4

	Survey year (year class)							
	1977	1978 (1982)	1979 (1983)	1980 (1984)	1981 (1985)	1982 (1986)	1983 (1987)	1984 (1988)
Age sex change started			3	4	4	4	4	4
Age most were male			3–4	4	4	4	4	4
Age most changed sex		4	4–5	5	5	5	5	5
Age sex change completed		4	5	5	5	5	5	
Age most were multiparous	5	5	5–6	6	6	6		
	1988	1989 (1995)	1990 (1996)	1991 (1997)	1992 (1998)	1993 (1999)	1994 (2000)	
Age sex change started			5	5	5	5	4	
Age most were male			5	5	5	5	5	
Age most changed sex		6	6	6	6	6	6	
Age sex change completed		6	6	6	6	6		
Age most were multiparous	7	7	7	7	7	7		

Table 2

Mean carapace length (mm) at age of year classes in SFA 13 as determined by modal analysis

Age (years)	Year class										Mean \pm S.D. (mm)	
	1977	1978	1979	1980	1981	1982	1983	1984	1985	1986		
2.11				14.42	14.59	13.48	14.14	14.98	14.70	13.87	14.31 (0.52)	
3.15			18.20	17.62	18.12	17.33	18.41	18.08	17.82		17.94 (0.37)	
4.13		21.47	21.30	19.81	20.49	20.26	21.54	20.64			20.79 (0.66)	
5.10	24.95	24.82	23.21	22.32	22.64	23.67	23.73				23.62 (1.0)	
6.16		26.24	24.43	24.79	25.59	25.71					25.35 (0.73)	
7.15												
8.15												
	1888	1989	1990	1991	1992	1993	1994	1995	1996	1997	1998	
2.22						14.19	14.72	14.00		15.56	15.94	14.88 (0.85)
3.22					17.37	18.28	18.00	17.58		18.84		18.01 (0.58)
4.22				20.08	20.49	21.29	20.16	19.52				20.31 (0.65)
5.22			21.85	22.86	23.00	21.75	21.87	21.60				22.15 (0.61)
6.22		24.71	24.75	23.03	24.18	23.69	24.46					24.14 (0.67)
7.22	26.05	25.47		26.18	25.19	26.12						25.80 (0.44)
8.22				26.88								26.88

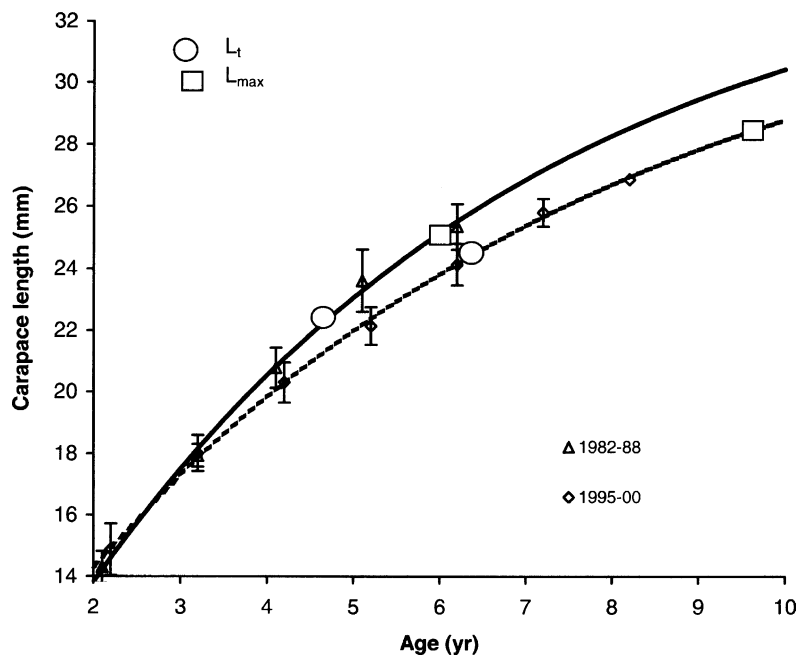


Fig. 5. Graph of the mean sizes for all identifiable year classes for Area 13 during the two time periods given in Table 2 including standard deviations, von Bertalanffy growth curves, and the means for size at transition (L_t) and maximum length (L_{max}).

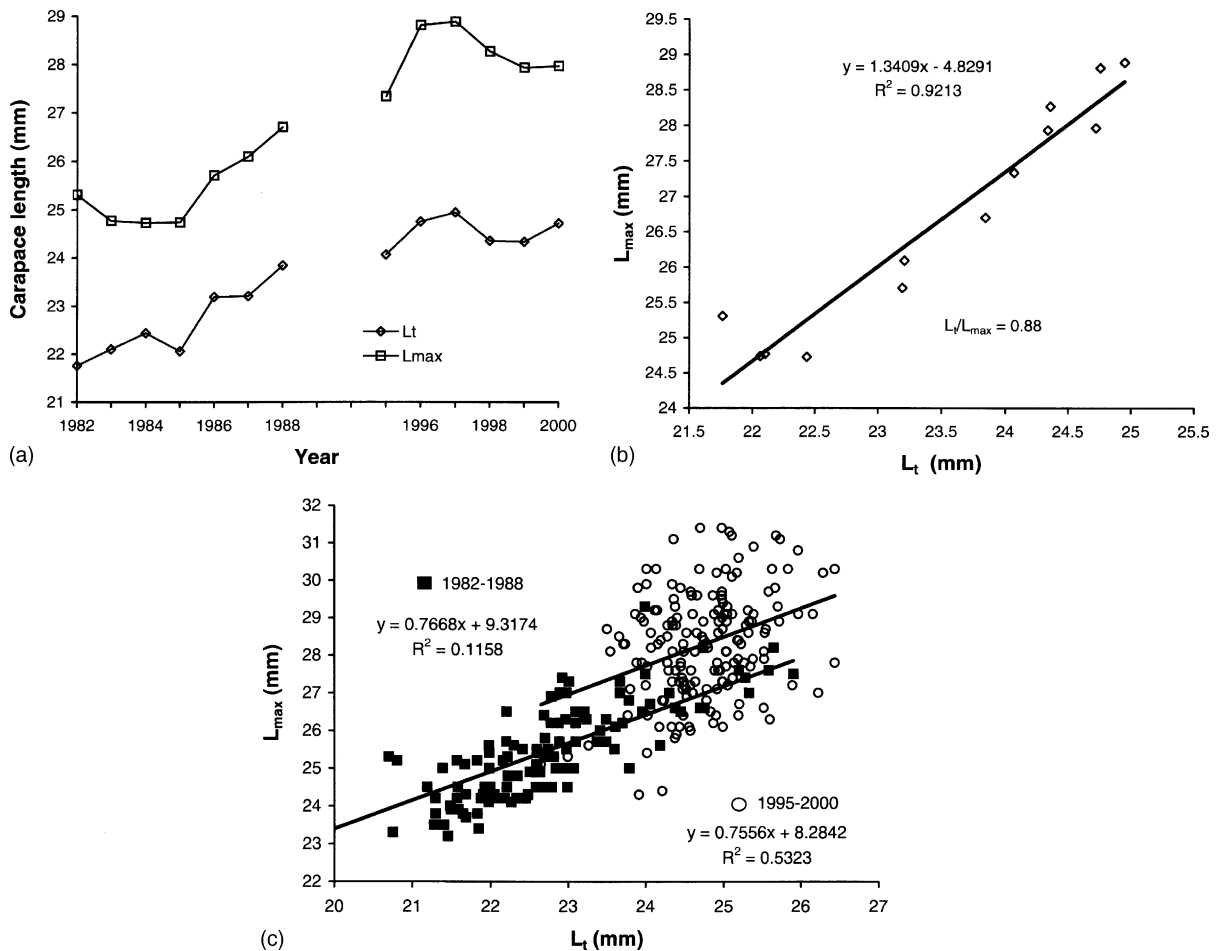


Fig. 6. Plots of L_t versus L_{max} including (a) overall annual means for the two time series, (b) regression for the annual means (** $P < 0.01$), and (c) individual sets for 1982–1988 and 1995–2000. The respective regressions in (c) are significant at ** $P < 0.01$ and * $P < 0.05$.

study periods indicated that the first period was one of low abundance for the *P. borealis* stock on the eastern Scotian Shelf (Fig. 7). Shrimp abundance appeared to be decreasing in the early 1980s, reached a minimum in 1985 and increased slightly or remained stable at low levels for the remainder of the period. Abundance increased beginning in 1988 and continued to increase throughout the 1990s. The later survey period was therefore one of high and increasing abundances, which averaged over four times that of the earlier period. In contrast, average L_t increased greatly throughout the earlier period. There are no L_t data between periods (1989–1992), but the high values at the end of

the first period approached the lower values of the second; consequently there appeared to have been only a slight increase between them. L_t values during the second period were high but variable, with no clear trend. Bottom temperatures on the shrimp grounds decreased during the first period and increased during most of the second period.

Although abundance (density) and L_t were directly related when data from both time periods were included ($R^2 = 0.424$, ** $P < 0.01$) there were no clear trends within periods (Fig. 8a). A negative correlation between these parameters was suggested for the earlier period; however, the relationship was not significant.

Table 3

Annual means for size at transition from male to female (L_t), maximum observed size (L_{\max}), age at transition, and measures of growth, including annual growth increment prior to transition, and the von Bertalanffy growth coefficient (K)

Year	L_t (mm)	L_{\max} (mm)	L_t/L_{\max}	Age at L_t (years)	Increment (mm)	K
1982	21.76	25.31	0.86	4.0	5.44	−0.49137
1983	22.10	24.77	0.89	4.5	4.91	−0.49515
1984	22.44	24.73	0.91	5.0	4.49	−0.47570
1985	22.06	24.74	0.89	5.0	4.41	−0.44476
1986	23.19	25.71	0.90	5.0	4.64	−0.46492
1987	23.21	26.10	0.89	5.0	4.64	−0.44044
1988	23.84	26.70	0.89	5.0	4.77	−0.44688
Mean \pm S.D. (mm)	22.66 (0.77)	25.44 (0.77)	0.89 (0.02)	4.79 (0.39)	4.76 (0.34)	−0.47 (0.02)
1995	24.07	27.34	0.88	6.0	4.01	−0.35393
1996	24.76	28.81	0.86	6.0	4.13	−0.32665
1997	24.95	28.89	0.86	6.0	4.16	−0.33192
1998	24.36	28.27	0.86	6.0	4.06	−0.32953
1999	24.34	27.93	0.87	6.0	4.06	−0.34162
2000	24.72	27.97	0.88	6.0	4.12	−0.35888
Mean \pm S.D. (mm)	24.53 (0.33)	28.20 (0.59)	0.87 (0.01)	6.0 (0)	4.0 (0.05)	−0.34 (0.01)

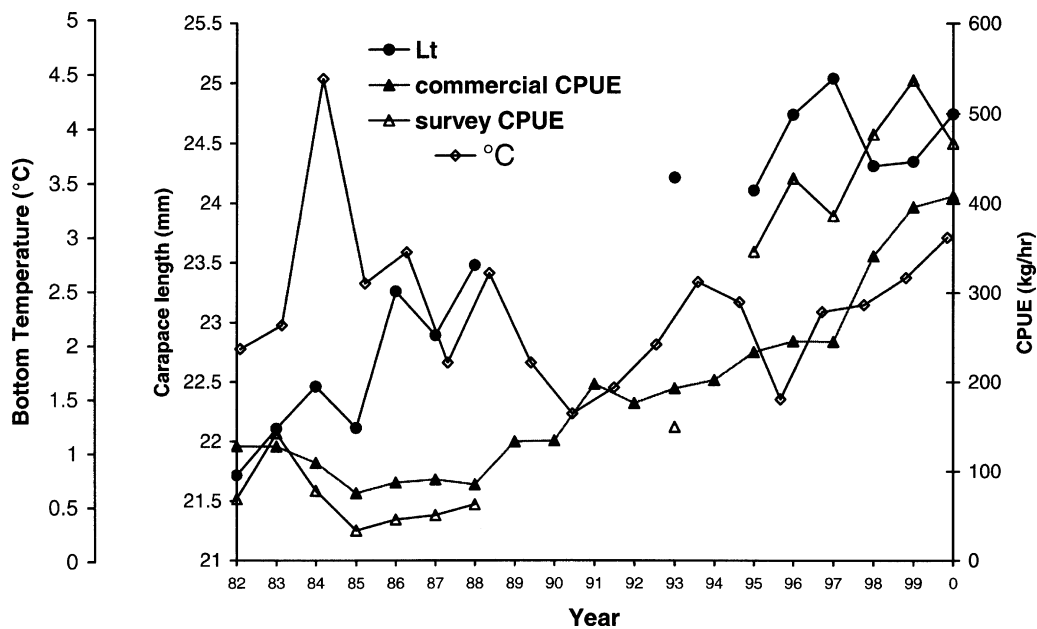


Fig. 7. Composite plots of bottom temperatures on the shrimp grounds, catches per unit of effort for commercial and survey vessels, and mean L_t (all areas combined) during both study periods.

The long-term (i.e. both time periods) correlation was considerably better between density and L_{\max} ($R^2 = 0.512$, ** $P < 0.01$) due mainly to a significant ($R^2 = 0.427$, * $P < 0.05$) positive relationship between these parameters in the later period (Fig. 8b).

4. Discussion

L_t/L_{\max} was approximately constant for *P. borealis* on the Scotian Shelf during two periods when L_t , L_{\max} and growth rates were very different. L_t/L_{\max}

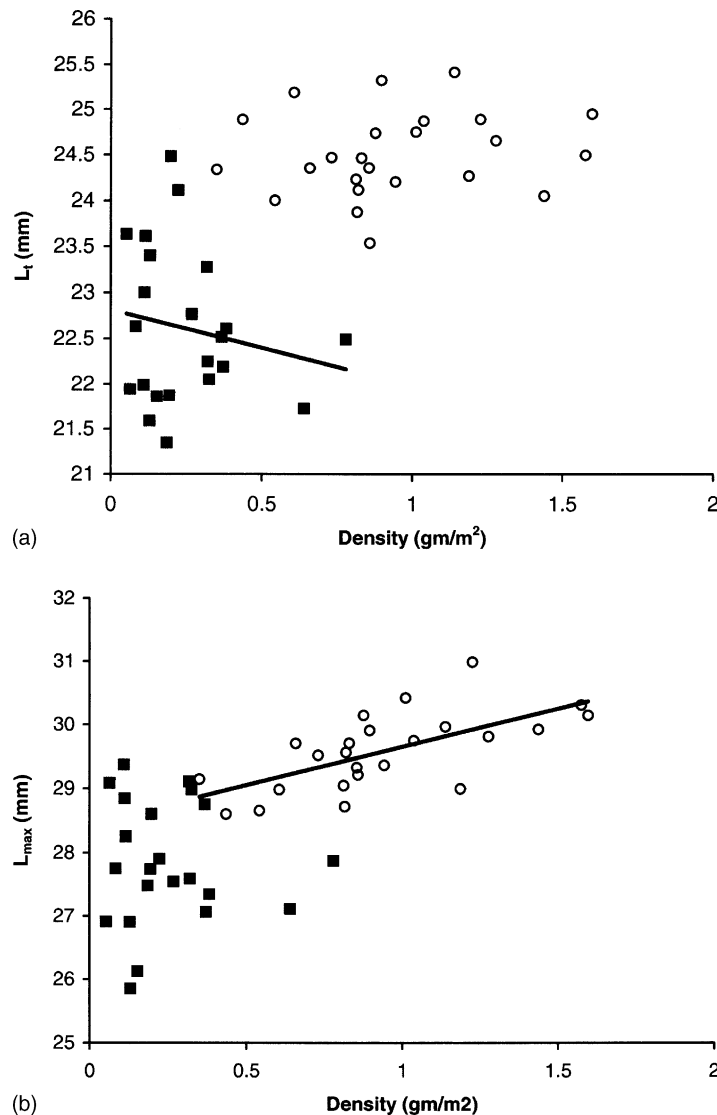


Fig. 8. Relationship between shrimp density and (a) size at transition L_t and (b) maximum shrimp size L_{max} . The two survey periods are shown as solid squares (1982–1988) and open circles (1995–2000). The regression line in (a) is for 1982–1988 data only and is non-significant, whereas the regression line in (b) is for the 1995–2000 data (* $P < 0.05$).

on the Scotian Shelf was also virtually identical to Icelandic stocks. These results support the theory of invariance in this ratio for *P. borealis* stocks (Charnov and Skúladóttir, 2000). The implication of this finding, i.e. that L_t and L_{max} can be taken as two points on a growth curve where L_{max} approximates the asymptotic length L_∞ in the von Bertalanffy equation, and that growth rates of pandalids can be determined

from L_t or L_{max} alone, was confirmed by comparing growth rates determined by two recognized methods, i.e. modal and deviation analysis, with those obtained from L_t and/or L_{max} . All three methods gave the same results, showing slower growth during the period of high abundance. The results are also consistent with Koeller et al. (2000a), who concluded that length at transition of *P. borealis* on the Scotian Shelf was

probably related to growth by demonstrating both density dependent and temperature effects on L_t .

Growth rates are difficult to obtain for pandalids as well as for other crustaceans. Deviation analysis requires the presence of a strong year class throughout a suitably long time series, whereas modal analysis depends on the ability to distinguish modes and correctly assign year classes to them. Consequently, pandalid growth rates are not often used in stock assessment models or are restricted to historical determinations. The association of L_t and L_{\max} with changes in growth means that growth rates can be compared between years for annual stock assessment purposes. Although L_{\max} is much easier to determine, the direct dependence of L_{\max} on L_t and their chronological order of occurrence in the life history means that L_{\max} is determined several years before maximum size is actually achieved (i.e. at the time of sexual transition). L_{\max} would therefore be more suitable for analyses where the need for real time information is less critical, e.g. spatial analyses such as stock identification (e.g. Skúladóttir, 1990) or the effects of environmental factors on growth. Changes in L_t would reflect more recent changes in growth and would therefore be more appropriate as an indicator of changes in population growth for annual “traffic light” assessments, such as those used for Canadian shrimp stocks in the North-west Atlantic (Koeller et al., 2000b), or more traditional approaches such as yield and eggs per recruit or production models (e.g. Armstrong et al., 1999).

L_t or L_{\max} were relatively poor indicators of changes in population size because the relationship was weak within time periods and only became obvious when data from both periods were considered. We conclude that L_t and L_{\max} are more suitable as indicators of individual growth. However, growth and abundance are related through density dependence (Koeller et al., 2000a) and this may be why a change in L_t is often associated with changes in abundance in stock assessments (e.g. Armstrong et al., 1999). The other reason for this association is due to the work of Charnov (1982), which provided the theoretical basis for linking L_t with abundance. On the Scotian Shelf, L_t was smaller, on average, during the period of low abundance in agreement with sex allocation theory (Charnov, 1982), which predicts that the population responds to a decrease in the abundance of females by decreasing L_t . However, on the Scotian Shelf, L_t

increased throughout the period of low abundance. If L_t had been used as an indicator of abundance at this time it would have been erroneously concluded that the population was increasing when in fact it did not do so until L_t approached its maximum value. We conclude that the increase in L_t during the period of low abundance was due to decreasing growth rates, probably in response to decreasing temperatures. L_t values were high and growth was low during the second period, probably in response to high densities and despite increasing temperatures. This is in agreement with Koeller et al. (2000a) who found that density was more important than temperature in determining L_t at high densities, whereas temperature was more important at low densities.

Our results suggest a mechanism for the negative and lagged correlations between temperature and population size or commercial catches, which appear to be common in stocks at the southern limits of their distribution (e.g. Clarke et al., 2000); increased temperatures result in an obligatory increase in growth rate, smaller L_t , decreased fecundity and, several years later, a decrease in population size. Other explanations for the negative relationships between temperature and shrimp abundance are numerous (Clarke et al., 2000) and include the possible influence of temperature on fecundity. Apollonio et al. (1986) speculated that temperature influences fecundity via water stratification and the different temperatures encountered by maturing females during vertical migrations. Our proposed mechanism is much more direct.

Since L_t is proportional to L_{\max} and fecundity is directly related to size (Shumway et al., 1985), fecundity will decrease with decreasing L_t . For example, using the carapace length versus egg numbers relationship given in Shumway et al. (1985), i.e. eggs = $-5234 + 285.4CL$, the average number of eggs carried by female shrimp on the Scotian Shelf was 1233 at L_t and 1767 at L_{\max} during the first period and 2027 and 2814 eggs during the second period, a difference of 39 and 43%, respectively. If it is assumed that annual fecundity in the two periods averaged midway between the minima and maxima above, i.e. 1500 and 2420 eggs per female for the first and second period and that females spawned annually throughout their life, then the total egg production per female would have been $1500 \times 2 \text{ years} = 3000$ eggs for the first period versus $2420 \times 3 \text{ years} = 7661$ for the second, a

difference of 142%! This egg loss would not be compensated at the population fecundity level, i.e. by the additional females generated by the shorter lifespan. The 6-year life span of the first period will produce $1 - (1/6)/(1/7) =$ only 17% more females and a similar increase in the number of eggs relative to the 7-year life span of the second period.

While our observational results agree with the invariance theory of L_t/L_{\max} (Charnov and Skúladóttir, 2000), and in general appear to support sex allocation theory (Charnov, 1982) as it pertains to pandalids, there are some theoretical inconsistencies between sex allocation theory and our theory on the cause of the negative relationship between temperature and abundance that require clarification. As a circum-polar, coldwater species, clearly warmer conditions are unfavorable for *P. borealis*. This is evidenced by population declines during warmer periods (Clarke et al., 2000) and smaller stock sizes in the southern limits of its distribution. In general, growth rate is directly proportional to temperature in most aquatic species. Age and size at maturity are generally inversely related to growth rate. Growth rate of *P. borealis* is also strongly density dependent (Koeller et al., 2000a). Consequently, the decrease in growth rate and concurrent increase in L_t during a period of high densities and colder temperatures (1995–2000) on the Scotian Shelf is not surprising. This is also consistent with sex allocation theory, which predicts that L_t will decrease during a period of decreasing abundance and vice versa. Although the proximate causes of a link between temperature, density, growth rate and L_t can easily be attributed to physiological processes, the ultimate evolutionary purpose is less clear in light of our results. In this regard, sex allocation theory predicts that pandalids decrease L_t to increase reproductive capacity during periods of low abundance, yet the present results suggest that population fecundity will actually decrease with L_t . The resolution of this inconsistency is beyond the scope of this paper and will require more precise calculations of population fecundity changes with L_t that also account for such factors as mortality and differences in fecundity at length between growth regimes. *P. borealis* fecundity at length can differ by as much as 30% between years (Shumway et al., 1985) and may accentuate or moderate the differences calculated above.

The fisheries management implications of Charnov and Skúladóttir (2000) and our findings are significant. The direct link of L_t to growth and fecundity presents the possibility of annual quantitative assessments using population models such as yield and eggs per recruit based on relatively simple L_t and/or L_{\max} measurements. Furthermore, it may be possible to set limit reference points for fisheries managers based on long-term measurements of these parameters during periods of low and high abundance, such as occurred on the Scotian Shelf.

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