

# Growth of juvenile lobster *Homarus americanus* off the Magdalen Islands (Quebec, Canada) and projection of instar and age at commercial size

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**ABSTRACT:** Juvenile American lobster *Homarus americanus* were quantitatively surveyed in the southeast Baie de Plaisance, Magdalen Islands, from 1995 to 2004. Lobster were collected by SCUBA, in summer and/or early fall after the annual settlement period. Growth for up to 3 yr following settlement was assessed by modal analysis of carapace length (CL)-frequency distributions and was confirmed for the first year by *in situ* rearing of Stage IV lobster collected from the plankton. In every sampling year, some modes (attributed to instars) were apparent in CL-frequency distributions up to 50 mm CL (estimated to be Instar XVI on average). The mean percent molt increment declined gradually from about 23% at Instar IV to about 15% at Instar XV. Strong year-classes could be tracked reasonably well for up to 2–3 yr after settlement. From this point, we projected growth to fishery recruitment and suggest that lobster reach commercial size at a higher instar and older age than previously believed. This is the first study to explain lobster juvenile growth in such detail, and it constitutes an essential step toward the understanding of potential settler-to-recruit relationships.

**KEY WORDS:** American lobster · *Homarus americanus* · Growth · Size-at-instar · Size-at-age

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## INTRODUCTION

The American lobster *Homarus americanus* has supported an important commercial fishery in eastern North America since the middle of the 19th century. Landings were at or near historical highs during the 1990s and into the early 2000s, following a steep and unforeseen increase through the 1980s. This increase probably resulted from changing environmental and ecological conditions that enhanced lobster productivity over broad regions, in conjunction with a technology-driven increase of fishing power and efficiency (reviewed in Fogarty & Gendron 2004). The increase was as striking as our inability to foresee it.

Forecasting trends in the abundance of commercial lobster was impossible because of the absence of egg-, larval-, or settler-recruit relationships. In recent years, however, the demonstration of a link between postlarval supply and benthic settlement (Incze et al. 1997) and the

recognition of spatial coherence in the abundance of postlarvae (either pelagic or benthic) and recruits to the fishery (Miller 1997, Steneck & Wilson 2001) have laid the foundation for the possible development of postlarvae/settler-recruit relationships. In parallel, progress has been made toward establishing time-series of lobster settlement intensity in Maine and Rhode Island, from which prediction of future recruitment to the fishery has been attempted (Wahle et al. 2004). Nevertheless, the difficulty of sampling postlarvae and early benthic stages, the uncertainty of age-at-recruitment and the possibly high level of variability of size-at-age (Wahle 2003) obscure the growth trajectory from settlement to recruitment and greatly complicate the task of forecasting recruitment for American lobster (Wahle et al. 2004). These caveats are compounded by a poor understanding of the post-settlement processes influencing survival during the multiyear time lag between settlement and harvestable size.

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The variability of lobster size-at-age is perceived already at the end of the first season of growth. There may be biological reasons for this variability. In any given region, lobster settling earlier in the season may overwinter at a larger size than late settlers because of their larger initial size (James-Pirri et al. 1998) and a longer season of growth and exposure to warmer temperatures that generally promote growth. Variability in size may also be modulated by intra- and intercohort competition and early establishment of dominance hierarchies among young-of-the-year (YOY) that affect growth (James-Pirri et al. 1998, Wahle et al. 2001, Paille et al. 2002). There may also be marked latitudinal gradients in the sizes and/or instars reached before the onset of the first winter, which reflect different temperature regimes affecting the timing of lobster hatching and settlement, as well as subsequent growth. Such gradients were initially proposed by Cobb & Wahle (1994) and later confirmed during field observations in southern New England (Incze et al. 1997, James-Pirri et al. 1998) and in the Gulf of Maine (Incze et al. 1997, Wahle & Incze 1997).

On the other hand, methodological reasons may also be partly responsible for the perceived variability in YOY lobster size after the first season of growth. James-Pirri et al. (1998) measured growth, established the size of Instars IV to XI of YOY lobster and inferred overwintering size from *in situ* experiments conducted in Rhode Island. In contrast, Hudon (1987) inferred size-at-instar from modal analysis of a size-frequency distribution (SFD) of lobster pooled from different times and sites in the Magdalen Islands (Gulf of St. Lawrence) and projected overwintering size from previously published growth curves.

In the present paper, we re-assess juvenile lobster growth at the Magdalen Islands using 2 *in situ* growth experiments and modal analysis of a 10 yr time-series of SFDs of lobster in the wild. We examine interannual variation of instar development and size after the first season of growth, provide an estimated growth trajectory for up to 3 yr following settlement, and project average instar and age at recruitment to the fishery. This work contributes to the understanding of variability of size-at-instar/age and of age-at-recruitment, which are initial steps towards the understanding of potential settler-to-recruit relationships.

## MATERIALS AND METHODS

**Study site and sampling.** The study was conducted in the southeast part of the Baie de Plaisance at the Magdalen Islands (Quebec) in the Gulf of St. Lawrence (Fig. 1), off a site called Les Demoiselles, which has been known as a lobster nursery ground since the study by Hudon (1987). The sampled site is a finite area of bedrock, boulders and cobbles, with patches of sand, spanning approximately 37.5 ha at a maximum depth of 5 m. The area is bounded south by shoreline and north, east and west by large sand flats, on which no juvenile lobster was seen during several day and night dives. Therefore, we assume there is no immigration of early juveniles into the area and lobster are not expected to leave this nursery until they become relatively large.

Water temperature on the south side of the Magdalen Islands has been recorded at a fixed station (47° 28.8' N, 61° 41.8' W) at a depth of 10 m below mean low water since 1994. Water temperature typically varies from -1 to 18°C over a year (Fig. 2A). The number of degree-days was calculated each year for the period 1 May to 31 October, when lobster growth is most likely to occur (Fig. 2B).

Lobster were collected by SCUBA divers in 1995 to 2001 and 2003 to 2004, after most or all settlement had occurred. Plankton surveys around the Magdalen Islands capture Stage IV larvae mostly in August (Hudon et al. 1986, Ouellet et al. 2001), indicating that

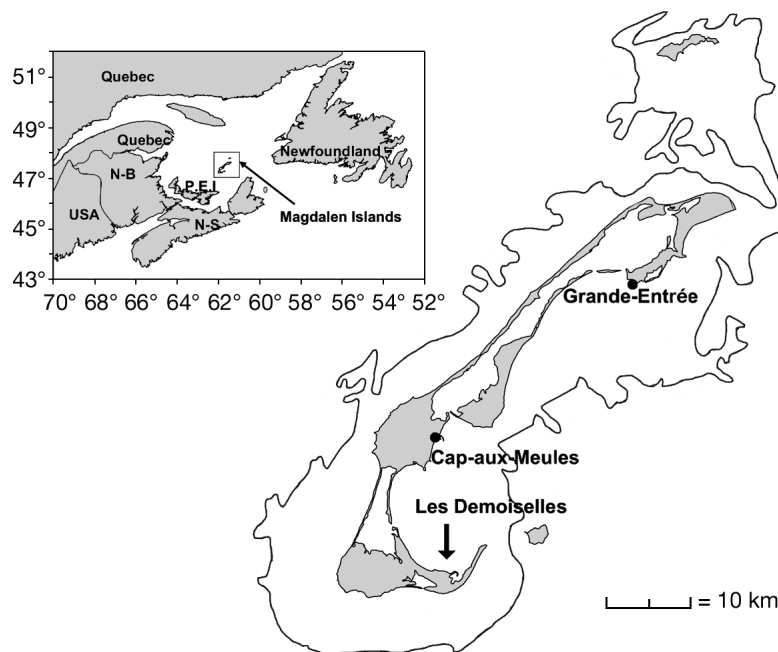


Fig. 1. Magdalen Islands, Quebec, in the southern Gulf of St. Lawrence, Canada, showing the 20 m isobath and location of the study site of Les Demoiselles (arrow)

settlement occurs mainly during that month. Sampling was done some time between the third weeks of August and September in most years, or from the end of August until the end of October in 1996 (Table 1).

Lobster were collected haphazardly in 1995, but starting in 1996 quantitative sampling was performed on 1 m wide belt transects oriented approximately perpendicular to the shore and covering depths of 2 to 5 m. An average distance of 46 to 83 m was sampled along each of 4 to 6 transects in each year (Table 1). Lobster were hand-picked by gently moving cobbles and digging around boulders to a depth of 10 to 15 cm. Lobster were brought to the surface for immediate in-field sex determination and measurement of carapace length (CL) to the nearest 0.01 mm with a caliper. Between 224 and 485 lobster, ranging from 4 to 80 mm CL, were sampled each year (Table 1). Additional samples were taken in July 1996 and in early August 1997, to assess within-season growth and intermolt duration.

**Controlled *in situ* growth experiments.** In 1997 and 1998, respectively, 50 and 19 plankton-caught Stage IV lobster, ranging in size from 3.9 to 5.5 mm CL, were held in captivity from early August to late October. Lobster were kept individually in PVC tubes (60 cm long and 10 cm in diameter). The 2 extremities of the tubes and 6 horizontally disposed 2 cm holes along the tubes were fitted with 2 mm NYTEX mesh for water circulation. Tubes were stacked horizontally, in groups of 6 to 8, separated vertically by 10 cm and horizontally by at least 1 m, and they floated just above the bottom in 3 m deep water at the sampling site. The volume and spacing of individual tubes were deemed sufficient to ensure spatially unconstrained growth and prevent neighbor effects. Lobster were fed 2 to 3

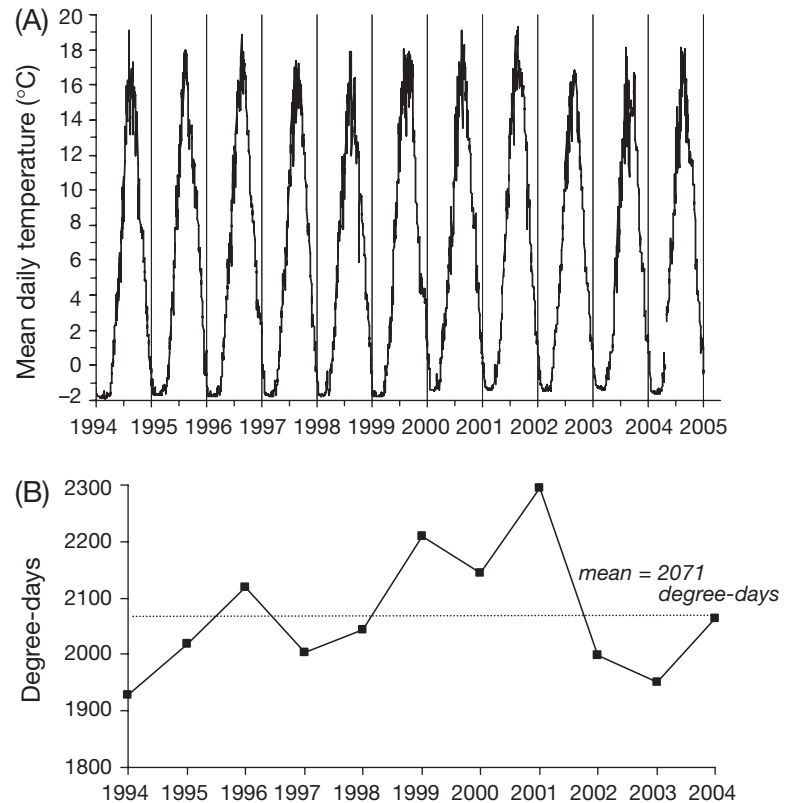


Fig. 2. (A) Water temperature in the southern part of the Magdalen Islands, Quebec, recorded daily at a depth of 10 m for the period 1994 to 2004 and (B) annual degree-days cumulated from late spring to fall (1 May to 31 October)

times a week, mostly with crushed small mussels, live or crushed juvenile rock crab and live amphipods, which are prominent elements of the natural diet of YOY at this site (Sainte-Marie & Chabot 2002). In 1997, lobster were measured once every 1 to 2 wk, to detect growth and instar progression, but no effort was made to obtain information on intermolt period. In 1998, the tubes were examined 2 to 3 times weekly for the presence of an exuvium; in such cases (or if the observer felt a molt had occurred), the lobster was measured and the date of molting was recorded as the half-way point between the preceding and current date of observation.

CL at each successive instar was related to initial CL of postlarvae by least-squares linear regression. Slopes of regressions were tested for homogeneity across all instars within years, and by instar between years, by analysis of covariance (ANCOVA) (Sokal & Rohlf 1995). The percent molt increment between successive instars ( $i$ ) was calculated as:

$$(CL_{i+1} - CL_i) / CL_i \times 100$$

Table 1. Details of diver sampling at Les Demoiselles, Magdalen Islands, Quebec, from 1995 to 2004

Year	Sampling period	No. of transects	Total area surveyed (m <sup>2</sup> )	No. of lobster caught
1995	21–25 Sep	Non-quantitative sampling		241
1996	28 Aug–31 Oct	6	497	388
1997	24 Aug–13 Sep	6	501	293
1998	18 Aug–3 Sep	6	309	389
1999	10–21 Sep	5	234	326
2000	8–16 Sep	6	283	366
2001	8–17 Sep	6	265	224
2003	17–23 Sep	5	250	485
2004	9–17 Sep	4	200	377

Mean size-at-instar and mean percent molt increment were compared between years using Student's *t*-test (Sokal & Rohlf 1995). Percent molt increment was calculated and mean CLs were compared only when there were at least 2 observations for any given instar.

**Analysis of growth from SFD.** Lobster from all transects surveyed in a given year were pooled together and SFDs of 1 mm CL classes for the full lobster size range and of 0.25 or 0.5 mm CL classes for lobster  $\leq 15$  mm CL were computed and then smoothed with a moving average on 3 size classes. Males and females were pooled together under the assumption that growth of immature lobster is similar between the sexes. Visual examination of SFDs revealed a number of more-or-less distinct modes up to ca. 50 mm CL that were interpreted as instars. Instar mean CL and standard deviation (SD) and the number of contributing individuals were determined by modal analysis using the MIX procedure (MacDonald & Pitcher 1979). This procedure iteratively adjusts a distribution model starting with reasonable inputs of number of modes and their estimated means, SD and numbers. Cumulated SFDs of best-fit normal curves were compared to the observed SFDs with a  $\chi^2$  test (Sokal & Rohlf 1995). Modal analysis of YOYs was calibrated with the size-at-instar obtained from the *in situ* growth experiments. For older lobsters, the analysis was done without calibration. In an attempt to overcome the inherent subjectivity of the exercise, we each performed modal resolution independently. Estimated mean size-at-instar and percent molt increment were compared to those of *in situ* reared YOY using Student's *t*-test. Percent molt increment was calculated as the relative increase in CL between successive instars within the same year-class (see below). Least-squares linear regression was used to relate mean percent molt increment to mean CL across instars.

We estimated intermolt period of early instars in 1997 from the additional sampling performed in early August, which extended over 3 wk from about the start of the settlement season. CL of YOY was regressed against their day of capture. Intermolt period was derived as the difference between predicted day of capture of lobsters at estimated mean  $CL_{i+1}$  and mean  $CL_i$  derived from the 1997 SFD analysis.

Year-classes were determined by identifying and tracking distinctive features of the SFDs through time. The age of each year-class was assigned as the number of years from settlement, starting with  $0^+$  representing the year-class in its settlement year. A  $0^+$  year-class was easily recognized in SFDs as a conspicuous mode or group of modes that was usually clearly separated from the preceding year-class. In the Magdalen Islands, molting begins in mid-June, with a peak in early July (Hudon 1987). Lobster settled in the population in the previous

year may molt during the summer period, before the next year-class starts to settle. Thus, there is generally very little size overlap between the late settlers and/or slow growers of a year-class and the early settlers and/or fast growers of the next year-class. The identification of year-classes (and contributing instars) above Age  $0^+$  was done iteratively, by following at first the strong year-classes (e.g. 1994, 1997 and 1999), which can be tracked more easily and for a longer period of time. Summer observations in 1996 helped to bracket the range of growth through 1 season. Information presented by Cowan et al. (2001) on the growth of tagged lobsters for up to 4 yr in the wild was also used to help identify cohorts and set their size limits. Estimated mean size-at-age was computed for each combination of year-class and sampling year, from the mean CL weighted by the number of individuals of all contributing instars. Mean size-at-age was computed up to Age  $3^+$ .

**Projections.** An estimation of instar at the legal (commercial) size of 83 mm CL was computed starting with 5.9 mm CL as the mean size of Instar V using the growth equation derived for Instars V to XV, and, for larger instars, using a mean percent molt increment of 15% based on observations of lobster growth in the southern Gulf of St. Lawrence (Comeau & Savoie 2001) and in the Magdalen Islands (L. Gendron unpubl. data). The age at legal size was estimated for the leading edge of each year-class starting from the inferred instar at Age  $3^+$  (or at Age  $2^+$  for 1999 and 2002) reached by a least 50% of lobster. Lobster at Instar XVI (ca. 50 mm CL) and more were assumed to molt once annually, based on Comeau & Savoie (2001), whereas lobster up to Instar XV were assumed to molt twice a year (i.e. a lobster at Instar XV in a given year would therefore be at Instar XVII 1 yr later).

## RESULTS

### Controlled *in situ* growth experiment

The mean CL ( $\pm$ SD) of Instar IV lobster placed in captivity in 1997 and 1998 was  $4.7 \pm 0.3$  and  $5.1 \pm 0.3$  mm, respectively. Postlarvae  $< 4.6$  mm CL were lacking in the 1998 sample (Fig. 3). By the end of the experiment in both years, after  $\sim 70$  d in captivity, the majority of surviving lobster had reached Instar VII. Only 6% in 1997 and 26% in 1998 reached Instar VIII. There was almost no overlap between the size distributions of the different instars in both years (Fig. 3). Regressions of CL at Instars V, VI and VII on CL at Instar IV were all significant ( $p < 0.05$ ), and, within years, the slopes of the regression lines were homogeneous (ANCOVA,  $F = 1.39$ ,  $p > 0.05$  for 1997 and  $F = 0.13$ ,  $p > 0.05$  for 1998). Similarly, slopes of the regressions for growth of individual instars were homogeneous between years ( $p \geq 0.2$  for

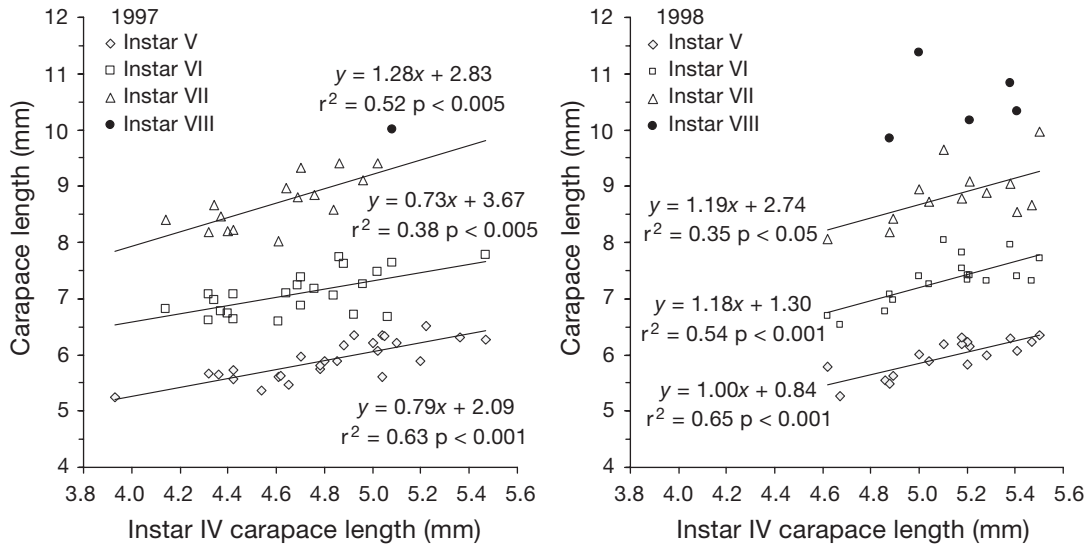


Fig. 3. *Homarus americanus*. Carapace length at Instars V, VI, VII and VIII as a function of carapace length at Instar IV for lobster in the *in situ* growth experiments in 1997 and 1998

each instar). Larger postlarvae maintained their size advantage through successive molts up to Instar VII. Mean size of Instars V to VII (Table 2A) did not differ significantly between 1997 and 1998 (Student's *t*-test,  $p > 0.05$  for each instar). The mean percent molt increment of Instars IV to VII ranged from 16.7 to 23.1% (Table 2B). In 1997, the percent molt increment was fairly constant at around 22 to 23% for Instars IV to VI. In 1998, the percent increment was more variable among instars and was less for Instar IV compared to 1997 (Student's *t*-test,  $p < 0.01$ ).

In the 1998 experiment, lobster continued to molt until mid- to late October, at temperatures ranging from 8 to 9.5°C, but intermolt period increased with instar number and with decreasing temperature (Fig. 4). Water temperature dropped from 16 to 18°C at the start to 8°C at the end of the experiment, and the mean ( $\pm$ SD) intermolt period was  $9.9 \pm 2.9$ ,  $12.3 \pm 2.4$ ,  $16.6 \pm 2.5$  and  $32 \pm 6.8$  d from Instars IV to V, V to VI, VI to VII and VII to VIII, respectively. The mean number of degree-days ( $\pm$ SD) required to grow from one instar to the next was  $174 \pm 34$  for Instars IV to V,  $187 \pm 36$  for

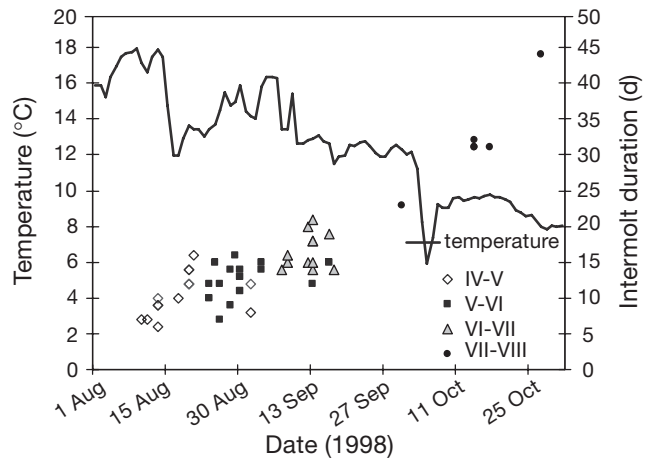


Fig. 4. *Homarus americanus*. Intermolt duration from Instars IV to VIII in relation to date and water temperature during the 1998 field growth experiment

Instars V to VI,  $253 \pm 36$  for Instars VI to VII, and  $367 \pm 57$  for Instars VII to VIII. A total of  $981 \pm 161$  degree-days was required to grow from Instar IV to VIII.

Table 2. *Homarus americanus*. Mean  $\pm$  SD (n) of (A) size-at-instar (carapace length, mm) and (B) percent molt increment of lobster in Instars IV to VIII from the *in situ* growth experiments in 1997 and 1998

(A) Size-at-instar	IV	V	VI	VII	VIII
1997	4.7 $\pm$ 0.3 (49)	5.9 $\pm$ 0.4 (26)	7.1 $\pm$ 0.5 (16)	8.7 $\pm$ 0.5 (16)	10.0 (1)
1998	5.1 $\pm$ 0.3 (18)	6.0 $\pm$ 0.3 (19)	7.4 $\pm$ 0.4 (19)	8.9 $\pm$ 0.5 (14)	10.5 $\pm$ 0.6 (5)
(B) Percent molt increment	IV→V	V→VI	VI→VII	VII→VIII	
1997	23.0 $\pm$ 5.5 (26)	22.4 $\pm$ 2.7 (7)	22.9 $\pm$ 2.9 (12)		
1998	16.7 $\pm$ 3.9 (18)	23.1 $\pm$ 3.8 (19)	19.6 $\pm$ 4.4 (14)	20.0 $\pm$ 5.5 (5)	

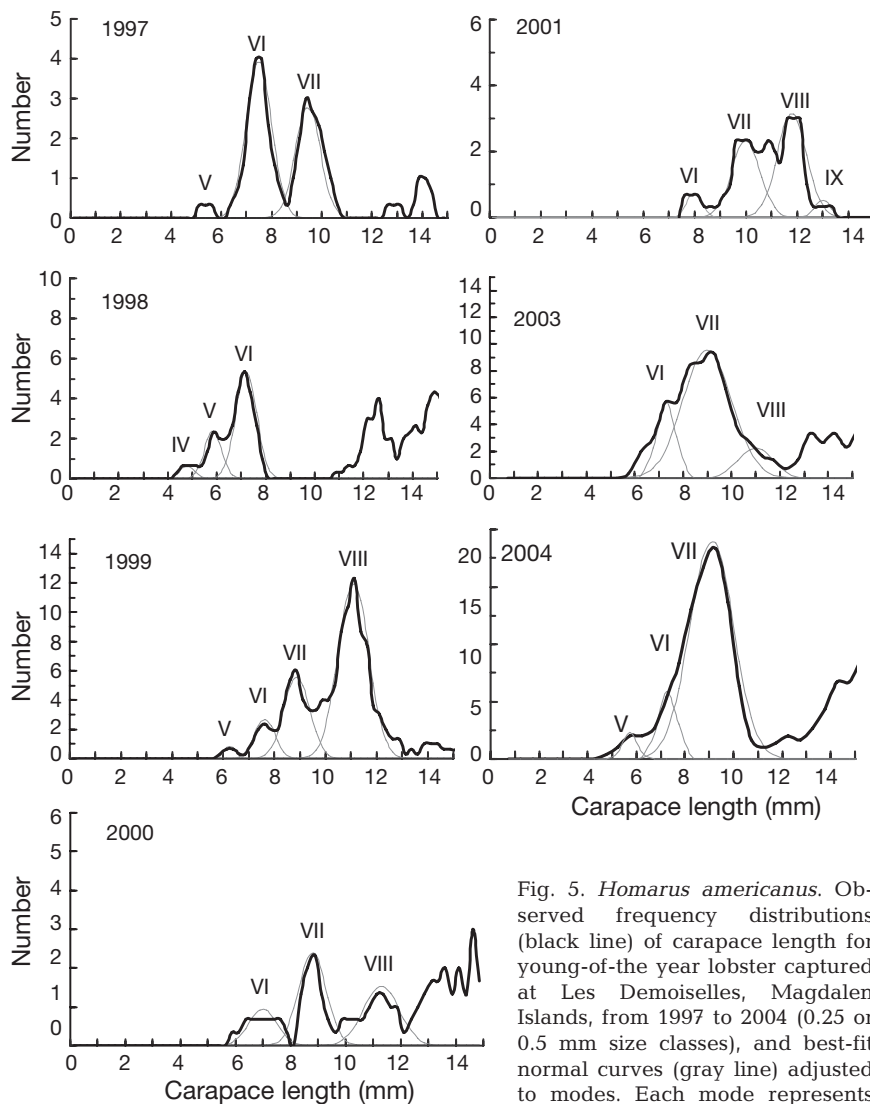


Fig. 5. *Homarus americanus*. Observed frequency distributions (black line) of carapace length for young-of-the-year lobster captured at Les Demoiselles, Magdalen Islands, from 1997 to 2004 (0.25 or 0.5 mm size classes), and best-fit normal curves (gray line) adjusted to modes. Each mode represents an instar designated by a roman numeral

### Size-at-instar and percent molt increment from SFD analysis

#### Young-of-the-year

YOY lobster were conspicuous in SFDs, usually as a group of multiple modes, ranging somewhere from 4 to 13.5 mm CL in all years. The visible modes of YOY in SFDs were attributed to Instars IV to VIII (Fig. 5). In certain years (e.g. 2003 and 2004), instars were identified in SFDs based on the results of the *in situ* growth experiment, even though their corresponding mode was not readily visible. Instar IV lobster were found only in 1998, when sampling was done earlier than usual, indicating that benthic settlement was still ongoing or had only recently ceased. Instar VIII lobster

were regularly found, but represented >50% of YOY only in 1999 and 2001. In 2001, 1 lobster of 13.5 mm CL was considered as belonging to Instar IX. For years when sampling continued into mid-September, YOY were most usually distributed among 3 instars (V to VII or VI to VIII). At the end of October 1996, 7 YOY were collected, ranging in size from 7.5 to 11.3 mm CL; 5 were between 8.2 and 9.2 mm CL, corresponding to Instar VII.

The mean ( $\pm$ SD) of CL for Instars IV to IX derived from the yearly SFD analyses are shown in Table 3A, except for years 1995 and 1996 given lack of quantitative sampling and lack of YOY, respectively. Only 7 YOY were collected in 1995, 4 of which ranged from 8.7 to 9.5 mm CL and most likely belonged to Instar VII. Mean size-at-instar was quite consistent through the years, except in 2001, when Instars VI, VII and VIII were larger than average. In 1997, Instars VI and VII were significantly larger in the wild than in the *in situ* growth experiment (Student's *t*-test,  $p < 0.01$  for each instar). In 1998, however, the mean CL of Instars IV to VI did not differ between the wild and the growth experiment (Student's *t*-test,  $p > 0.05$  for each instar). The mean CL of Instar VIII was 0.5 to 1.8 mm more in the wild (1999 to 2003) than in the growth experiments (1997 and 1998).

Percent molt increments were computed for each year (Table 3B). In 1998, the percent molt increment from Instar IV to V was greater in the wild (22.9%, but  $n = 2$ ) than in the *in situ* growth experiment (16.7%). In general, the percent molt increment from Instars V to VI and VI to VII was slightly greater in the wild (20.6 to 29.3%, except 1 outlier of 17.1%) than in the growth experiments (19.6 to 23.1%; Table 2B). The percent molt increment from Instars VII to VIII ranged from 19.2 to 28.4% in the wild and was generally higher than in the 1998 growth experiment (20.0%).

The regression of CL on the day of capture for YOY collected in 1997, including those from early August, had a positive ( $0.125 \text{ mm CL d}^{-1}$ ) and highly significant slope ( $r^2 = 0.60$ ,  $p < 0.001$ ,  $n = 36$ ). From this regression, the intermolt period was estimated to be 12.8 d from Instars IV (4.2 mm CL) to V (5.8 mm CL), 13.6 d from Instars V to VI (7.5 mm CL) and 16.0 d from Instars VI

Table 3. *Homarus americanus*. Mean  $\pm$ SD (n) of (A) size-at-instar (carapace length, mm) and (B) mean percent molt increment of lobster in Instars IV to IX from the benthic census carried out at Les Demoiselles, Magdalen Islands, from 1997 to 2004 (values estimated from size-Frequency distribution analyses shown in Fig. 5)

(A) Size-at-instar	IV	V	VI	VII	VIII	IX
1997 <sup>a</sup>	4.2 (1)	5.8 $\pm$ 0.3 (3)	7.5 $\pm$ 0.5 (22)	9.5 $\pm$ 0.48(15)		
1998	4.8 $\pm$ 0.3 (2)	5.9 $\pm$ 0.4 (8)	7.2 $\pm$ 0.4 (21)			
1999		6.3 $\pm$ 0.2 (2)	7.6 $\pm$ 0.4 (11)	8.9 $\pm$ 0.5 (28)	11.1 $\pm$ 0.7 (72)	
2000			7.0 $\pm$ 0.5 (8)	8.8 $\pm$ 0.5 (18)	11.3 $\pm$ 0.7 (15)	
2001			8.0 $\pm$ 0.4 (3)	9.9 $\pm$ 0.6 (15)	11.8 $\pm$ 0.6 (15)	13.5 (1)
2003			7.3 $\pm$ 0.4 (10)	9.0 $\pm$ 1.0 (42)	11.0 $\pm$ 0.7 (6)	
2004		5.8 $\pm$ 0.3 (3)	7.3 $\pm$ 0.3 (11)	9.1 $\pm$ 0.9 (80)		
(B) Percent molt increment	IV→V	V→VI	VI→VII	VII→VIII		
1997		29.3	26.7			
1998	22.9	22.0				
1999		20.6	17.1	24.7		
2000			25.7	28.4		
2001			23.8	19.2		
2003			23.3	22.2		
2004		25.9	24.7			

<sup>a</sup>Including 1 Instar IV and 2 Instar V lobster from early August 1997

to VII (9.5 mm CL). These values are similar to those obtained in the 1998 *in situ* growth experiment (see above).

#### Juveniles

SFDs and adjusted modes for all lobster sampled between 1995 and 2004 are shown in Fig. 6. Few lobster >60 mm CL were collected, because they probably leave the nursery. In each year, the cumulated SFD of best-fit normal curves did not differ from the observed SFD ( $\chi^2$ ,  $p > 0.9$ ). The mean ( $\pm$ SD) of CL and the number of lobster for each instar derived from modal analyses are given in Table 4. Assignment of instar numbers to modes for juveniles followed from the YOY modal analyses. For some years, instars were identified based on their presence in other SFDs, even though their corresponding mode was not readily visible.

Instars were assigned to the different year-classes by following modal progression through the years, starting with what appeared to be a strong year-class. For example, the 1994 year-class was seen as a composite of 3 modes (Instars X, XI and XII) in the 1995 SFD (Fig. 7) that was separated easily from the 1995 year-class (<12 mm CL). Separation from the previous 1993 year-class was less obvious, and the upper limit of the 1994 year-class was set around 26 mm CL, which corresponds roughly to Cowan et al.'s (2001) observations of lobster growth after 2 yr. Three modes were again visible in July 1996, corresponding to Instars XI,

XII and XIII, suggesting that 1 molt had occurred since the previous fall. In September 1996, 3 modes were still visible as Instars XII, XIII and XIV. This suggests that lobster in Instars X, XI and XII could molt twice a year, and the year-class was inferred to have progressed by 2 instars. In fall 1997, Instars XIV, XV and XVI were attributed to the 1994 year-class (Fig. 6), suggesting that lobster at Instars XIII and XIV might also molt twice a year. The pattern of modal progression described for the 1994 year-class was also seen in the other strong year-classes of 1997, 1999 and 2002. In general, the weaker year-classes of 1996, 1998 and 2000 were more difficult to track and seemingly exhibited a narrower size range caused possibly by temporally restricted settlement or overlap with the neighboring stronger year-classes.

The size progression from Instar IV to XVI determined for each year-class appears relatively consistent among years (Fig. 8). The intercohort differences in size-at-instar for YOY (e.g. the larger individuals of the 2001 year-class) did not appear to become more pronounced over time. Projection of growth from Instar V (overall mean of 5.9 mm CL) to minimum legal size of 83 mm CL suggests lobster could, on average, start recruiting to the fishery at Instar XX (mean of 85.1 mm CL), with intervening average CLs of 48.7, 56.0, 64.4 and 74.0 mm at Instars XVI, XVII, XVIII and XIX, respectively.

A regression of mean percent molt increment on mean premolt CL was done for Instars IV to XV (Fig. 9). The mean percent molt increment ( $y$ ) was negatively correlated with mean CL following the equation  $y = -0.25\text{CL} + 25.4$  ( $r^2 = 0.87$ ,  $p < 0.001$ ).

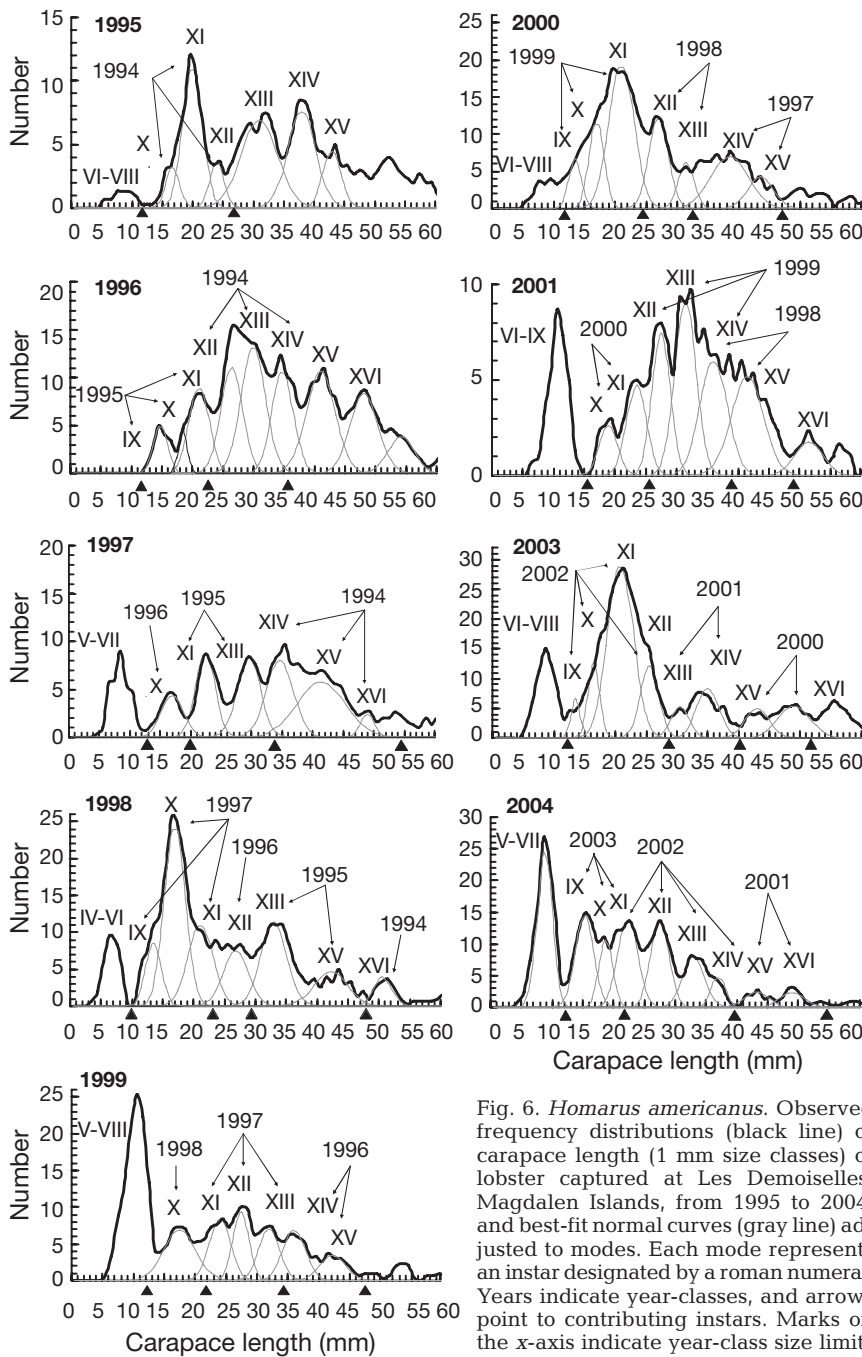


Fig. 6. *Homarus americanus*. Observed frequency distributions (black line) of carapace length (1 mm size classes) of lobster captured at Les Demoiselles, Magdalen Islands, from 1995 to 2004, and best-fit normal curves (gray line) adjusted to modes. Each mode represents an instar designated by a roman numeral. Years indicate year-classes, and arrows point to contributing instars. Marks on the x-axis indicate year-class size limits

**Size-at-age**

The progression of year-classes through time appears to have been different from one year-class to the other. As mentioned above, by the end of the first season of benthic life, we estimated that >50% of lobster in the 1999 and 2001 year-classes had reached Instar VIII. Two years later, respectively, 71 and 100% of lobster in these year-classes had apparently reached Instar XIII (Table 5). In contrast, a majority of Age 2<sup>+</sup> lobster from

year-classes 1996, 1997, 1998 and 2002 only reached Instars XI and XII. These differences in growth translate into different mean sizes-at-age. At Age 2<sup>+</sup>, mean CL varied between an estimated 26.2 mm (1995 year-class) and 33.6 mm (2001 year-class) (Table 5). At Age 3<sup>+</sup>, when lobsters probably start to leave the nursery, differences in size-at-age were still apparent. We infer that all lobster from the 2001 year-class had reached Instar XV, compared to <50% of lobster from year-classes 1995, 1996 and 1997. Estimated mean CL at Age 3<sup>+</sup> varied between 36.0 and 46.1 mm. However, the mean size at Age 3<sup>+</sup> may be underestimated if the larger lobster of a cohort have already vacated the nursery.

Based on the largest instar reached by at least 50% of lobster at Age 3<sup>+</sup> (see Table 5), we projected growth to obtain an estimate of the age at which the leading edge of each year-class could reach Instar XX (most probable instar at commercial size) and start recruiting to the fishery. The majority of lobster of the 2000 and 2001 year-classes could reach Instar XX at Age 7<sup>+</sup>, whereas the 1995, 1996 and 1997 year-classes would not reach Instar XX until they were 1 yr older, at Age 8<sup>+</sup>.

**DISCUSSION**

We have presented a revised assessment of juvenile growth and inferred the growth trajectory from settlement to commercial size for American lobster *Homarus americanus* in the Magdalen Islands. This work is the first to combine controlled *in situ* growth experiments for YOY and modal analyses from long-term field observations of juveniles at 1 site. The size-at-instar, percent molt increment and intermolt period were consistent between the *in situ* growth experiments and the wild population. The gradual but slight divergence in the size of successive instars obtained from SFD analysis compared to the *in situ* growth experiments may reflect suboptimal holding conditions or repeated manipulation (see James-Pirri et al. 1998). Nevertheless, the largely congruent data



Table 4. *Homarus americanus*. Mean  $\pm$  SD (n) of size-at-instar (carapace length, mm) of lobster in Instars IX to XVI from the benthic census carried out at Les Demoiselles, Magdalen Islands, from 1995 to 2004 (values estimated from SFD analyses shown in Fig. 6). Italicized years in table represent year-classes

	IX	X	XI	XII	XIII	XIV	XV	XVI
1995		16.7 $\pm$ 1.1 (9) <i>1994</i>	20.0 $\pm$ 1.6 (45) <i>1994</i>	24.0 $\pm$ 1.2 (11) <i>1994</i>	31.0 $\pm$ 3.0 (53)	38.0 $\pm$ 2.3 (44)	43.0 $\pm$ 0.5 (19)	
1996	14.8 $\pm$ 1.2 (15) <i>1995</i>	18.5 $\pm$ 0.7 (8) <i>1995</i>	21.1 $\pm$ 1.6 (36) <i>1995</i>	26.4 $\pm$ 1.8 (50) <i>1994</i>	30.0 $\pm$ 2.0 (67) <i>1994</i>	34.8 $\pm$ 1.7 (47) <i>1994</i>	41.0 $\pm$ 2.4 (63)	48.1 $\pm$ 2.3 (48)
1997		17.0 $\pm$ 1.8 (20) <i>1996</i>	22.4 $\pm$ 1.6 (35) <i>1995</i>		29.5 $\pm$ 1.9 (40) <i>1995</i>	34.6 $\pm$ 2.2 (44) <i>1994</i>	41.4 $\pm$ 3.9 (57) <i>1994</i>	49.0 $\pm$ 1.2 (7) <i>1994</i>
1998	13.5 $\pm$ 1.3 (28) <i>1997</i>	17.0 $\pm$ 1.7 (105) <i>1997</i>	21.1 $\pm$ 2.0 (55) <i>1997</i>	26.8 $\pm$ 2.1 (39) <i>1996</i>	33.0 $\pm$ 2.1 (60) <i>1995</i>		42.2 $\pm$ 2.7 (32) <i>1995</i>	50.6 $\pm$ 1.4 (14) <i>1994</i>
1999		17.5 $\pm$ 2.6 (45) <i>1998</i>	23.5 $\pm$ 1.7 (35) <i>1997</i>	27.4 $\pm$ 1.3 (31) <i>1997</i>	32.0 $\pm$ 1.7 (30) <i>1997</i>	36.0 $\pm$ 1.8 (31) <i>1996</i>	42.2 $\pm$ 2.1 (18) <i>1996</i>	
2000	13.5 $\pm$ 1.0 (17) <i>1999</i>	17.0 $\pm$ 1.2 (36) <i>1999</i>	21.0 $\pm$ 2.0 (97) <i>1999</i>	27.0 $\pm$ 1.6 (49) <i>1998</i>	31.5 $\pm$ 1.3 (20) <i>1998</i>	38.5 $\pm$ 3.0 (53) <i>1997</i>	43.5 $\pm$ 2.1 (22) <i>1997</i>	
2001		19.0 $\pm$ 1.5 (10) <i>2000</i>	23.5 $\pm$ 1.9 (19) <i>2000</i>	27.5 $\pm$ 1.5 (28) <i>1999</i>	31.5 $\pm$ 1.8 (40) <i>1999</i>	36.0 $\pm$ 2.4 (33) <i>1999-98</i>	41.5 $\pm$ 2.6 (34) <i>1998</i>	51.5 $\pm$ 2.5 (10) <i>1997</i>
2003	13.5 $\pm$ 0.7 (12) <i>2002</i>	16.5 $\pm$ 1.0 (30) <i>2002</i>	20.8 $\pm$ 2.1 (150) <i>2002</i>	25.5 $\pm$ 1.5 (46) <i>2002</i>	30.5 $\pm$ 1.5 (20) <i>2001</i>	35.0 $\pm$ 1.8 (38) <i>2001</i>	43.0 $\pm$ 2.0 (25) <i>2000</i>	49.0 $\pm$ 2.6 (35) <i>2000</i>
2004	15.3 $\pm$ 1.5 (55) <i>2003</i>	18.8 $\pm$ 1.1 (30) <i>2003</i>	22.3 $\pm$ 1.6 (55) <i>2003-02</i>	27.5 $\pm$ 1.5 (52) <i>2002</i>	33.0 $\pm$ 1.8 (35) <i>2002</i>	37.0 $\pm$ 1.1 (13) <i>2002</i>	43.2 $\pm$ 2.0 (12) <i>2001</i>	49.0 $\pm$ 2.0 (12) <i>2001</i>

from these 2 sources form a sound foundation for resolving/interpreting subsequent instars in the SFDs of wild juvenile lobster. In an attempt to overcome the absence of calibration for modal analysis of lobster >1 yr old, SFDs were interpreted independently in the present study. The resulting interpretation rests on the overall coherence of modal patterns and should not be viewed piecewise.

#### Molt increment and intermolt duration

Little information is available on the molt increment and intermolt period of YOY and juvenile lobster in their natural habitat. Despite increasing numbers of YOY censuses over the past years (e.g. Cowan 1999, Wahle et al. 2004), detailed studies of early and juvenile lobster growth are scarce. Most often, Mauchline (1977) is the standard reference for describing lobster growth. However, his regression equation of molt increment against CL (Fig. 9) is a composite of 2 incomplete data sets, neither of which actually measured early juvenile growth. The first is Templeman's (1948) hand-drawn relationship of percent molt increment on CL, which was fitted to data for planktonic Instars III and IV and lobster  $\geq$  50 mm CL by transposing the shape of the growth curve obtained for *Cancer magister* by MacKay & Weymouth (1935). Percent molt increments of planktonic instars are generally high (up to 35%; see Ouellet & Allard 2002) and their use may overestimate molt increment, especially for early benthic stages. The second set of data contributing to Mauchline's (1977) regression equation was taken from Wilder (1953, 1963) and represents percent molt

increments for lobster  $\geq$  55 mm CL. As for the regression equation of intermolt period on CL presented by Mauchline (1977), it is based on Templeman's (1948) laboratory growth study done at a constantly warm temperature range of 19 to 21°C.

There are substantial differences between our interpretation of growth of juvenile lobster at the Magdalen Islands and that proposed by Hudon (1987). The relationship of percent molt increment to CL obtained in the present study differs from Hudon's (1987) in that it is more regular and exhibits a gradual and significant decline with increasing lobster CL. Unlike Hudon (1987), our SFDs showed considerable structure within years and consistency across the years, which facilitated resolution of modes. Our data do not show the 'growth spurt' that Hudon (1987) suggested was due to a change from active pelagic to sedentary benthic lifestyle. We attribute the large oscillation in the percent molt increment of early benthic instars reported in Hudon (1987) to the fact that the mode corresponding to Instar VII was not resolved and that the 12 mm CL mode attributed to Instar VII corresponded in fact to Instar VIII. As for the temporal component of YOY growth, Hudon (1987) borrowed values from Mauchline (1977), resulting in an estimate of intermolt duration from Instars VII to VIII much shorter than our actual measurements, which incorporate the effects of decreasing fall temperatures. Hudon (1987) predicted the intermolt period to be 19 d, whereas it was 32 d in our 1998 growth experiment.

Temperature plays a key role in determining crustacean growth, and, in general, the growth rate of a species increases with temperature because the intermolt period is shortened (Kurata 1962, Hartnoll 2001).

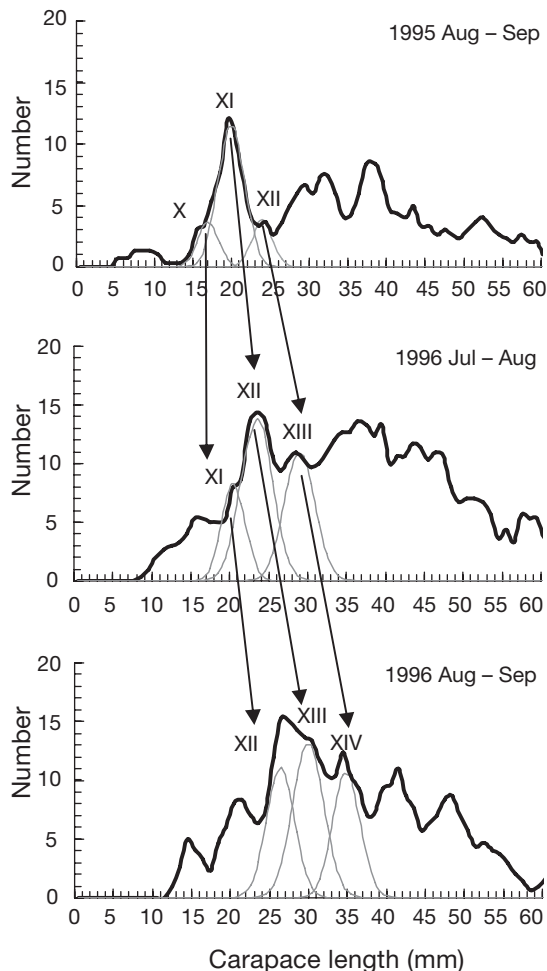


Fig. 7. *Homarus americanus*. Instar composition of year-class 1994 observed in fall 1995 and summer and fall 1996, showing modal progression from Instars X, XI and XII in 1995 to Instars XII, XIII and XIV in 1996

Increasing temperature also frequently reduces the molt increment, but this antagonistic effect on growth rate usually does not offset the relatively more important reduction of intermolt period (Hartnoll 1982, 2001). However, excessively high (post-optimum) temperatures may eventually cause a reduction of growth rate by increasing intermolt period (Hartnoll 1982), and this is true of rock lobsters in particular (Thomas et al. 2000).

In the American lobster, the growth rate is reported to be proportional to temperature within the range of 8 to 25°C (Aiken 1977). Templeman (1936) hypothesized from his observations of larval growth in nature that the molt increment would be reduced at warmer temperatures. Ouellet & Allard (2002) documented substantial within-year variability in the size of postlarvae (Instar IV) in the plankton at the Magdalen Islands and suggested that higher temperatures favored smaller planktonic lobster larvae. The molt increment for

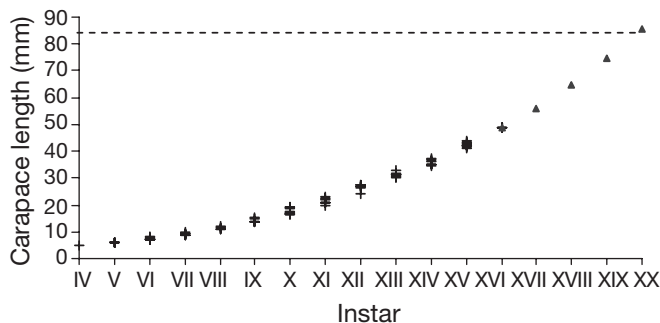


Fig. 8. *Homarus americanus*. Mean size at Instars IV to XVI (+) estimated for year-classes 1994 to 2004 from the analysis of size-frequency distributions shown in Fig. 6, and projected size at Instars XVII to XX (▲) assuming a molt increment of 15%. Dashed line represents the current minimum legal size (83 mm CL) in the Magdalen Islands lobster fishery

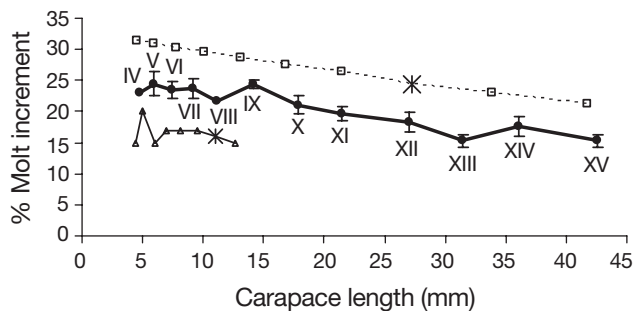


Fig. 9. *Homarus americanus*. Mean ( $\pm$ SE) of percent molt increment expressed as a function of mean premolt carapace length at instar calculated from data in Tables 3 & 4. Dashed line represents the growth equation from Mauchline (1977), and the thin line represents molt increments reported by James-Pirri et al. (1998), both starting with Instar IV. Asterisks represent Instar X

Instars IV to XI was conspicuously less and resulted in YOY lobster being much smaller at instar in the warmer waters (mean 19.7°C, range 13.4 to 24.5°C from July to November 1995) off Rhode Island (Fig. 9, data from James-Pirri et al. 1998) than in the cooler waters (mean 12.5°C, range 5.9 to 17.9°C from July to November 1998) off the Magdalen Islands. However, contrary to expectation, the intermolt periods for Instars V to VI initially were not shorter off Rhode Island than at the Magdalen Islands. It is only at Instar VII that the intermolt period became substantially longer at the Magdalen Islands (mean 32 d), with the onset of cool fall temperatures, than in Rhode Island (mean 16.5 d).

### Size of YOY at onset of winter

The size that a lobster reaches before the end of its first season of growth may be critical for winter survival and competitiveness with individuals of the next year's cohort, and it contributes to the time required to

Table 5. *Homarus americanus*. Estimated mean size (carapace length, mm) and instar composition at age for year-classes 1994 to 2004 (from SFD analyses shown in Fig. 6). The instar selected for projection of age at fishery recruitment from Age 3+ is underlined

	0+	1+	2+	3+
1994		22.3	30.2	39.3
		X: 16 %	XII: 31 %	XIV: 41 %
		XI: 67 %	XIII: 41 %	<u>XV: 53 %</u>
		XII: 17 %	XIV: 28 %	XVI: 6 %
1995		19.2	26.2	36.0
		IX: 25 %	XI: 47 %	<u>XIII: 67 %</u>
		X: 15 %	XII: 0 %	XIV: 0 %
		XI: 60 %	XIII: 53 %	XV: 33 %
1996		16.0	26.8	38.2
		X: 100 %	XII: 100 %	<u>XIV: 63 %</u>
				XV: 37 %
1997	8.3	17.9	27.6	39.7
	V: 3 %	IX: 12 %	XI: 37 %	<u>XIV: 76 %</u>
	VI: 57 %	X: 54 %	XII: 32 %	XV: 24 %
	VII: 40 %	XI: 34 %	XIII: 31 %	
1998	6.7	17.5	28.3	41.5
	IV: 7 %	X: 100 %	XII: 71 %	XIV: 31 %
	V: 26 %		XIII: 29 %	<u>XV: 69 %</u>
	VI: 67 %			
1999	10.1	19.1	31.8	
	V: 4 %	IX: 11 %	XII: 29 %	
	VI: 8 %	X: 24 %	<u>XIII: 39 %</u>	
	VII: 24 %	XI: 65 %	XIV: 32 %	
	VIII: 64 %			
2000	9.4	22.2		45.8
	VI: 20 %	X: 35 %		XV: 44 %
	VII: 44 %	XI: 65 %		<u>XVI: 56 %</u>
	VIII: 36 %			
2001	10.8		33.6	46.1
	VI: 6 %		XIII: 35 %	XV: 50 %
	VII: 38 %		XIV: 65 %	<u>XVI: 50 %</u>
	VIII: 53 %			
	IX: 3 %			
2002		20.8	28.6	
		IX: 5 %	XI: 26 %	
		X: 13 %	<u>XII: 37 %</u>	
		XI: 63 %	XIII: 28 %	
		XII: 19 %	XIV: 9 %	
2003	8.9	18.5		
	VI: 18 %	IX: 45 %		
	VII: 73 %	X: 25 %		
	VIII: 9 %	XI: 30 %		
2004	8.9			
	V: 3 %			
	VI: 12 %			
	VII: 85 %			

recruit to the fishery. In Rhode Island, depending on the time of settlement, YOY are expected to reach Instars VIII to X by the end of the first season of growth, corresponding to sizes of 8 to 12.5 mm CL. Most YOY lobster at our study site probably overwintered at Instar VII (mean 8.8 to 9.9 mm CL) or VIII (11.0 to 11.8 mm CL). This is considerably smaller than the average overwintering size of 14.5 mm CL (Instar VIII) inferred by Hudon (1987). This discrepancy can

be explained by an extrapolation based on incorrect sizes-at-instar and underestimated intermolt periods as explained above. In the colder waters of the Gulf of Maine, Incze & Wahle (1991) observed in September that YOY lobster formed a clear mode at 7 to 8 mm CL, which may correspond to Instar VI. There, YOY lobster are expected to reach Instar VII with  $\leq 10.5$  mm CL before winter (Incze et al. 1997, Wahle & Incze 1997).

First-year growth and YOY overwintering size at the Magdalen Islands is certainly subject to some interannual variability, most probably linked to temperature. YOY lobster were on average 1 instar less developed in 2003 and 2004 compared to 1999 and 2001, although the sampling periods were similar in timing and extent. The 1999 and 2001 year-classes may have benefited from above-average water temperature, which could have extended the season of growth and, in addition, favored early settlement. Indeed, retrocalculation of mean settlement date using the number of degree-days for growth from Instars IV to VIII suggests that postlarvae started to settle around 16–18 July in 1999 and 2001 compared to 7–8 August in 2003 to 2004. The date of settlement depends on the date of hatching and on the larval development rate, and the time required to attain the postlarval stage from hatching is inversely related to temperature during the planktonic phase (Templeman 1948). Additionally, size of YOY at the onset of winter may also depend, in part, on the size at settlement. James-Pirri et al. (1998) observed that postlarvae settling earlier in the season tended to be larger than those settling later, possibly because they were also larger at hatching.

Our field data are perhaps not always representative of the full growth potential of YOY before the onset of winter. The growth season of YOY was reported to extend into October (Wahle et al. 2004) and even into November (Cowan et al. 2001) in the Gulf of Maine, which in fall is similarly cold to the Magdalen Islands. At our site, sampling was terminated by the third week of September, when temperature was still 12 to 14°C. Molt-ing can occur until the temperature drops to approximately 5°C, and then molt induction is blocked (Aiken & Waddy 1986). In all years we sampled, there were apparently ample degree-days left for any Instar IV, V and VI lobster to make an additional molt between September and the time of onset of the critical temperature low. This is especially true of the warmer years (1999 and 2001).

### Projections

Projections indicate that commercial legal size in the Magdalen Islands fishery (83 mm CL) would most likely be reached at Instar XX. Lobster of a year-class could achieve commercial size by Ages 7+ or 8+ and become

available to the spring fishery the following year, approximately 8 to 9 yr after settlement. Females that become sexually mature before 83 mm CL would need an additional year before entering the fishery because of a 2 yr reproductive cycle, with 1 yr of spawning/brooding alternating with 1 yr of molting. Our projection is more conservative than Hudon's (1987) suggestion that lobster could enter the fishery at Ages 4<sup>+</sup> to 6<sup>+</sup>, for a commercial size of 76 mm CL in those years. Obviously, our projection of age at commercial size does not capture all the variability in the growth process and does not provide an estimation of the range of ages at recruitment, which could be fairly large as reported by Sheehy (2001) for *Homarus gammarus*. We projected from inferred instar composition at Age 3<sup>+</sup>, and it is likely that lobster start to leave the nursery area near or at that age. Therefore, larger instars may have been under-represented in our samples, which could cause an underestimation of size-at-age. Moreover, projections were made assuming that all instars of a year-class grow equally after Age 3<sup>+</sup>. At this stage, in the absence of direct measurements of the age of lobster, our projection cannot be validated. The technique to assess lobster age (Sheehy et al. 1996, 1999) was not yet available when we initiated this study and has yet to be applied and validated with American lobster, following from Wahle et al.'s (1996) work.

### CONCLUSIONS

The present study contributes to the understanding of growth of American lobster *Homarus americanus* from Instars IV to XVI, i.e. from benthic settlement to approximately 3 yr of age. Based on long-term field observations and *in situ* growth experiments, this work provides new and precise information on size-at-instar and percent molt increment, and some reasonable inferences about interannual variability in the growth trajectory of juvenile lobster. We have also critically reviewed current concepts about lobster early growth, emphasizing at the same time the scarcity of fine-resolution studies of growth of early benthic stages. Our work was concentrated in a nursery area, hence processes involved after lobster leave the nursery area and the ways in which they affect growth are still uncertain and warrant further investigation.

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### LITERATURE CITED

- Aiken DE (1977) Molting and growth in decapod crustaceans with particular reference to the lobster *Homarus americanus*. Div Fish Oceanogr Circ (Australia, CSIRO) 7:41–73
- Aiken DE, Waddy SL (1986) Environmental influence on recruitment of the American lobster, *Homarus americanus*: a perspective. Can J Fish Aquat Sci 43:2258–2270
- Cobb JE, Wahle RA (1994) Early life history and recruitment processes of clawed lobsters. Crustaceana 67:1–25
- Comeau M, Savoie F (2001) Growth increment and molt frequency of the American lobster (*Homarus americanus*) in the southwestern, Gulf of St. Lawrence. J Crustac Biol 21:923–936
- Cowan DF (1999) Method for assessing relative abundance, size distribution, and growth of recently settled and early juvenile lobsters (*Homarus americanus*) in the lower intertidal zone. J Crustac Biol 19:738–751
- Cowan DF, Solow AR, Beet A (2001) Patterns in abundance and growth of juvenile lobster, *Homarus americanus*. Mar Freshw Res 52:1095–1102
- Fogarty MJ, Gendron L (2004) Biological reference points for American lobster (*Homarus americanus*) populations: limits to exploitation and the precautionary approach. Can J Fish Aquat Sci 61:1392–1403
- Hartnoll RG (1982) Growth. In: Abele LG (ed) The biology of Crustacea. Academic Press, New York, p 111–196
- Hartnoll RG (2001) Growth in Crustacea — twenty years on. Hydrobiologia 449:111–122
- Hudon C (1987) Ecology and growth of postlarval and juvenile lobster, *Homarus americanus*, off Îles de la Madeleine (Quebec). Can J Fish Aquat Sci 44:1855–1869
- Hudon C, Fradette P, Legendre P (1986) La répartition horizontale et verticale des larves de homard (*Homarus americanus*) autour des îles de la Madeleine, golfe du Saint-Laurent. Can J Fish Aquat Sci 43:2164–2176
- Incze LS, Wahle RA (1991) Recruitment from pelagic to early benthic phase in lobsters *Homarus americanus*. Mar Ecol Prog Ser 79:77–87
- Incze LS, Wahle RA, Cobb JS (1997) Quantitative relationships between postlarval production and benthic recruitment in lobsters, *Homarus americanus*. Mar Freshw Res 48:729–743
- James-Pirri MJ, Cobb JS, Wahle RA (1998) Influence of settlement time and size on postsettlement growth in the American lobster (*Homarus americanus*). Can J Fish Aquat Sci 55:2436–2446
- Kurata H (1962) Studies on the age and growth of Crustacea. Bull Hokkaido Reg Fish Res Lab 24:1–115
- MacDonald PDM, Pitcher TJ (1979) Age-groups from size-frequency data: a versatile and efficient method of analysing distribution mixtures. J Fish Res Board Can 36:987–1001
- MacKay DCG, Weymouth FW (1935) The growth of the Pacific edible crab, *Cancer magister* Dana. J Biol Board Can 2:41–88
- Mauchline J (1977) Growth of shrimps, crabs and lobsters — an assessment. J Cons Int Explor Mer 37:162–169

- Miller RJ (1997) Spatial differences in the productivity of American lobster in Nova Scotia. *Can J Fish Aquat Sci* 54: 1613–1618
- Ouellet P, Allard JP (2002) Seasonal and interannual variability in larval lobster *Homarus americanus* size, growth and condition in the Magdalen Islands, southern Gulf of St. Lawrence. *Mar Ecol Prog Ser* 230:241–251
- Ouellet P, Lefavre D, Allard JP (2001) Lobster (*Homarus americanus*) larvae abundance and post-larvae availability to settlement at the Magdalen Islands, southern Gulf of St. Lawrence (Quebec). In: Tremblay MJ, Sainte-Marie B (eds) Canadian lobster Atlantic wide studies (CLAWS) symposium: abstracts and proceedings summary. *Can Tech Rep Fish Aquat Sci* 2328:14–18
- Paille N, Sainte-Marie B, Brêthes JC (2002) Behavior, growth and survival of stage V lobsters (*Homarus americanus*) in relation to shelter availability and lobster density. *Mar Freshw Behav Physiol* 35:203–219
- Sainte-Marie B, Chabot D (2002) Ontogenetic shifts in natural diet during benthic stages of American lobster (*Homarus americanus*), off the Magdalen Islands. *Fish Bull* 100: 106–116
- Sheehy MRJ (2001) Implications of protracted recruitment for perception of the spawner–recruit relationship. *Can J Fish Aquat Sci* 58:641–644
- Sheehy MRJ, Shelton PMJ, Wickins JF, Belchier M, Gaten E (1996) Ageing the European lobster *Homarus gammarus* by the lipofuscin in its eyestalk ganglia. *Mar Ecol Prog Ser* 143:99–111
- Sheehy MRJ, Bannister RCA, Wickins JF, Shelton PMJ (1999) New perspectives on the growth and longevity of the European lobster (*Homarus gammarus*). *Can J Fish Aquat Sci* 56:1904–1915
- Sokal RR, Rohlf FJ (1995) *Biometry*. WH Freeman, New York
- Steneck RS, Wilson CJ (2001) Large-scale and long-term, spatial and temporal patterns in demography and landings of the American lobster, *Homarus americanus*, in Maine. *Mar Freshw Res* 52:1303–1319
- Templeman W (1936) Local differences in the life history of the lobster (*Homarus americanus*) on the coast of the maritime provinces of Canada. *J Biol Board Can* 2:41–88
- Templeman W (1948) Growth per molt in the American lobster. *Bull Nfld Gov Lab* 18:26–47
- Thomas CW, Crear BJ, Hart PR (2000) The effect of temperature on survival, growth, feeding and metabolic activity of the southern rock lobster, *Jasus edwardsii*. *Aquaculture* 185:73–84
- Wahle RA (2003) Revealing stock–recruitment relationships in lobsters and crabs: Is experimental ecology the key? *Fish Res* 65:3–32
- Wahle RA, Incze LS (1997) Pre- and post-settlement processes in recruitment of the American lobster. *J Exp Mar Biol Ecol* 217:179–207
- Wahle RA, Tully O, O'Donovan V (1996) Lipofuscin as an indicator of age in crustaceans: analysis of the pigment in the American lobster *Homarus americanus*. *Mar Ecol Prog Ser* 138:117–123
- Wahle RA, Tully O, O'Donovan V (2001) Environmentally mediated crowding effects on growth, survival and metabolic rate of juvenile American lobsters (*Homarus americanus*). *Mar Freshw Res* 52:1157–1166
- Wahle RA, Incze LS, Fogarty MJ (2004) First projections of American lobster fishery recruitment using a settlement index and variable growth. *Bull Mar Sci* 74:101–114
- Wilder DG (1953) The growth rate of the American lobster (*Homarus americanus*). *J Fish Res Board Can* 10:371–412
- Wilder DG (1963) Movements, growth and survival of marked and tagged lobsters liberated in Egmont Bay, Prince Edward Island. *J Fish Res Board Can* 20:305–318

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