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Growth, survivorship, life-span, and sex change in the hermaphroditic shrimp *Lysmata wurdemanni* (Decapoda: Caridea: Hippolytidae)

Abstract *Lysmata wurdemanni* (Gibbes) is a protandric simultaneous hermaphrodite. All individuals first mature as a male-phase individual (MP) and then later change to a female-phase individual (FP) that spawns and broods embryos but can also mate as a male. A Gulf of Mexico population was sampled monthly for 1 year and bimonthly the next. Estimates of basic population parameters were obtained from cohort analysis to reveal possible factors explaining the unusual sexual biology of *L. wurdemanni* as well as the broad variation in the size (age) of change from MP to FP. Growth rates of individuals from cohorts varied from 4–7 mm carapace length year^{-1}. Growth of small MPs in the laboratory was somewhat faster but concordant with growth rates estimated from field samples. The period from recruitment to >50% sex change in cohorts varied from 3 months to 1 year. In the laboratory, the size and interval to sex change was similar to that of the most rapidly changing cohort observed. Survivorship of cohorts was high until later in life; life-span was estimated to be 12–18 months. Rates of sex change were highest from late winter through spring, in time for the spring–summer breeding season. The size and age of sex change in cohorts were related to the season of recruitment. MPs recruited from late winter to mid-spring rapidly changed to FPs at a relatively small size. A majority of MPs recruited in the summer and autumn did not change to FPs until the following late winter to spring, and they did so at a larger size. Rates of sex change were not correlated with the sexual composition of the population. We conclude that seasonal factors related to female breeding greatly influence sex change in *L. wurdemanni*. We found no evidence to support demographically influenced and socially mediated environmental sex determination, which has been suggested for *L. wurdemanni* and other sex-changing caridean shrimps.

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Introduction

Sex change from male to female (protandry) is not uncommon in caridean shrimps (Bauer 2000). A protandric individual first matures as a male-phase individual (MP) and then changes into a female-phase individual (FP) later in life. Sex-changing individuals develop vitellogenic oocytes in their gonads and lose male characteristics such as cincinnuli on the first pleopods and appendices masculinae on the second pleopods. Similar to protandric species, an individual of the hippolytid shrimp *Lysmata wurdemanni* develops first as an MP and then later changes to an FP (Bauer and Holt 1998). However, FPs of *L. wurdemanni* retain functional male gonopores, the ejaculatory ducts persist, and the testicular portions of the gonads (ovotestes) continue to produce sperm. Mating experiments confirmed that FPs of *L. wurdemanni* are outcrossing simultaneous hermaphrodites, capable of mating as a male or as a female with subsequent spawning of eggs (Bauer and Holt 1998). They are, however, incapable of self-fertilization. This sexual system was termed "protandric simultaneous hermaphroditism" (PSH) by Bauer (2000). In spite of the reproductive advantages of PSH, this sexual system appears to be quite rare in caridean shrimps. This sexual system has been confirmed to date only in *L. wurdemanni* (Bauer and Holt 1998) and *L. amboinensis* (Fiedler 1998). Based on reproductive morphology, it is probable that PSH is widespread in the genus *Lysmata* (Bauer 2000) and occurs in the hippolytid *Exhippolysmata ensirostris* (Kagwade 1982).

The size at which sex change occurs in *L. wurdemanni* is quite variable, ranging from 5.0 mm carapace length (CL)

to 11.5 mm CL (size of transitional individuals; present study). Variability in the age and/or size at which sex change occurs might be explained by environmental sex determination (ESD) based on the sexual composition of the population and presumably mediated by social interactions (Charnov et al. 1978; Charnov 1981, 1982; Charnov and Anderson 1989; Bauer 2000). This kind of ESD is well documented in sex-changing fishes (Shapiro 1979; Chan and Yeung 1983; Ross 1990) and was suggested by Bauer (2000) for *L. wurdemanni*. Lin and Zhang (2001) performed experiments that indicated, in their view, ESD in *L. wurdemanni* based on the demographic environment. Alternately, the timing of sex change may be genetically fixed and occurs when an individual reaches a certain age or size, as suggested by rearing experiments in the protandric caridean *Pandalus danae* (Marliave et al. 1993). Genetic variation in the timing of sex change might be maintained by frequency-dependent selection (*P. borealis*; Bergström 1997). Seasonal variation in physical factors affecting breeding may be responsible for delayed sex change in *L. wurdemanni* during certain seasons of the year (Bauer 2002a).

Other than description of basic population structure and breeding biology (Bauer 2002a, 2002b), there is little information on the population biology of *L. wurdemanni*, a species with a seemingly quite advantageous but rare sexual system (PSH). The purpose of this study was to describe some fundamental life-history characteristics of this species, including growth, survivorship, life-span, rate and timing of sex change, and the possible relation of the latter with the relative frequency of sexual morphs in the population. We wanted to determine if there are any striking features of the population biology of this species that might shed light on the evolution of its unusual sexual system. Additionally, information on its population biology may help to explain why there is so much variation in the size (age) of sex change in *L. wurdemanni*.

Materials and methods

Collections and measurements

Population samples of *Lysmata wurdemanni* were taken from the rock jetty in Port Aransas, Texas (27°50′N; 97°03′W) from June 1999 to June 2000 and bimonthly from August 2000 to June 2001. Shrimps were collected during lower tides (−0.5 ft mean sea level) at night, when the shrimps are active and move out into tide pools and under ledges of boulders on the perimeter of the rock jetty (Bauer 2002b). Shrimps were collected in tide pools with hand dipnets and from under ledges with a long-handled dipnet. The nets used had 1 mm mesh and effectively collected the smallest (newly recruited) members of the population (Bauer 2002a, 2002b). There was no apparent segregation of individuals into size or age groups, all individuals captured were retained as part of the sample, and thus samples taken are assumed to represent random samples of the population (Bauer 2002a, 2002b). Time spent by each person participating in sample collection was recorded. After collection, the samples were preserved in 10% formalin for 1–2 days and then transferred to 70% ethyl alcohol for permanent storage.

Size of individuals was measured and recorded as CL, defined as the distance from the posterior-most margin of the eye orbit to the mid-dorsal posterior margin of the carapace. The sexual phase of individuals was determined as in Bauer and Holt (1998): MPs

have appendices masculinae on the second pleopods and cincinnuli (coupling hooks) on the first pleopods; sex-changing individuals (transitionals) show MP characteristics externally but vitellogenic oocytes are observable in the anterior (ovarian) portions of the gonads; FPs have no or reduced appendices masculinae on the second pleopods, lack cincinnuli on the first pleopods, vitellogenic oocytes may be present in the ovotestes, and embryos may be attached to (incubated on) their pleopods.

Cohort analysis, growth and life-span

The mixture analysis method (MIX; Macdonald and Pitcher 1979; Macdonald and Green 1988) was used to identify cohorts (population components) within size-frequency distributions constructed from population samples. The MIX program computes a mixture of normal distributions and compares it to the size-frequency data of a sample. The program requires that the user specify the number of components within the distribution. To avoid bias in the number of components chosen, each sample was analyzed multiple times with different numbers of components. For each component of the mixture, representing a cohort, the mean CL (and standard deviation) and the proportion of the total sample represented by that component (cohort) were calculated. Through a series of iterations the optimal combination of these parameters was achieved for the entire mixture. For each combination of solutions, the MIX program generated a goodness-of-fit chi-square statistic and the probability of the hypothesis of no difference between the mixture distribution and the original size-frequency distribution. The solution generating the highest *P*-value best described the number of cohorts and their parameters for each sample. After analysis was completed for all samples, the resulting size-frequency diagrams were compared. Beginning with cohorts on the far right of the histogram (presumably the oldest), cohorts of a sample were matched with what appeared to be the same cohorts in samples before and after. Each cohort was identified with a letter designation.

The mean CL of a cohort during the first month it appeared was the initial observation in estimation of growth. Subsequent observations of that cohort over time were recorded as the mean CL at the time interval from the initial observation. Cohorts with a mean CL of ≤ 4.7 mm were considered as newly recruited, following Bauer (2002b) for the size at which recruitment onto the jetties occurs (individuals catchable by sampling methods). Life-span at the sampling location was estimated by measuring the amount of time the cohorts persisted from recruitment until extinction. Only newly recruited cohorts were used in the estimation of life-span.

Survivorship

The abundance (catch per unit effort) of the population for a sample was estimated by dividing the total number of shrimps collected by the number of person-hours spent in collecting. The total abundance was then multiplied by the relative proportions of each cohort (obtained from the MIX analysis) to determine the abundance of each cohort for that sample. The decline in a cohort's abundance (survivorship) was recorded as a fraction of its initial abundance. The initial abundance of a cohort was taken from the first or second sample, whichever was higher, in which the cohort was identified, that is, the sample in which the cohort was considered fully recruited. A regression of survivorship against time was calculated for each cohort. To construct survivorship curves, survivorship values for cohorts were multiplied by 100, and plots of survivorship from an initial value of 100 (100% initial cohort abundance) were made on a semi-logarithmic scale to generate survivorship curves. Survivorship curves were made only for cohorts for which the regression of survivorship on time was statistically significant (*P* < 0.05).

Proportion of sexual morphs and rate of sex change

The proportions of MPs (including transitionals) and FPs for each cohort in each sample were estimated by counting the number of MPs and FPs in the sample belonging to that cohort. The change in

proportions of sexual morphs in a cohort from one sampling period to the next is the rate of sex change and was calculated using the formula: $(P_2-P_1)/(T_2-T_1)$ where P_1 and P_2 are the proportions of FPs in the cohort at time 1 (T_1, in months) and time 2 (T_2), respectively. Only cohorts that were changing sex were used in this analysis, that is, cohorts that were above the physiological minimum size of sex change (mean CL of cohort > 5.0 mm) and in which the proportion of FPs was increasing from one sample to the next.

Laboratory observations on growth and time to sex change

Growth and time to sex change of small MPs were measured in the laboratory for comparison with values obtained from cohort analysis. Because of the possibility that growth rate and time to sex change might be influenced by competitive or social interactions, individuals were observed in two treatments, "Group" and "Individual." In the Group treatment ($n=25$), individuals were maintained in three 38-l aquaria in two groups of 10 and one group of the remaining 5, rather than a single group of 25 in one aquarium, because preliminary observations suggested significant losses from cannibalism when densities exceed 10 shrimps per 38-l aquarium. Approximately half the water in the aquaria was changed weekly. In the Individual treatment ($n=25$), each shrimp was kept in a separate container, a 500-ml plastic cup perforated with 2–3 mm diameter holes to allow water flow, placed on a water table with recirculating water. Both treatments were maintained under a long-day (14 h light) photoperiod, a water temperature of 26°C, with water salinity of 34–36‰. Shrimps were fed daily with half of a food pellet (Wardley shrimp pellets, 0.06–0.08 g pellet^{-1}). Individuals utilized in these observations were collected in Port Aransas, Texas, in September 2001. The initial mean size of MPs was 5.3 mm CL (SD ±0.6) in the Group treatment and 5.6±0.6 mm CL in the Individual treatment. Observations were terminated after 18 weeks when most individuals had changed to FPs and the remaining MPs showed no signs of impending change.

To identify and follow individuals in the Group treatment, internal elastomer tags were used (Godin et al. 1996). Elastomer, a bio-neutral polymer, was injected as a small spot or strip into abdominal muscle with a hypodermic syringe. The tags were placed in one of four possible locations using one of three different colors.

In the two treatments, each individual was measured to the nearest 0.1 mm CL at the first observation. In the Group treatment, all individuals were removed weekly, rapidly measured, and briefly examined for ovarian development (presence or absence of vitellogenic oocytes in the anterior portion of the ovotestes). Individuals were removed when they had changed to FP, indicated by the presence of embryos under the abdomen. In the Individual treatment, each shrimp was observed daily for molting (presence or absence of a molt skin or exuviae) and gonadal condition. When an individual changed to an FP, it was removed, along with its pres-pawning molt skin (indicating size of its transitional stage).

Growth rate of individuals in the Group treatment is reported as the weekly mean increase in CL from the initial size measured at the beginning of the observations. The overall growth of shrimps in the Individual treatment was determined by dividing the total growth of each individual by the length of time each shrimp was observed. The mean of these individual growth rates is reported.

Results

Cohort analysis

Of the 17 samples collected between June 1999 and June 2001, 15 contained a sufficient number of individuals for cohort analysis. The analysis using the MIX program generated a mixture distribution for samples with a histogram and fitted curves corresponding to cohorts

(Fig. 1). Eight cohorts were identified and followed over successive samples. Each cohort was assigned a letter designation from "A" (oldest cohort) to "H" (most recently recruited cohort). An additional two cohorts were identified in the final sample and assigned the letter designations "I" and "J". The mean size (carapace length) of cohorts A and B was well past maximum recruitment size (4.7 mm CL) when the sampling began. Cohorts C, D, and E each recruited during the sampling period and went extinct before the end of the sampling periods. For these latter three cohorts, growth, survivorship, and sex change could be observed over their entire life-span. Cohorts F and G recruited during the sampling period but had not yet gone extinct before the end of the sampling project. Because the mean size of cohort H was above recruitment size when first identified, it was not used in estimates of life-span or in the growth key (below). Cohorts I and J, only observed in a single (the final) sample, were not used in the following analyses.

Growth

For each cohort, a simple linear regression of mean CL (millimeters) on time (years) was calculated to describe cohort growth (Fig. 2). The slope of the regression line yields the growth rate (millimeters per year). All regressions were statistically significant ($P<0.05$), and r^2 values (square of Pearson correlation coefficient) were ≥0.91. The cohorts varied in growth rate from 4.0 to 6.7 mm year^{-1} (median = 5.4; Fig. 2). Combining the growth data for newly recruited cohorts (cohorts C–G; Fig. 3), a linear regression of age on size (CL) was calculated that allows estimation of age from carapace length (growth key). The regression equation of the growth key is: age in years = (0.16)(CL)−0.63 ($P<0.001$, $r^2=0.92$). For any given size, the lower and upper limits for age can be estimated from the 95% confidence limits on the slope and y-intercept of this equation, 0.02 and 0.05, respectively.

Growth rates were also obtained from laboratory observations on living shrimps. For the Group treatment (Fig. 4), growth (increase in CL per week) is given by the slope of the regression equation: increase in CL = b(time in weeks) + a, where b is the slope and a is the y-intercept (Fig. 4). For the Group treatment, the growth rate was 0.20 mm ± 0.01 week^{-1}. For the Individual treatment, calculated from the total growth from the initial to final observation divided by the time span of observations, the mean growth rate was 0.19 ± 0.07 mm week^{-1}. Extrapolated to yearly values, growth rates were 10.4 mm year^{-1} and 9.9 mm year^{-1} for the Group and Individual treatments, respectively.

Life-span

Life-span is defined as time from first recognition of a cohort to its disappearance from the samples. Cohort F was the longest-persisting cohort (1.3 years) and its
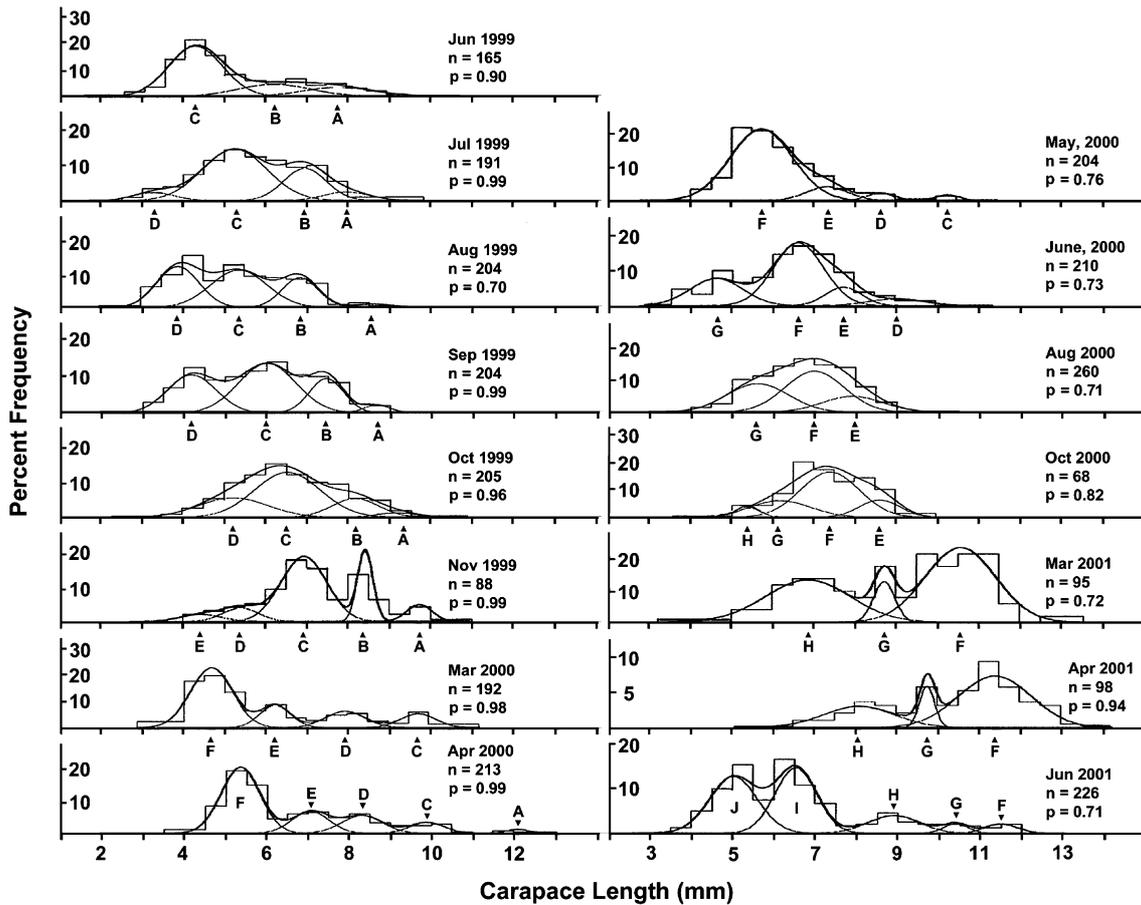
Fig. 1 *Lysmata wurdemanni.* Cohorts identified from size-frequency distributions (histogram) from samples taken at Port Aransas, Texas, using mixture analysis (MIX). *Upper case letters* are used for identified cohorts; *n* number of individuals in the sample; *p* probability of goodness-of-fit of the mixture distribution (cohort curves) with the observed size-frequency distribution

mean CL was 11.5 ± 0.4 mm when last observed (Fig. 2). This cohort had not yet gone extinct by the end of the study and its abundance had declined to 15.5% of its initial value. Cohort G also had not disappeared by the end of the sampling period (Fig. 1). When last observed (June 2001), it had been in the population for 1 year (1.02 years), its mean CL was 10.4 ± 0.3 mm, and its abundance had declined to 34.1%. Cohorts C, D, and E, which were followed from recruitment to extinction, persisted for 0.91 years (C) and 0.92 years (D and E). The mean CLs of cohorts C, D, and E at their final observation were 10.1 ± 0.3 mm, 9.1 ± 0.7 mm, and 8.5 ± 0.5 mm, respectively. In the April 2001 sample, there were several very large individuals with carapace lengths from 13 to 14 mm. The ages of these individuals, using the growth key, are estimated at 1.4 to 1.6 years.

Survivorship

Survivorship was calculated for five cohorts, three with a life-span slightly less than 1 year (cohorts C, D, and E)
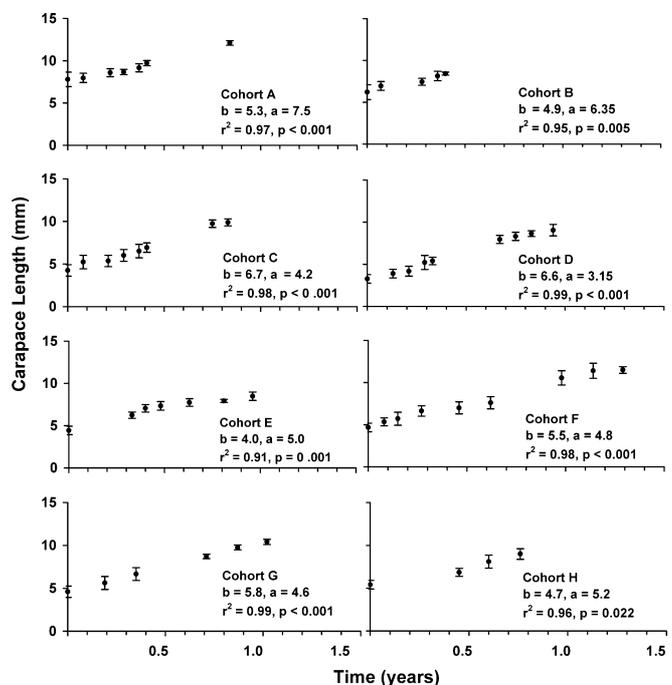

Fig. 2 *L. wurdemanni.* Growth plots for eight cohorts using the mean carapace length of each cohort at the time of sampling. *Error bars* represent standard deviations. Regressions of mean carapace length on time were calculated. The slope (*b*) represents the growth rate per year; *a* y-intercept; *p* probability of no significant regression; r^2, square of Pearson correlation coefficient
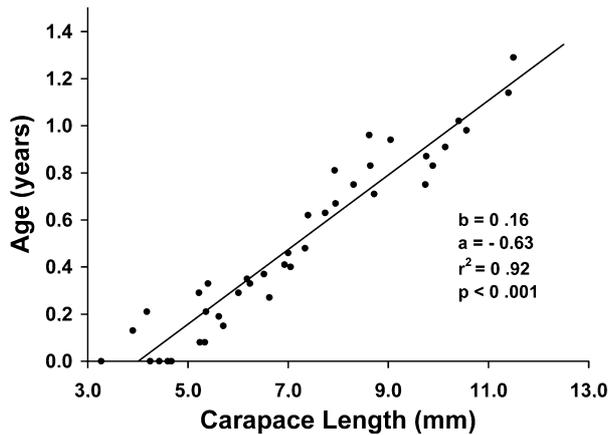
Fig. 3 *L. wurdemanni*. Growth key based on the regression of mean carapace length of a cohort on its age (time from recruitment in years) for all samples in which it occurred. *Data points* (n = 40) are from cohorts C–G, which were considered newly recruited on their first observation; *a* y-intercept; *b* slope; *p* probability of no significant regression; r^2, square of Pearson correlation coefficient
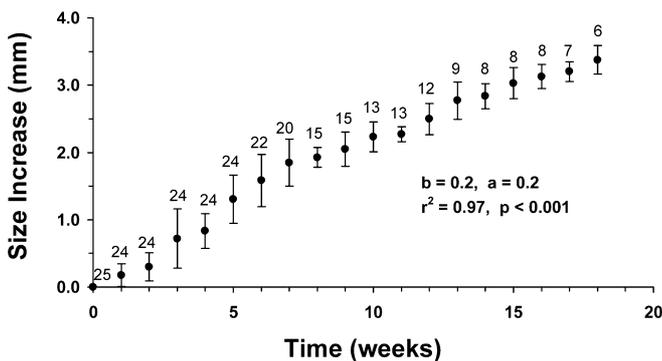

Fig. 4 *L. wurdemanni*. Growth of male-phase individuals (MPs) from the Group treatment. Values plotted are the mean increase in carapace length ($\pm$ SD) from the initial size observation. *Numbers above error bars* are the number of individuals (n) measured at each observation, which decreased from the original n = 25 as MPs changed to the female phase or suffered mortality; *a* y-intercept; *b* slope; *p* probability of no significant regression; r^2, square of Pearson correlation coefficient

Table 1 *Lysmata wurdemanni*. Coefficients for the regression of survivorship (fraction of initial cohort abundance) on time in years for cohorts C–F; *a* y-intercept; *b* slope; *P* probability of no significant regression; r^2 square of Pearson correlation coefficient

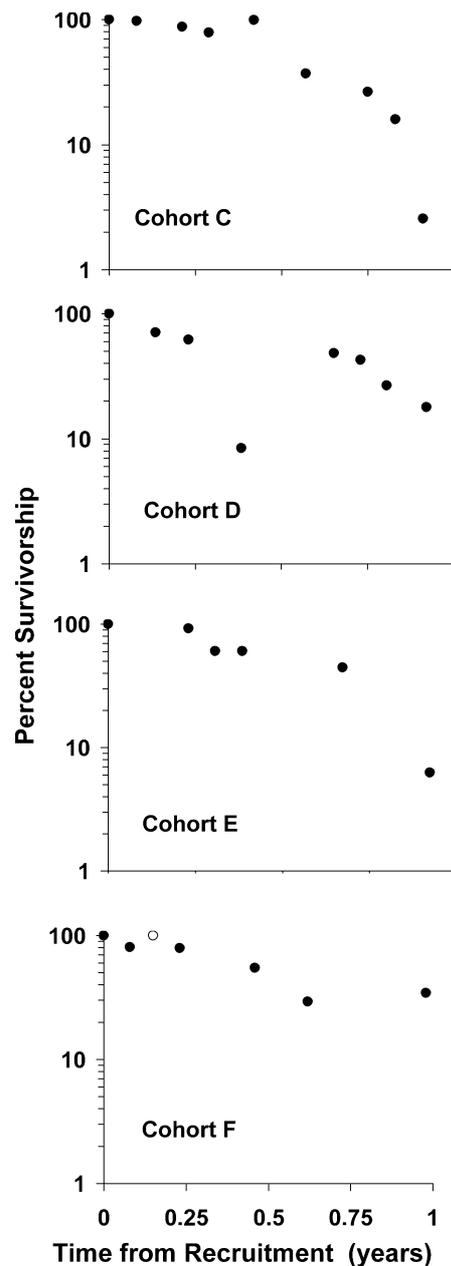| Cohort	b	a	r^2	P
C	−1.12	1.11	0.88	< 0.001
D	−0.66	0.79	0.56	0.03
E	−0.99	1.02	0.93	0.002
F	−0.84	1.02	0.68	0.02

Fig. 5 *L. wurdemanni*. Plots of survivorship over time in cohorts from 100% survivorship at full recruitment in cohorts C–F. Semi-logarithmic plots are used to visualize survivorship curves. The single *unfilled data point* in cohort F represents a value greater than 100% (127%); this value was adjusted to 100% for this figure

and two with a life-span over 1 year (cohorts F and G). A regression of survivorship on time was calculated: survivorship, as the fraction of initial cohort abundance, is calculated as b(time in years) $+ a$, where b (slope) is the survivorship per year and a is the y-intercept. Regressions for cohorts C, D, E, and F were statistically significant ($P < 0.05$; Table 1) but the regression for cohort G was not ($P = 0.09$). Survivorship curves are shown in Fig. 5 for cohorts C, D, E, and F.

Sex change

The proportion of FP shrimps in the individual cohorts showed a general pattern of increase with time from recruitment, with most cohorts at 100% FP at their final

observation (Fig. 6). However, in the late summer and autumn months, this pattern reversed (cohorts A, E, F), with an increase in the proportions of MP shrimp. In the spring, however, the pattern of increasing FPs in the cohorts resumed.

Regressions of the rate of sex change in a cohort on both its mean CL and the percentage of FPs in the entire sample in the first of two successive samples (T_1) were not significant (Fig. 7A, B). The average rate of sex change was 26.8% during the late winter, 28.2% in the spring, 9.5% in the summer, and 9% in the autumn (Fig. 7C).

The size and age (time from recruitment) at which sex change occurred was highly variable among cohorts. In cohorts C–H, the mean size at which > 50% of the

cohort changed to FP varied from 6.6 ± 0.63 mm CL (cohort F) to 10.4 ± 0.3 mm CL (cohort G), with a median of 8.6 mm CL (Table 2). The age (time from recruitment) at which > 50% of the population changed to FP varied from 0.27 years (cohort F) to 1.02 years (cohort G), with a median of 0.75 years for the six cohorts (Table 2). The period from recruitment of a cohort to sex change in a majority of its individuals varied with the season of recruitment, as illustrated for cohorts E–G (Fig. 8). Cohort E recruited in November 1999, and its individuals remained mainly male phase over the winter but a majority changed to female phase by May 2000 at a mean cohort size of 7.3 mm CL. Cohort F recruited in March 2000 and a majority its individuals changed to FP by June 2000 at a mean CL of 6.6 mm. Cohort G

Fig. 6 *L. wurdemanni.*
Diagrams showing the proportions (percentages) of MP (*unfilled*) and FP (*filled*) individuals in cohorts A–H in the sampling period (June 1999 to June 2001). The percentage of each sexual morph is given above the *pie diagrams* (MPs on the left, FPs on the right). Cohort A was not identified in the March 2000 sample but was observed in the samples before and after

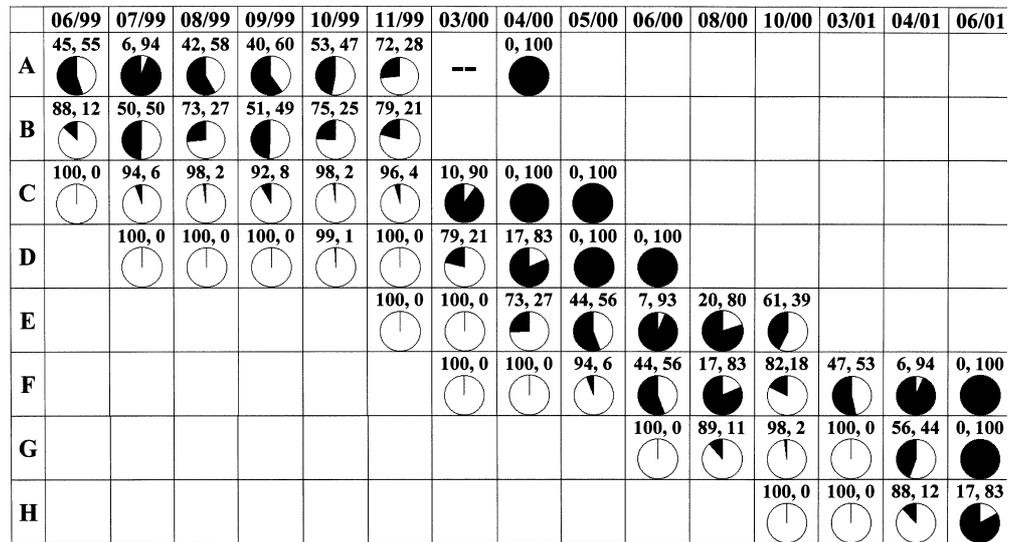|	06/99	07/99	08/99	09/99	10/99	11/99	03/00	04/00	05/00	06/00	08/00	10/00	03/01	04/01	06/01
A	45, 55	6, 94	42, 58	40, 60	53, 47	72, 28	--	0, 100							
B	88, 12	50, 50	73, 27	51, 49	75, 25	79, 21									
C	100, 0	94, 6	98, 2	92, 8	98, 2	96, 4	10, 90	0, 100	0, 100						
D		100, 0	100, 0	100, 0	99, 1	100, 0	79, 21	17, 83	0, 100	0, 100					
E							100, 0	100, 0	73, 27	44, 56	7, 93	20, 80	61, 39		
F								100, 0	100, 0	94, 6	44, 56	17, 83	82,18	47, 53	6, 94	0, 100
G											100, 0	89, 11	98, 2	100, 0	56, 44	0, 100
H													100, 0	100, 0	88, 12	17, 83

Fig. 7A–C *L. wurdemanni.*
Rates of sex change in cohorts related to mean body size, sexual composition, and season. The rate of sex change of a cohort (increase in proportion of FP individuals in successive sampling periods T_1 and T_2) is plotted against **A** the mean carapace length of the cohort at T_1 and **B** the percentage of FPs in the entire population sample at T_1. **C** Average rate of sex change of cohorts grouped by season. *Error bars* are standard deviations; *n* number of observations; *p* probability of no significant regression of the rate of sex change on the independent variable in **A** and **B**; r^2 square of the Pearson correlation coefficient

A r² = 0.04, p = 0.41, n = 21
Rate of Sex Change vs Carapace Length (mm)

B r² = 0.005, p = 0.76, n = 21
Rate of Sex Change vs Percent FPs in Sample

C Average Rate of Sex Change vs Season: winter (Feb-Mar) n = 6, spring (Mar-Jun) n = 8, summer (Jun-Sep) n = 3, autumn (Sep-Nov) n = 4
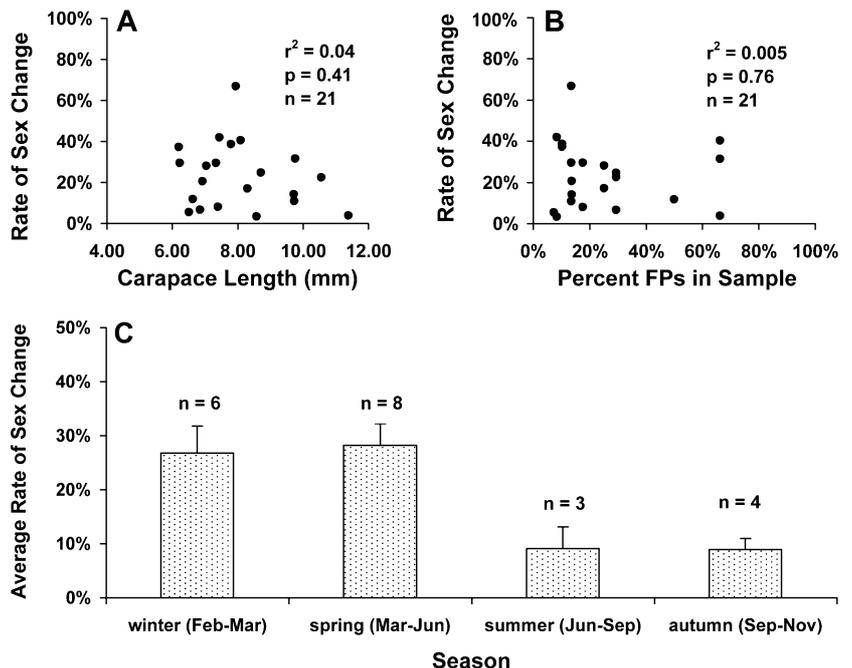
Table 2 *L. wurdemanni*. Size and age at which >50% of a cohort had changed from the male phase to the female phase. *SD* standard deviation

Cohort	Carapace length ± SD (mm)	Age (years)
C	9.7 ± 0.4	0.75
D	8.3 ± 0.5	0.75
E	7.3 ± 0.5	0.48
F	6.6 ± 0.6	0.27
G	10.4 ± 0.3	1.02
H	9.0 ± 0.7	0.76

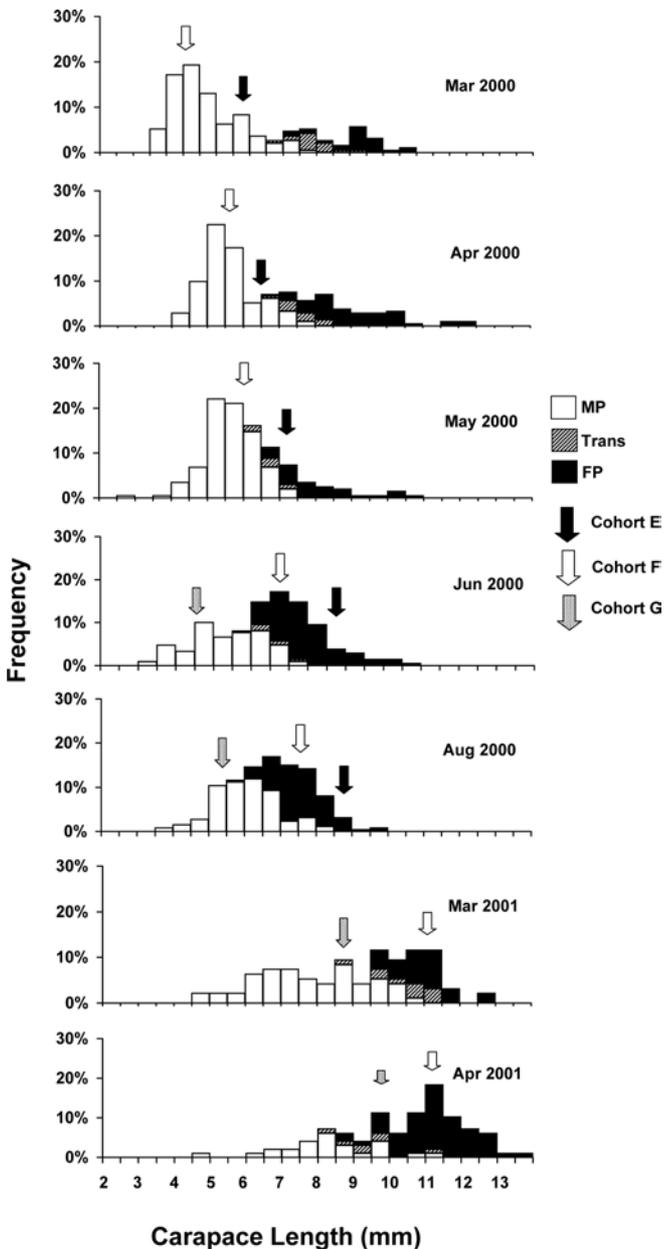**Fig. 8** *L. wurdemanni*. Comparison of the timing of sex change in cohorts E–G, recruited at different times of the year during the period March 2000 to April 2001. *Arrows* point to the mean carapace length of the cohort

recruited in June 2000, and most individuals remained in the male phase in the autumn and winter. A majority of FPs in cohort G was not observed until June 2001 at a mean CL of 10.4 mm. Cohorts C and D also were recruited in the summer and did not reach 50% FP until the following spring. This general pattern of recruitment and sex change is diagrammed in Fig. 9.

Size at sex change was estimated more directly from the size of transitional MPs, that is, individuals changing to FP at their next molt. The mean size of transitionals from field samples was 8.2 mm (Table 3). The size of and time to sex change was observed in small MPs reared in the laboratory. In the Group treatment, 16 of the original 25 individuals changed sex during the 18 weeks of observation. Of those that did not change, 4 died and 5 remained MPs. The percentage of shrimps from each group of 10, 10, and 5 that changed sex was 89%, 63%, and 75%, respectively. Nineteen of the shrimps maintained in the Individual treatment changed sex. One individual died and 5 others remained MPs. The mean size of sex change was 7.6 mm CL in the Group treatment and 7.2 mm CL in the Individual treatment (Table 3). The time to sex change was 9.8 weeks in the Group treatment and 9.4 weeks in the Individual treatment (Table 3). Extrapolated to years,
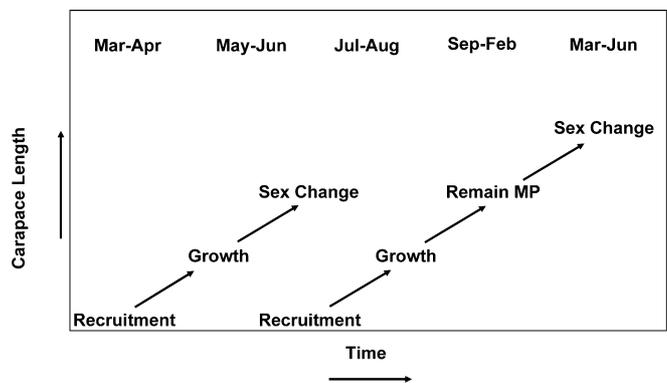

Fig. 9 *L. wurdemanni*. Two patterns of sex change based on timing of recruitment

Table 3 *L. wurdemanni*. The size at and time to sex change from male-phase individual (*MP*) to female-phase individual based on observations of transitional individuals from field samples and on MPs changing to the transitional stage in laboratory observations (Group and Individual treatments). The initial MP size and the time to sex change could not be determined for transitionals from field samples. *CL* carapace length; *n* number of individuals; *SD* standard deviation

Source of MPs	n	Initial size (mm CL)	Mean size sex change (mm CL ± SD)	Mean time sex change (weeks)
Population samples	102	–	8.2 ± 1.5	–
Group treatment	16	5.3 ± 0.6	7.6 ± 1.1	9.8 ± 4.2
Individual treatment	19	5.7 ± 0.6	7.2 ± 0.4	9.4 ± 2.4

time to sex change was 0.19 years and 0.18 years in the Group and Individual treatments, respectively.

Discussion

Estimates of growth, survivorship, and timing of sex change of individuals from male phase (MP) to female phase (FP) in a population of *Lysmata wurdemanni*, a protandric simultaneous hermaphrodite, are summarized in Fig. 10. Estimates of growth and timing of sex change obtained by cohort analysis of the population sampled for 2 years are concordant with those observed on living shrimps in laboratory culture. Growth rates of MPs reared both in groups and individually under optimal conditions for growth and sex change (Lin and Zhang 2001; Bauer 2002b) were 10 mm CL year^{-1} versus 4–7 mm CL year^{-1} in cohorts from field samples in the present study. In the laboratory, MPs somewhat larger than minimum recruitment size changed to FP at a size and age similar to that of the field cohort in which sex change was most rapid. Thus, although sample sizes were sometimes low and the cohort analysis used (MIX; Macdonald and Pitcher 1979) involves some subjectivity, as in even more complex cohort analysis programs, we feel that our estimates of basic population parameters are at least good approximations.

Growth to and timing of sex change in *L. wurdemanni* were linked to the season at which recruitment occurred rather than to size of individuals in a cohort. The highest rates of sex change to FP were found in cohorts in the late winter through spring, in time for the major breeding season (Bauer 2002b) of spring and summer. Individuals from cohorts recruited in late winter through mid-spring grew quickly, with sex change occurring earlier at a smaller size than in those from cohorts recruited in the summer or early autumn. A majority of individuals

recruited in summer and autumn remained MPs until the late winter or spring of the following year, changing sex at a larger size. At one extreme, a majority of individuals in cohort F, recruited in the late winter, changed to FP 3 months later in the late spring at a mean CL of 6.6 mm. At the other extreme, in Cohort G recruited in mid-June, a majority of FPs in the cohort was not attained until 1 year later. Overwintering individuals changing sex at a larger size produce larger broods as FPs, since brood size increases with body size in female-phase and female carideans (Bauer 1991), including FPs of *L. wurdemanni* (personal observation). Overwintering MPs recruited in the previous summer and autumn are exposed to a longer time to predation before changing from MP to FP. However, survivorship curves of cohorts from this study most resemble "type I" curves (Deevey 1947), in which survivorship is relatively high until older age (larger size). An overwintering MP has a good chance of changing to FP and successfully producing a few larger broods before death. Life-span of cohorts varied from 11 months to at least 16 months, with maximum individual life-span estimated at 19 months. These values are similar to those estimated by more subjective methods for gonochoristic warm-temperate species from shallow-water habitats (e.g., Kikuchi 1962; Bauer 1976; Alon and Stancyk 1982).

Although MPs are capable of changing to the female-phase simultaneous hermaphrodite at a relatively small size, there is considerable variability in the size (age) of sex change in *L. wurdemanni*. In this study, the smallest MP observed was 2.5 mm CL and the largest was 11.5 mm CL. Transitional individuals, MPs in which change to FP will occur at the next molt, ranged from 5.0 to 11.5 mm CL, while FPs varied in size from a minimum of 5.5 mm CL to 14.2 mm CL. A majority of sex-changing (transitional) individuals were between 6.5 and 8.5 mm CL. Thus, most MPs change to FPs at a larger size than the minimum possible with a consider-

Fig. 10 *L. wurdemanni*. Size/age life-history summary of the population sampled at Port Aransas, Texas, based on the growth key, survivorship, and sex-change data
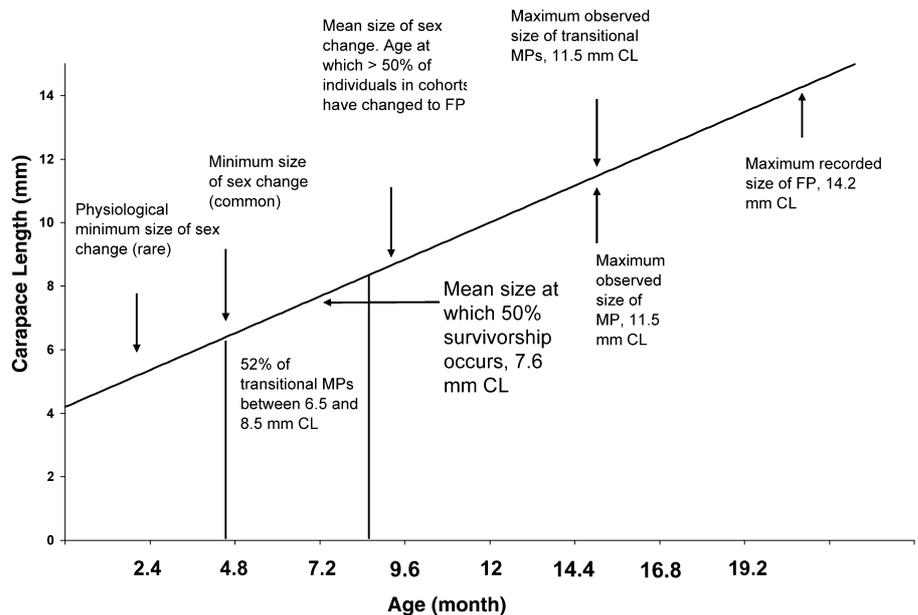
able amount of variation. There are no primary males, that is, all MPs larger than 5.0 mm CL have ovotestes and are physiologically capable of changing to FPs. Even the largest transitional MPs may change to FPs if they do not suffer mortality before their next molt. There are no primary females, as in some sex-changing species (Bauer 2000), that is, all individuals go through a male phase, although it may be brief. In the study of Bauer and Holt (1998), all FPs examined, from the smallest to the largest, had ovotestes and male ejaculatory ducts.

Given the reproductive advantages of simultaneous hermaphroditism, it is difficult to envision why many MPs, capable of only mating as a male, do not change as soon as morphologically possible to an FP, which can mate successfully both as male and female (Bauer and Holt 1998). Change of an MP to FP at a larger size might be explained by some selective advantage for MPs, such as large MP male mating advantage. Charnov et al. (1978) and Charnov (1981, 1982) suggested that variation in the size (age) of sex change in protandric pandalid species varies with the sexual composition of the population. When FPs are abundant in a population, small MPs might delay sex change because reproductive success as an MP could be higher than that as an FP in this demographic situation. An individual may father (inseminate) several broods as an MP but can only produce one brood as an FP per breeding season in the boreal protandric pandalids. When FPs are not abundant, it may be adaptive for an MP to change to FP as quickly as possible, since insemination of an FP spawn is assured but mating opportunities as an MP would be rare and competition for those opportunities would be high. In this study on *L. wurdemanni*, the rate of sex change from MP to FP in cohorts was not related to the proportion of FPs in the population, so that demographically influenced environmental sex determination, as proposed by Charnov et al. (1978) and Charnov (1981, 1982) for pandalids is not supported. Furthermore, no adaptive advantage promoting the evolution of larger MP size, such as male mating advantage, has been demonstrated (Bauer 2002a). No experimental evidence to date supports the hypotheses of Charnov et al. (1978), Charnov (1981, 1982), and Charnov and Anderson (1989) about variation in size (age) of sex change in protandric pandalids (Marliave et al. 1993; Bergström 1997).

The evidence from our study and from Bauer (2002a) suggests that delayed change from MP to FP in *L. wurdemanni* is a consequence of the timing of recruitment and growth (Fig. 9). MPs recruited early in the breeding season grow rapidly and quickly change to FPs at a relatively small FP size by the late spring and early summer. However, most MPs recruited in the summer do not change to FPs until the late winter or the following spring. In gonochoristic carideans, juvenile females reaching reproductive size late in or outside of the breeding season do not attain the reproductive "breeding dress" (Höglund 1943) until the following year (next breeding season). Similarly, most MPs of *L. wurdemanni* that become large enough to change sex by the autumn and winter do not change to FPs because both the proximate factors stimulating this change to female breeding capability and the ultimate factors favoring embryo production and larval survival are suboptimal (Bauer 2002a, 2002b). As in females of gonochoristic carideans, development and maintenance of the breeding dress during the nonbreeding season would be inadaptive. These summer-recruited MPs grow to large size as sex change is delayed until late winter and spring, with production of broods and release of larvae into the plankton during the spring and early summer when conditions for larval survival are presumably high. Two proximate factors influencing female breeding, water temperature and photoperiod, may account for the seasonal variation in sex change of *L. wurdemanni*. Bauer (2002a) showed that sex change in laboratory populations of MPs was significantly higher with increasing or high water temperatures and long-day photoperiod, simulating late-winter, spring, and early summer conditions, than with decreasing temperatures and short-day photoperiod, simulating autumn and early-winter conditions. Other seasonally varying factors may be involved. In the protandric hermaphrodite *Hippolyte inermis*, Zupo (2000, 2001) found that seasonal variations in diet determined whether a newly recruited individual matured first as a male, later changing to female, or as a primary female without a male phase. On the other hand, preliminary experiments by Lin and Zhang (2001) suggest, unlike those of Marliave et al. (1993) with *Pandalus danae*, that the probability that a young MP will change to FP is influenced by the sexual composition of the surrounding population (demographically influenced ESD). We propose that more extensive and varied experiments are required to test this latter hypothesis.

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