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REPRODUCTIVE ECOLOGY OF A PROTANDRIC SIMULTANEOUS HERMAPHRODITE, THE SHRIMP *LYSMATA WURDEMANNI* (DECAPODA: CARIDEA: HIPPOLYTIDAE)

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ABSTRACT

The temporal pattern of population abundance, breeding, and recruitment of the marine shrimp *Lysmata wurdemanni* is described and analyzed. A population inhabiting the rock jetty in Port Aransas, Texas, U.S.A., was sampled monthly for one year and then bimonthly in a second. Abundances were greatest in the summer, declining during the fall to zero values in early winter, with increases in the late winter and early spring. The disappearance of the population in early winter is attributed to its movement beneath the jetty or to some other location inaccessible to sampling. When the population reappeared in late winter to early spring, it contained a high proportion of larger (older) individuals. The breeding season was seasonal but extended. Most female-phase individuals (FPs) incubated broods of embryos continuously during the warmer months (spring through early fall). Spawning of a new brood occurred soon after hatching of the previous one, as shown by the significant positive correlation between the degree of embryonic development (nearness to hatching) in an FP and the degree of ovarian maturation (nearness to spawning) in its ovotestes. Male-phase individuals (MPs) changing to FPs were found throughout most of the year. Their relative abundance was greatest in late winter to early spring when a group of large MPs, far past minimum FP size, finally changed sex. Recruitment occurred primarily in the spring and summer in both years, although its timing and intensity varied between years. The observed pattern of breeding, recruitment, and population abundances of *Lysmata wurdemanni* is what might be expected of a primarily tropical species living in an area transitional between the tropical Caribbean and warm temperate Gulf of Mexico biogeographical provinces. The breeding pattern of this shrimp, with an unusual hermaphroditic sexual system, is not strikingly unusual or different from that of gonochoristic shallow-water carideans.

Although most caridean shrimp species have separate sexes (gonochory), there are numerous species with protandric hermaphroditism, in which individuals develop first as males and then later change to females (Bauer, 2000). The hippolytid shrimp *Lysmata seticaudata* (Risso, 1816) was considered protandric (Spitschakoff, 1912; Dohrn, 1950; Charniaux-Cotton and Payen, 1985) in spite of the unique presence of testes, male ducts, and sperm in the gonads (ovotestes) of female-phase individuals (FPs) (Berreur-Bonnenfant and Charniaux-Cotton, 1965; Charniaux-Cotton, 1975). Bauer and Holt (1998) described retention of male ducts by FPs in the Western Atlantic *Lysmata wurdemanni* (Gibbes, 1850). Mating experiments demonstrated that FPs function as male and female, but they cannot fertilize themselves (outcrossing simultaneous hermaphrodites). Bauer (2000) termed this novel sexual system "protandric simultaneous hermaphroditism" (PSH). Morphological evidence in other *Lysmata* species (Bauer, 2000) and breeding observations in *L. amboinensis* (De Man, 1888) by Fiedler (1998) indicate that the PSH is widespread in the genus.

Theoretical models have been developed to explain various aspects of protandry in pandalid shrimps (Charnov, 1979, 1981, 1982; Charnov *et al.*, 1978; Charnov and Anderson, 1989). The environmental (social) control of sex determination suggested by these models has not been supported by empirical studies (Marliave *et al.*, 1993). Bergström (1997) proposed the alternative hypothesis that variations in sex change are gentotypically fixed and subject to frequency-dependent selection. Allen (1959) reviewed variation in protandry of *Pandalus borealis* Krøyer related to temperature and latitude. In *Lysmata wurdemanni*, the size (age) at which male-phase individuals (MPs) change to the FP simultaneous hermaphrodite is variable (Bauer and Holt, 1998; Bauer, 2000). To understand whether sex change is environmentally labile or under strict genetic control, as well as to understand the evolution of the PSH in *L. wurdemanni* and other *Lysmata* species, models incorporating empirical data on population structure, growth, mortality, differential reproductive success among sexual morphs, and breeding need to be developed. This paper addresses the basic reproductive biology of *L. wurdemanni*. The purpose of the study was to describe and analyze seasonality of breeding, recruitment, and abundance in a population from the northwestern Gulf of Mexico.

MATERIALS AND METHODS

The population of *Lysmata wurdemanni* at Mustang Island, Port Aransas, Texas, U.S.A. (27°50′N, 97°03′W) was sampled monthly from June 1999 through June 2000 and then bimonthly (as low night tides and weather permitted) from August 2000 through June 2001. Collections were taken along the rock jetty on the north end of Mustang Island (south side of inlet known as Aransas Pass). It was possible to collect these shrimps only at night, when they are active, and at negative tides, when their tidepool and rock ledge habitat is accessible. Shrimps were taken with 1-mm mesh dipnets, either directly when seen under the light of headlamps or indirectly by scraping deep under rock ledges. Shrimps were preserved in 10% Formalin after collection, later washed with running water, and stored in 70% ethanol. The collecting effort (total number of person-hours spent in collection), temperature, and salinity were recorded at each sampling.

Body size was measured as carapace length (CL), the distance from the posterior edge of the eye orbit to the mid-dorsal posterior edge of the carapace. Sexual phase was identified by examining the endopods of the first two pleopods (Bauer and Holt, 1998). Male-phase individuals (MPs) have cincinnuli (coupling hooks) on pleopod 1, whereas female-phase individuals (FPs) lack them completely. The appendix masculina of pleopod 2 is well developed in MPs but highly reduced or absent in FPs. Transitional-phase individuals have MP characters externally, but there is visible development (filling with vitellogenic oocytes) of the ovarian portions of the gonads (ovotestes). Transitionals change to the female phase at their next molt (Bauer and Holt, 1998).

In many caridean species, a female spawns soon after the hatching of incubated embryos produced in a previous spawning (successive spawning or continuous breeding; Bauer, 1986, 1989; Bauer and Abdalla, 2001). Spawning pattern can be inferred in preserved material by observations on the ovarian condition of females incubating embryos at different developmental stages (Bauer and VanHoy, 1996). To determine the spawning pattern of incubating FPs of *Lysmata wurdemanni* taken in monthly samples, ovarian condition of the ovotestes was staged as in Bauer (1986) for ovaries, from stage 1 (no vitellogenic oocytes visible) to stage 4 (complete filling of the space available for vitellogenic oocytes). Development of embryos incubated by FPs was scored from stage 1 (newly spawned) to stage 4 (close to hatching) (Bauer, 1986).

Abundances were estimated by dividing the sample abundance (number of shrimps) by the collecting effort. Individuals just entering the population (recruits) were defined as individuals smaller than 4.5 mm CL.

RESULTS

Population Abundances

Population numbers were high during the summer months, declined through the fall to lows in early winter, and increased again in the spring (Fig. 1A). Abundances were positively correlated with water temperature (Fig. 2A) [Spearman rank correlation coefficient $r_s = 0.52$, P ($r_s = 0$) < 0.025] but not with salinity (Fig. 2B; $r_s = 0.19$, $P > 0.10$). No shrimps were collected in the December and January samples of Year 1 (June 1999 to May 2000), and only a single individual was collected in the early winter (December) sample of Year 2 (June 2000 through June 2001). The population increase in the late winter and early spring always included individuals of large size (Fig. 3, February–April 2000; Fig. 4, March–April 2001).

Breeding Pattern of the Population

The abundance of FPs carrying embryos followed a similar pattern as that of population abundances, with highs in the summer months declining in the fall to zero values in the winter, and with increasing abundances in the spring (Fig. 1B). In the first year of sampling, the percentage of FPs with embryos was highest in the spring and summer months, with a decline during the fall (Fig. 5). In the second year, the summer highs in FPs with broods persisted through the October 2000 sample, with a low value in the late winter (March 5, 2001) increasing to spring and summer highs in the April and June 2001 samples. The percentage of FPs with embryos was positively correlated with water temperature ($r_s = 0.46$, $P < 0.05$).

The percentage of MPs changing to FPs (transitionals) showed its highest values from late winter to mid-spring in both years (Fig. 6). Samples taken in winter and early spring contained very large MPs changing to FP (Figs. 3, 4). Intermediate to low values for transitionals were found in May–July samples, with values declining to zero in October and November 1999 but with a high value in October 2000. The percentage of transitionals was negatively correlated with water temperature ($r_s = -0.531$, $P < 0.025$).

Spawning Pattern of Individual FPs

Female-phase individuals incubating broods near hatching (embryo stages 3 and 4) nearly all had ovotestes filling with or full of vitello-

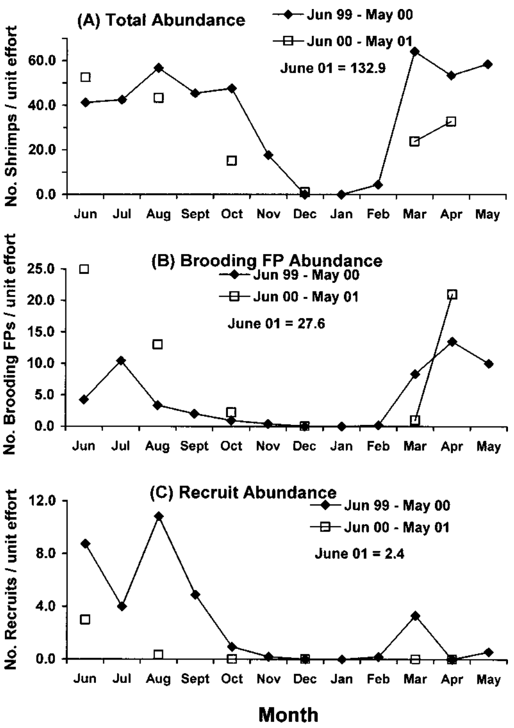

Fig. 1. Abundance estimates (number of individuals in sample/collecting effort) of (A) all individuals, (B) female-phase individuals (FPs) carrying broods of embryos, and (C) newly recruited individuals of the *Lysmata wurdemanni* population from Port Aransas, Texas. The absence of a data point for a given month indicates that no sampling was conducted. The data for the June 2001 sample is given in the figure legend.

genic oocytes (ovarian stages 2–4) (Fig. 7), indicating another spawning at the next molt. Those FPs with recently-spawned (stage 1) embryos had no ovarian development, whereas some FPs with stage 2 embryos showed some filling of the ovarian part of the ovotestes with vitellogenic oocytes (Fig. 7). The ovarian stage of FPs was positively and significantly correlated with the developmental stage of embryos in the their brood (r_s = 0.675; 0.005 < P < 0.01).

Recruitment

Recruitment was high in the summer of 1999, declining during the fall to zero values in the winter (Fig. 1C; Figs. 3, 4). In 2000, low recruitment occurred in February, March, not in April, and then again in May and June. In the bimonthly samples taken thereafter, there were a small number of recruits in August 2000 and then there was no recruitment through the late winter (March 5, 2001) and spring (April 28, 2001) samples until the last sample, June 21, 2001. The presence of small MPs in the June 2001 sample, but not in the previous one, indicates an episode of recruitment with growth between samples (Fig. 4). Recruitment values were highly correlated with temperature (r_s = 0.80, $P < 0.001$) but not with salinity (r_s = 0.20, $P > 0.10$).

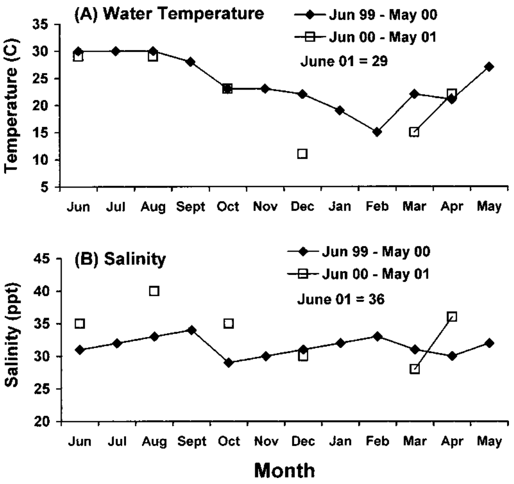

Fig. 2. Water temperature (A) and salinity (B) measurements taken during sampling of the *Lysmata wurdemanni* population from Port Aransas, Texas. The absence of a data point for a given month indicates that no sampling was conducted. The data for the June 2001 sample is given in the figure legend.

DISCUSSION

Breeding and recruitment of *Lysmata wurdemanni* generally followed the seasonality typical of shallow-water shrimps from the Gulf of Mexico (Linder and Anderson, 1956; Wood, 1967; Bauer, 1992; Bauer and Lin, 1994; Bauer and Van Hoy, 1996; Bauer and Abdalla, 2001). Breeding effort is highest in the spring and summer, with late spring and summer recruitment. However, a well-defined seasonal pattern was obscured by low abundances from late fall to early spring. These declines in abundance are apparently not due to a simple winter reduction from mortality and a lack of recruitment. Many individuals reappearing in the late winter and early spring were quite large (10–14 mm CL), older individuals. Very large (>8.5 mm CL) MPs and transitionals, well past the size at which most MPs change to FP (approximately 6–7 mm carapace length; Bauer and Holt, 1998), were collected at this time.

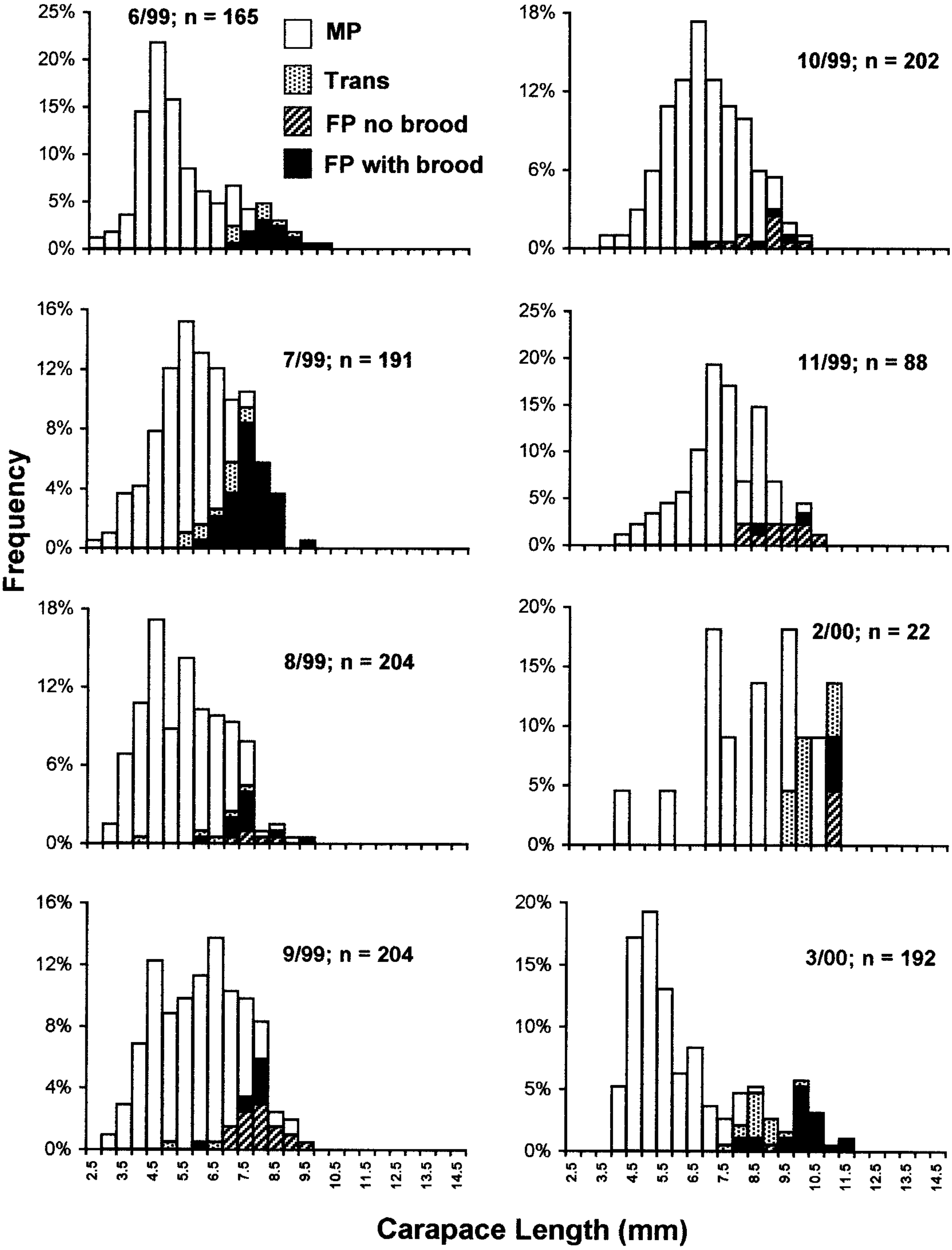

Fig. 3. Size-frequency diagrams constructed from monthly samples of *Lysmata wurdemanni*, June 1999 to March 2000. MP, male phase; FP, female phase; Trans, transitional MP.

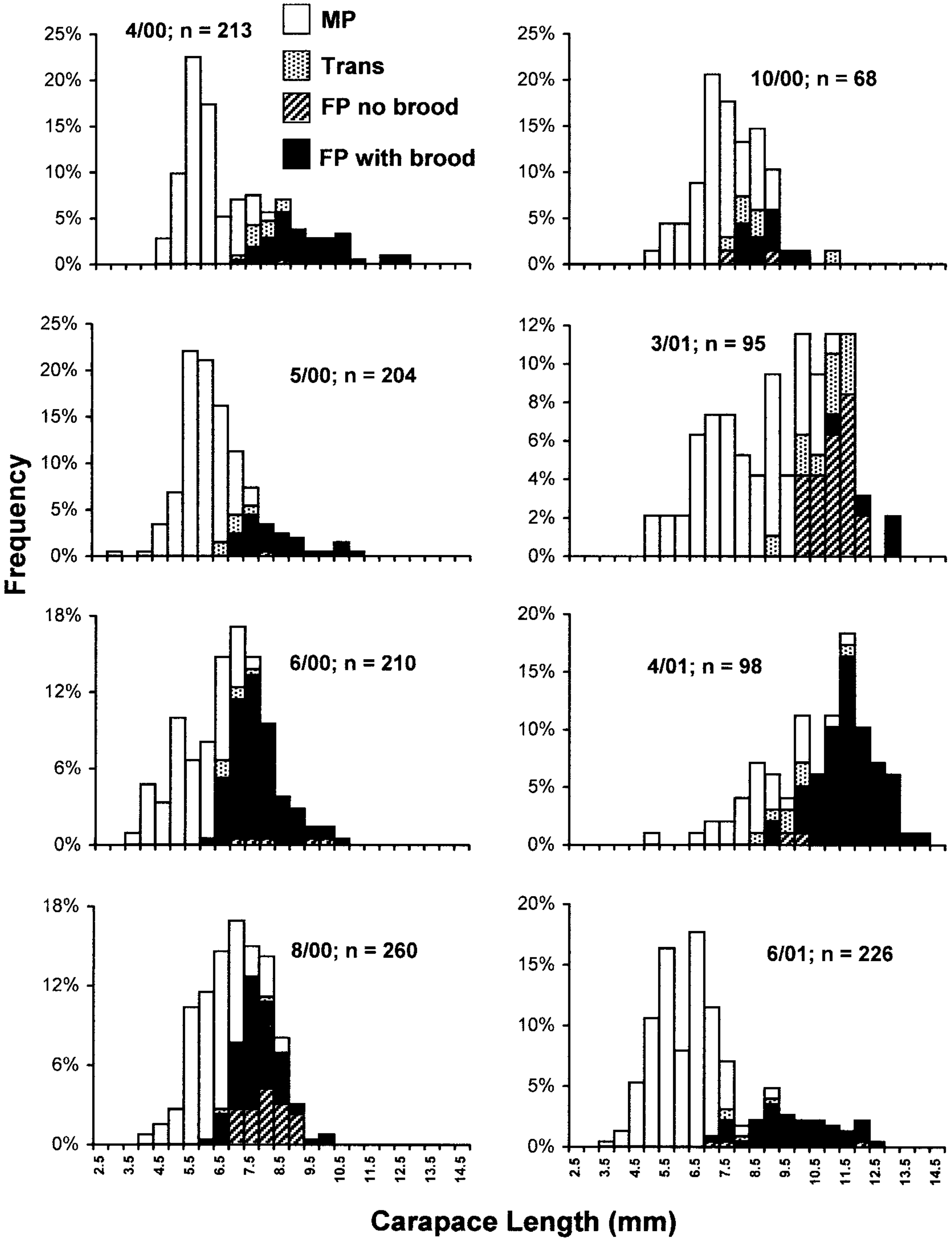

Fig. 4. Size-frequency diagrams constructed from monthly samples of *Lysmata wurdemanni*, April 2000 to June 2001. MP, male phase; FP, female phase; Trans, transitional MP.

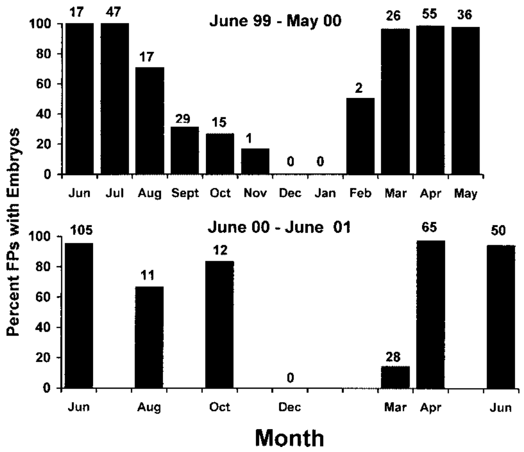

Fig. 5. Percentage of female-phase individuals (FPs) incubating embryos in population samples from June 1999 to June 2001. Months in which sampling occurred are listed on the abscissa. The total number of FPs is given above the histogram bar for each monthly sample.

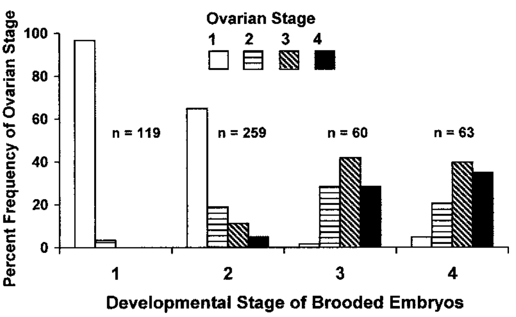

Fig. 7. The relationship between the ovarian condition of a female-phase individual and the developmental stage of embryos that it is brooding. In stage 1 ovarian condition, no vitellogenic oocytes are observed; in stage 4 (near spawning), the ovarian portion of the gonad is filled with vitellogenic oocytes. For embryonic development, stage 1 is recently spawned and stage 4 is near hatching. *n*, number of FPs with embryos in developmental stage 1, 2, 3, or 4.

It is not known where the population goes during the winter months. Seasonal migrations of shrimps and other decapods are well known (Allen, 1972). However, individuals of *Lysmata wurdemanni* are very thigmotactic, perching on and clinging to rocky boulders and ledges. In the northwestern Gulf of Mexico, nearshore hard substrates are man-made structures, such as rock jetties (Britton and Morton, 1989) and oil platform supports. These small shrimps would have to migrate, exposed to predation, over vast expanses of sand bottom to move to some other hard substrate. Lardies *et al.* (1998) reported that ovigerous females of the alpheid *Betaeus emarginatus* (H. Milne Edwards, 1837) migrated from rock tidepools during the summer, probably to nearby subtidal kelpbeds to release larvae. Some nonovigerous females, at least, remained behind. In contrast, all sexual morphs and individuals of *L. wurdemanni* disappeared at a time unfavorable to reproduction. I hypothesize that the winter population of *L. wurdemanni* simply moves farther beneath the rock jetty at Port Aransas, which is about 50 m wide at its base (Britton and Morton, 1989). Because sampling is restricted to the outer edges of the jetty, the shrimps would not be accessible. Why the shrimps would move farther under the jetty during the winter, if they do, is unknown. Although abundances and water temperature were correlated, the water temperatures

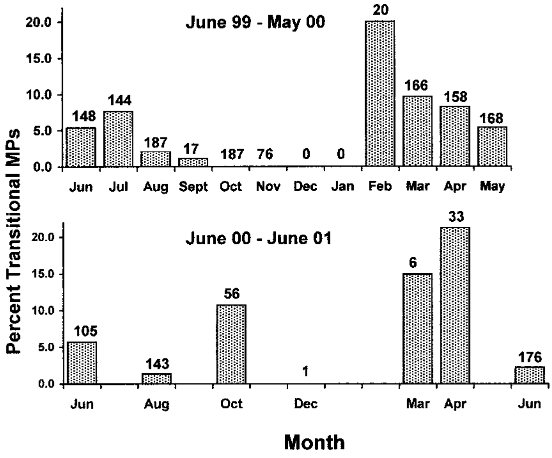

Fig. 6. Percentage of male-phase individuals (MPs) transitional between MP and FP. Months in which sampling occurred are listed on the abscissa. The total number of MPs is given above the histogram bar for each monthly sample.

in two of three months with zero abundance (December 1999, 22°C; January 2000, 19°C) were warmer than two months (February 2000, 15°C; March 2001, 15°C) in which shrimps were taken in collecting. Abundances showed no correlation with salinity, which varied within a relatively narrow range. The population may be moving under the jetty in winter in response to seasonality in other physical factors or biological ones such as food supply or predators.

The breeding season extended through much of the year, with highest numbers of incubating FPs and highest percentages of the FP population with embryos in spring and summer. The proportion of FPs with embryos declined in the fall and winter. This pattern is typical of carideans in shallow-water habitats in the Gulf of Mexico (Wood, 1967; Bauer and Van Hoy, 1996; Bauer and Abdalla, 2001).

Once breeding began in individual FPs, broods were produced continuously. The ovarian portion of the ovotestes filled with vitellogenic oocytes as the embryos from a previous spawn developed. Laboratory observations on mating in *L. wurdemanni* (see Bauer and Holt, 1998) showed that FPs hatch embryos from a previous spawning, molt and mate within one or two days, and then spawn within hours of mating. Production of a new brood within a few days after hatching of a previous one is common in many (Bauer, 1989, 1992; Bauer and Van Hoy, 1996), although not all (Bauer and Abdalla, 2001), shallow-water carideans from warm temperate and tropical habitats.

Another indicator of potential breeding activity in this hermaphroditic species is the relative abundance of transitional individuals changing from MP to FP. Transitionals have male characters externally, but the gonad fills with vitellogenic oocytes, and spawning takes place in the next molt, at which female secondary sexual characteristics appear. Although transitionals were collected in the summer months, the greatest percentage of MPs changing to FPs occurred in late winter and spring. At this time, overwintering large MPs finally changed to FP, along with smaller MPs just reaching the minimum size of change. Large MPs must change at this time to breed as FPs in the short life span still available to them.

Recruitment primarily occurred during the summer months during both years, although at a much higher level in the first year of sampling. The 1-mm mesh of nets used in collecting was small enough to sample the smallest possible recruits. Zhang *et al.* (1998) reared larvae of *Lysmata wurdemanni* and reported that newly metamorphosed postlarvae were 7 mm total length, corresponding to 1.7 mm carapace length (CL), nearly the size of the smallest individuals (2.5 mm CL) collected in this study.

Lysmata wurdemanni is a tropical Western Atlantic species that extends into warm temperate areas in both hemispheres (Williams, 1984). The population studied is near the northern edge of the species range in the Gulf of Mexico. This species is rarely or sporadically found in the north-central Gulf of Mexico on suitable rocky substrates (personal observation), probably because of low nearshore salinities, seasonally much lower than those of Port Aransas (this study) and other Texas rock jetties (Brinton and Morton, 1989). The seasonality in breeding, recruitment, and population abundances of *L. wurdemanni* appears more variable than that of warm temperate carideans from the Gulf of Mexico, such as *Palaemonetes pugio* Holthuis, 1949 (Wood, 1967). Many shallow-water carideans in the tropical Western Atlantic breed throughout the year, with individual females continuously producing broods during a relatively short life span (<1 year) (Bauer, 1989). Like tropical species, breeding is continuous in *L. wurdemanni* during the several months of warm water temperature in the western Gulf of Mexico. However, breeding effort and production of larvae by the population decreases or ceases during the winter.

Multiple population sources for larvae may account for the observed variability in recruitment. The Port Aransas population occurs in a biogeographical region transitional between tropical (Caribbean) and warm temperate Gulf faunas. Currents carrying larvae are principally from the south (tropical) in the summer but from the north in the winter (Felder and Chaney, 1979), and the intensity of these currents may vary from year to year. Some recruitment may come from tropical populations in the Caribbean where caridean recruitment is episodic in spite of continuous, year-round breeding (Bauer, 1989). Some recruits may come from the Port Aransas population itself and from scattered populations to the north.

In summary, the breeding and recruitment of *Lysmata wurdemanni* is what might be expected of a tropical species on the edge of its distributional range, where environmental factors acting on reproduction and recruitment are quite different from those in the central part of the range. There is little about the breeding and recruitment of *L. wurdemanni*, a protandric simultaneous hermaphrodite, that distinguishes its reproductive ecology from that of gonochoristic species in a similar geographic situation.

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