

PROTANDRIC SIMULTANEOUS HERMAPHRODITISM IN THE MARINE SHRIMP *LYSMATA CALIFORNICA* (CARIDEA: HIPPOLYTIDAE)

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A B S T R A C T

To investigate the extent of protandric simultaneous hermaphroditism (PSH) in the genus *Lysmata*, observations were made on the sexual system of *L. californica*, a species from the warm-temperate eastern Pacific. Observations on a large number of female-phase individuals (FPs) from a museum collection indicated that FPs with broods containing advanced embryos spawn again (successively) soon after brood hatching. Female-phase individuals maintained in pairs went through successive cycles of embryo brooding concomitant with gonadal vitellogenesis, hatching, molting, and spawning. Time-lapse video observations confirmed that FPs are able to copulate as males and inseminate postmolt, respawning FPs. Prespawning FPs maintained alone did not produce successful broods of embryos. Thus, FPs of *L. californica* are outcrossing simultaneous hermaphrodites. Size-frequency distributions of sexual phases showed that individuals develop first in the male phase (MP) and then change to the female phase. Individuals apparently change from MP to FP in a single molt, as shown by (a) “transitional” individuals that were fully MP externally but whose ovotestes were full of vitellogenic oocytes and (b) a distinct change in the presence/absence and growth of pleopod characters from MP to FP. Female-phase individuals retain male gonopores from the MP phase, and relative growth of male ejaculatory ducts is similar in MPs and FPs. Pleopod flanges related to embryo attachment and incubation are somewhat masculinized in FPs of *L. californica*. The sexual system of *L. californica* is similar to that of *L. wurdemanni* from the Gulf of Mexico and *L. amboinensis* from the Indo-West Pacific. Protandric simultaneous hermaphroditism is probably widespread if not ubiquitous in the genus *Lysmata*.

Sexual systems may vary greatly within genera of caridean shrimps (Bauer, 2000). In the genus *Pandalus*, for example, all individuals of some species are protandric hermaphrodites whereas in other species, a mix of protandric individuals and primary females may occur (Bergström, 2000). In the hippolytid *Thor manningi* Chace, 1972, 50% of individuals are primary males, while the other 50% are protandric, developing first as males and then changing to females (Bauer, 1986). However, *Thor dobkini* Chace, 1972, and *Thor floridanus* Kingsley, 1878, are gonochoristic, with no evidence of sex change (Bauer and VanHoy, 1996). Female-phase individuals (FPs) of the “protandric” genus *Lysmata* retain the testicular portions of the gonads and male ducts from the male phase after changing to the terminal female phase (*L. seticaudata* (Risso, 1816) from European waters, Spitschakoff, 1912; Berreur-Bonnenfant and Charniaux-Cotton, 1965; *L. grabhami* (Gordon, 1935) from Madeira and the Canary Islands, Wirtz, 1997; *L. wurdemanni* (Gibbes,

1850) from the western Gulf of Mexico, Bauer and Holt, 1998; *L. amboinensis* (De Man, 1888) from Hawaii, Fiedler, 1998). Mating experiments with *L. wurdemanni* (see Bauer and Holt, 1998) and *L. amboinensis* (see Fiedler, 1998) demonstrated that FPs copulate successfully as males but do not fertilize themselves. Thus, FPs of these species are outcrossing, functional simultaneous hermaphrodites. Bauer (2000) proposed that this sexual system (“protandric simultaneous hermaphroditism,” or PSH) may be widespread if not ubiquitous in species of *Lysmata*.

Lysmata californica (Stimpson, 1866) occurs in caves and under ledges of rocky reefs from the low intertidal to the shallow subtidal from southern California (Point Conception) to the Galapagos (Jensen, 1995). They occur in aggregations, often in association with the moray eel *Gymnothorax mordax* (Ayres, 1859) and are facultative cleaners of fish and other organisms such as the spiny lobster *Panulirus interruptus* Randall, 1839 (Limbaugh *et al.*,

1961). Bauer (2000) illustrated gonads of "male" and "female" *L. californica*, showing them to be ovotestes. It was proposed that *Lysmata* species with such gonads are, as in *L. wurdemanni* and *L. amboinensis*, functional simultaneous hermaphrodites in the female phase. In this study, we tested the hypothesis of PSH in *L. californica* with observations on mating and breeding, reproductive morphology, and size-frequency distribution of population samples.

MATERIALS AND METHODS

Live shrimps were obtained with fine-mesh (1 mm) aquarium nets from the pier flume at the Scripps Institution of Oceanography (SIO), La Jolla, during June 4–8, 2001. The covered flume periodically conducts seawater from an intake at the end of the pier into the SIO seawater system, and the shrimps are found in pools on the floor of the flume when the flow is nil. At SIO, shrimps were maintained at a water temperature of 20–22°C and a salinity of 34 ppt on a laboratory water table with a continuous flow from the seawater system. Some specimens taken on the pier flume were transported in oxygenated collecting bags to the University of Louisiana at Lafayette (ULL), where they were maintained in recirculating aquaria in seawater with temperature at 24°C and salinity at 35 ppt. In both laboratories, shrimps were fed fish food (shrimp pellets) daily.

Observations on breeding were taken from June 7 to September 21, 2001, on three pairs of female-phase (FP) individuals maintained in 35-cm long × 25-cm wide × 15-cm deep over-flow tanks on an SIO laboratory water table. Daily observations were taken on the presence or absence of (a) incubated embryos held beneath the abdomen; (b) a mass of vitellogenic oocytes in the gonad (visible through the cephalothoracic exoskeleton in dorsal view); and (c) exuviae from molting. At the SIO laboratory, one FP was specifically maintained in isolation and observed through three molting cycles for possible spawning and successful brood production.

Observations on copulation were recorded at the ULL laboratory for two pairs of FPs with time-lapse video as in Bauer and Holt (1998). For each observation, two FPs with brooded embryos, one near spawning (gonad full of vitellogenic oocytes) and the other not, were placed and maintained in a partitioned space 25 cm long × 24 cm wide × 15 cm deep within a 38-L aquarium. Videos were made using a time-lapse video recorder and an infrared-sensitive surveillance video camera equipped with an 8- or 12.5-mm lens. Day and night illumination was provided with overhead fluorescent lights and infrared lamps (880 nm), respectively. Activities were recorded from the placement of a FP pair into the aquarium until after molting (2 days (d), 3 d) and spawning of the prespawning FP occurred.

To test the hypothesis that FPs can fertilize themselves, 10 FPs incubating embryos and near a spawning were maintained individually in 38-L aquaria at the ULL laboratory. Observations were made on the occurrence of embryo hatching, the prespawning molt (2–8 d; median = 4 d from placement into observation chamber, $n = 10$), and, for the next 1–6 days (median = 2.5 d, $n = 10$), the presence or absence of (a) attached eggs or incubated embryos and (b) a mass of vitellogenic oocytes in the gonads.

Preserved specimens for observations on reproductive morphology and size-frequency distributions were obtained from different sources: (1) a mixed sample containing individuals taken from the pier flume June 4–8, 2001, including those used for mating observations and preserved up to one year later, plus three MPs collected from the flume in January, 1999 (SIO flume 1); (2) a sample collected from the SIO pier flume on July 23, 2002 (SIO flume 2); (3) a sample from the SIO Benthic Invertebrate Collections (SIO-BIC), taken from tidepools north of SIO in La Jolla, February 2, 1916, by P. S. Barnart (BIC catalog # 2570); and (4) a sample from the Natural History Museum of Los Angeles County (NHMLAC), taken at the Southern California Edison Plant, Huntington Beach, California, on August 8, 1970, by C. Swift, R. Lavenberg, and J. Fitch (NHMLAC catalog # AHF 1970-16).

The sexual phase of specimens was operationally defined and determined as in Bauer and Holt (1998) by the presence (male phase) or absence (female phase) of cincinnuli (coupling hooks) on the endopods of the first pleopods. In specimens from all samples, carapace length (CL) was measured as the distance from posterior edge of the eye orbit to the middorsal posterior border of the carapace. The presence or absence of incubated embryos, cincinnuli on the endopods of the first pleopods, appendices masculinae on the endopods of the second pleopods, and gonopores on the coxae of the fifth pereopods was recorded. To describe the ontogeny of sexual characters, morphometric observations were made on all FPs collected in SIO flume samples 1 and 2 ($n = 25$), 22 MPs preserved from flume sample 1, and 3 MPs selected at random from flume sample 2 to have an equal sample size (25) of FPs and MPs. All FPs used in the morphometric analysis had reproduced as females: they either had a brood of embryos held beneath the abdomen or had been observed with a brood at some time before their preservation. Morphometric observations reported are the number of cincinnuli on the endopod of pleopod 1, the length of the appendix masculina on pleopod 2, the number of appendix masculina spines, the width of the ejaculatory duct, and the width of the basipod flange of the second pleopod (Bauer and Holt, 1998). The former three observations were made at 100× with a compound microscope and the latter two at 50× with a stereomicroscope. Pearson correlation coefficients (r) of these measures with carapace length were calculated along with the probability of no correlation ($r = 0$); probabilities adjusted for multiple testing (Bonferroni procedure) are reported. Allometry of growth in the above sexual characters was investigated using the log transformation of the allometric growth equation $Y = \alpha X^\beta$ [$\log(Y) = \beta \log(X) + \log(\alpha)$] where β is the slope and α is the Y -intercept of the regression equation; in this study, Y = measure (in mm) or counts of the sexual character and X = carapace length (mm). Log transformation for ejaculatory duct width, appendix masculina length, and flange width was of the form " $\log(Y + 1)$ " because many Y values were less than 1. Positive allometry, negative allometry, and isometry are indicated by $\beta > 1$, $\beta < 1$, and $\beta = 1$, respectively (Gould, 1966; Kuris *et al.*, 1987; Harvey and Pagel, 1991). All regression lines were statistically significant ($P \leq 0.007$). Their slopes (β) with lower and upper 95% confidence intervals are reported.

Additional observations were made on the simple presence or absence of ejaculatory ducts by dissection of all specimens from flume sample 2 not used in the morphometric analysis. Neither dissections nor destructive measurements were taken on the two museum samples, which were used solely for making size-frequency distributions of

sexual phases, identified by observations on pleopod morphology as described above.

The NHMLAC sample contained many FPs with broods of embryos, so that the hypothesis of successive spawning could be tested (Bauer, 1986; Bauer and Abdalla, 2001). For each incubating FP, observations were made on the degree of embryonic development and the degree of "ovarian" development (filling of the ovotestes with vitellogenic oocytes). As in Bauer and Holt (1998), embryonic development was scored from 1 (recently spawned embryos) to 4 (embryos near hatching); ovarian development was scored from 1 (no mass of vitellogenic oocytes observable through the carapace) to 4 (vitellogenic oocytes completely filling the cephalothoracic space posterior to the eyes and dorsal to the cardiac stomach).

RESULTS

Observations on Breeding and Copulation

The FPs maintained in pairs on the SIO water table went through repeated cycles of molting, spawning, and brood incubation concomitant with filling of the gonads with vitellogenic oocytes (prespawning gonads). There were 24 molts among individuals of the three pairs during the thirteen weeks of observations. In 22 of the 24 molts, prespawning gonads were observed in the FP before the molt; in 20 of these 22 molts, a brood of embryos was observed under the abdomen of the molting FP for at least one week after the molt, indicating successful fertilization of spawned eggs and their subsequent development as embryos.

Time-lapse video observations on two FP pairs at ULL showed that the nonspawning FP copulated as a male with the prespawning FP. In each of the two pairs, the nonspawning FP chased and then grasped the prespawning FP shortly (1 min 56 sec; 38 sec) after the posthatching, prespawning molt of the latter. Spawning occurred 1 h 47 min after the molt of the prespawning FP in one pair and 2 h 33 min in the other pair. In both cases, the spawning FP was maintained for one week before preservation; embryonic development of spawned broods was observed in both FPs.

Ten prespawning FPs with vitellogenic gonads incubating a brood of previously spawned embryos were maintained individually in aquaria (ULL laboratory) through embryo hatching and a posthatching, prespawning molt. No evidence of spawning was observed within one day after the molt in any of these FPs. There was neither attachment of embryos nor an emptying of the vitellogenic oocytes from the gonads. Seven of these individuals were followed from 2–6 d (median = 3 d) after the prespawning molt. The vitellogenic oocytes

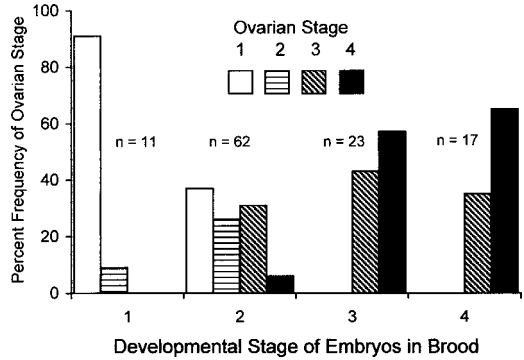


Fig. 1. Degree (stage) of ovarian development (nearness to next spawning) in female-phase individuals of *Lyasmata californica* incubating broods of embryos. Stages of ovarian development (filling of ovotestes with vitellogenic oocytes) range from 1 (no vitellogenic oocytes apparent) to 4 (ovotestes full of vitellogenic oocytes). The developmental stage of embryos in a brood (nearness to hatching) varies from 1 (newly spawned) to 4 (fully developed, close to hatching).

remained in the gonad but showed a blanching of their characteristic green color and a disappearance of distinct cell membranes, perhaps evidence of necrosis and/or reabsorption.

One individual maintained at the SIO laboratory began to show vitellogenic gonads in its second year of captivity. This virgin FP, maintained in isolation, was then followed through three consecutive molt cycles. In each cycle, the gonads filled with vitellogenic oocytes during the intermolt, molting occurred, but, unlike the isolated ULL FPs, eggs were spawned and attached to the pleopods. However, the apparently unfertilized eggs disappeared from the pleopods within a few days.

Spawning Pattern

Female-phase individuals incubating embryos were abundant (113 of 125 FPs) in the NHMLAC sample from August, 1970, permitting a test of the hypothesis of successive spawning by individual FPs. Ovotestes of FPs with recently spawned embryos showed little or no ovarian development whereas FPs carrying embryos near hatching (embryo stages 3 and 4) were filling or were full of vitellogenic oocytes (Fig. 1). The hypothesis of no association between stage of embryonic development and stage of ovarian development is rejected (G -test, χ^2 (9 d.f.) = 89.4, $P < 0.001$). Eight FPs in the sample carried no embryos but had significant ovarian development (stage 3 or 4). In six of these eight FPs, membranes of hatched embryos

and, in four of these six FPs, a few unhatched or undeveloped embryos were attached to the pleopods, indicating that the posthatching, prespawning molt had not yet occurred. Four other FPs carried no embryos, and vitellogenic oocytes were not apparent in their ovotestes.

Variation of Sexual Characters with Sexual Phase and Size

Male gonopores with flap-like opercula were observed on the coxae of the fifth pereopods (last walking legs) of all FPs ($n = 167$) and all MPs > 3.1 mm ($n = 272$). In 20 of 29 individuals ≤ 3.1 mm CL (SIO flume samples), gonopores were not visible in observations using a stereomicroscope (to $50\times$). Other male characters were poorly developed in these small individuals ("juvenile MPs") with ejaculatory ducts not visible upon dissection in 7 of 29, no appendices masculinae in 12, and no cincinnuli on the pleopod 1 endopods in 25. Only two of these individuals (3.0, 3.1 mm CL) showed full MP characters. Two other somewhat larger individuals (3.4, 3.5 mm CL) lacked cincinnuli but otherwise showed male characters. All other individuals with fully developed appendices masculinae had cincinnuli on the pleopod 1 endopods and were classified as MPs. All the very small individuals lacking one or more male characters are obviously newly recruited individuals and were classified as MPs in the size-frequency distributions (Fig. 2). Upon dissection, all individuals > 3.1 mm CL (152 MPs, 25 FPs) from the SIO flume samples had ejaculatory ducts leading to the gonopores on the coxae of the fifth pereopods.

The FPs incubating embryos invariably lack cincinnuli on the endopods of the first pleopods, both in *L. californica* (this study) and *L. wurdemanni* (Bauer and Holt, 1998). Thus, the absence of cincinnuli on the first pleopods of specimens without embryos was used to classify such individuals as FPs. In the SIO-BIC sample, taken in a winter month (February), none of 17 individuals classified as FPs carried embryos. All either lacked or had reduced appendices masculinae, an FP characteristic. However, 5 of the 17 had a few to several cincinnuli on the first pleopods, an MP characteristic. Given that they were within the size range of FPs observed with embryos in *L. californica* in this study (8.6 to 15.4 mm CL, $n = 167$ FPs) and that appendices masculinae were absent or reduced, these anomalous individuals were classified as FPs in the size-frequency distributions (Fig. 2).

The MPs that will change to FPs at the next molt ("transitionals," Bauer and Holt, 1998) are individuals with external MP characters but with the ovarian portion of the gonad visibly filled with vitellogenic oocytes. Two transitional MPs (6.8 and 8.4 mm CL) were found in the SIO flume 2 sample and another (11.0 mm CL) was identified in the NMHLAC sample.

Variations in sexual characters among individuals of different body sizes were compared in 25 MPs and 25 FPs from the SIO flume samples (Fig. 3). In the samples used for morphometric observations, all individuals identified as FPs by previous embryo production lacked cincinnuli on the pleopod 1 endopods. In the MPs, identified by lack of brood production and by the presence of cincinnuli on the first pleopods, the number of cincinnuli was positively correlated with carapace length (CL), the measure of body size, (Fig. 3A) ($r = 0.80$, $P < 0.001$), and the slope (β) of the log-transformed allometric growth equation indicates positive allometry ($\beta = 1.36 \pm 0.38$). The length of the appendix masculina, a male sexual character in carideans, was positively correlated with size in MPs ($r = 0.97$; $P < 0.001$) but negatively correlated in FPs ($r = -0.73$; $P < 0.001$) (Fig. 3B). The growth of the appendix masculina was negatively allometric in MPs ($\beta = 0.37 \pm 0.03$) and much more so in FPs ($\beta = -0.49 \pm 0.19$) (Fig. 4). The number of appendix masculina spines (Fig. 3C) increased with size in MPs ($r = 0.73$; $P < 0.001$), but their increase was negatively allometric ($\beta = 0.37 \pm 0.14$). In FPs, there were few or no spines on the highly reduced appendices masculinae present in most FPs, and the correlation between appendix spine number and size is not statistically significant ($r = -0.48$; $P = 0.07$). The slope of the growth equation ($\beta = -1.59 \pm 1.11$) shows the highly negative growth (reduction and loss) of appendix masculina spines in FPs (Fig. 4). However, all FPs had male ejaculatory ducts, and the size (width) of FP ejaculatory ducts was positively correlated with size ($r = 0.54$; $P < 0.024$) as it was in MPs ($r = 0.91$; $P < 0.001$) (Fig. 3D). Growth of the ejaculatory ducts was negatively allometric in both MPs ($\beta = 0.41 \pm 0.08$) and FPs ($\beta = 0.26 \pm 0.17$), with extensive overlap in 95% confidence limits on slopes of the MP and FP allometric regressions (Fig. 4). The width of the pleopod flange, a character associated with female reproduction (Höglund, 1943; Bauer, 1986) was positively correlated

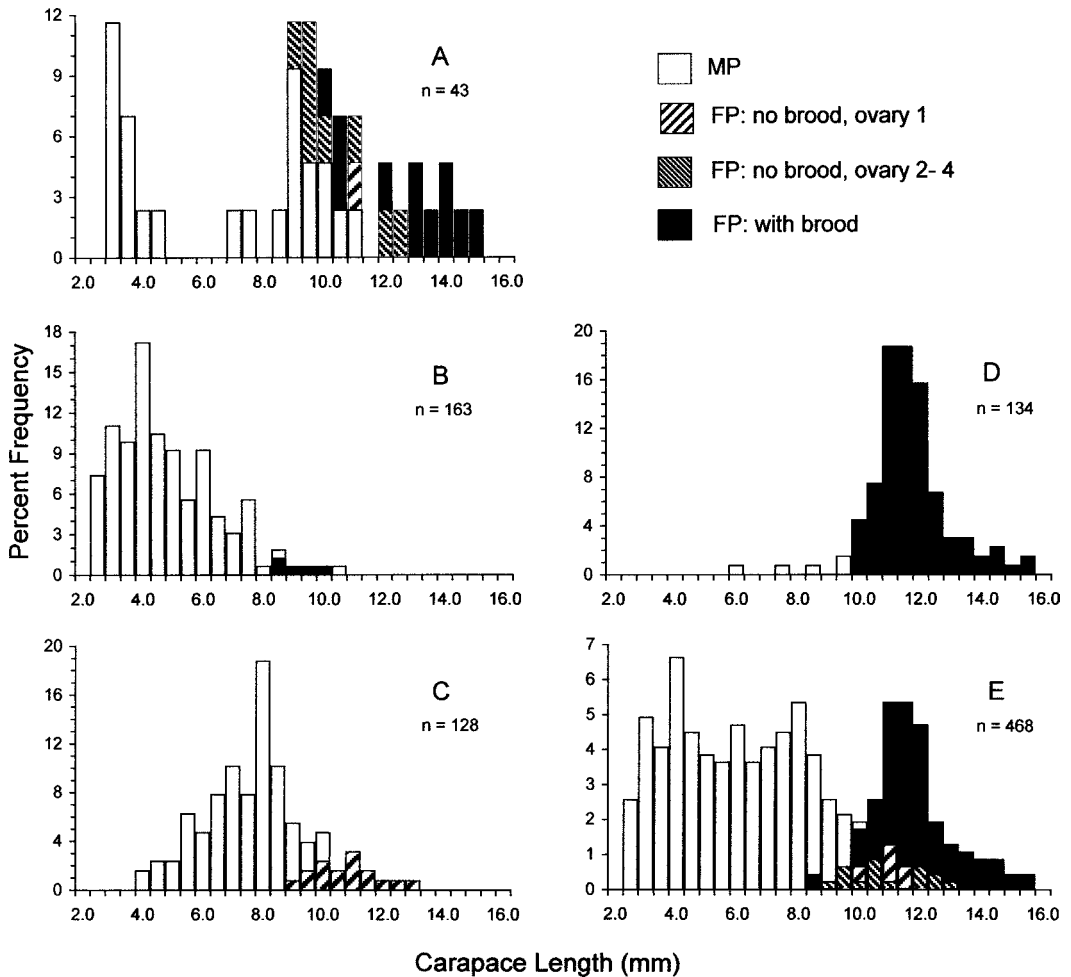


Fig. 2. Size-frequency distributions of sexual morphs in *Lysmata californica* with the reproductive condition of female-phase individuals. A, SIO flume sample 1 (a mixed sample containing individuals collected on the SIO pier flume June 4–8, 2001, including those used for mating observations and preserved up to one year later, plus 3 MPs collected from the flume in January, 1999); B, SIO flume sample 2 (July 23, 2002); C, SIO-BIC sample (Feb. 2, 1916); D, NHMLAC sample (August 8, 1970); E, composite sample of A–D. FP, female-phase individual; MP, male-phase individual.

with size in both MPs ($r = 0.90$; $P < 0.001$) and FPs ($r = 0.84$, $P < 0.001$) (Fig. 3E). However, growth in pleopod flanges was more negatively allometric in MPs ($\beta = 0.15 \pm 0.03$) than in FPs ($\beta = 0.31 \pm 0.10$) (Fig. 4).

Size-Frequency Distributions of Sexual Morphs

In all samples, MPs composed the size classes of smaller body size and FPs those of larger body size with some overlap (Fig. 2). In the composite of all samples (Fig. 2E), MPs (including juvenile MPs) ranged in size from 2.5 mm to 11.2 mm CL, and FPs from 8.6 mm to 15.4 mm CL. In the SIO flume 2 sample,

specifically taken as a population sample, and in the two museum collection samples, the sex ratio was highly biased (Fig. 2B–D). In the SIO flume 2 sample, taken in July, 2002, and the SIO-BIC sample, collected in February 1916, there were very few FPs (Fig. 2B, C). In contrast, the NHMLAC sample, collected in August 1970, was composed almost completely of FPs (Fig. 2D).

DISCUSSION

The sexual system of *Lysmata californica* is clearly protandric simultaneous hermaphroditism. Size-frequency distributions show that individuals first develop as males (male phase = MP);

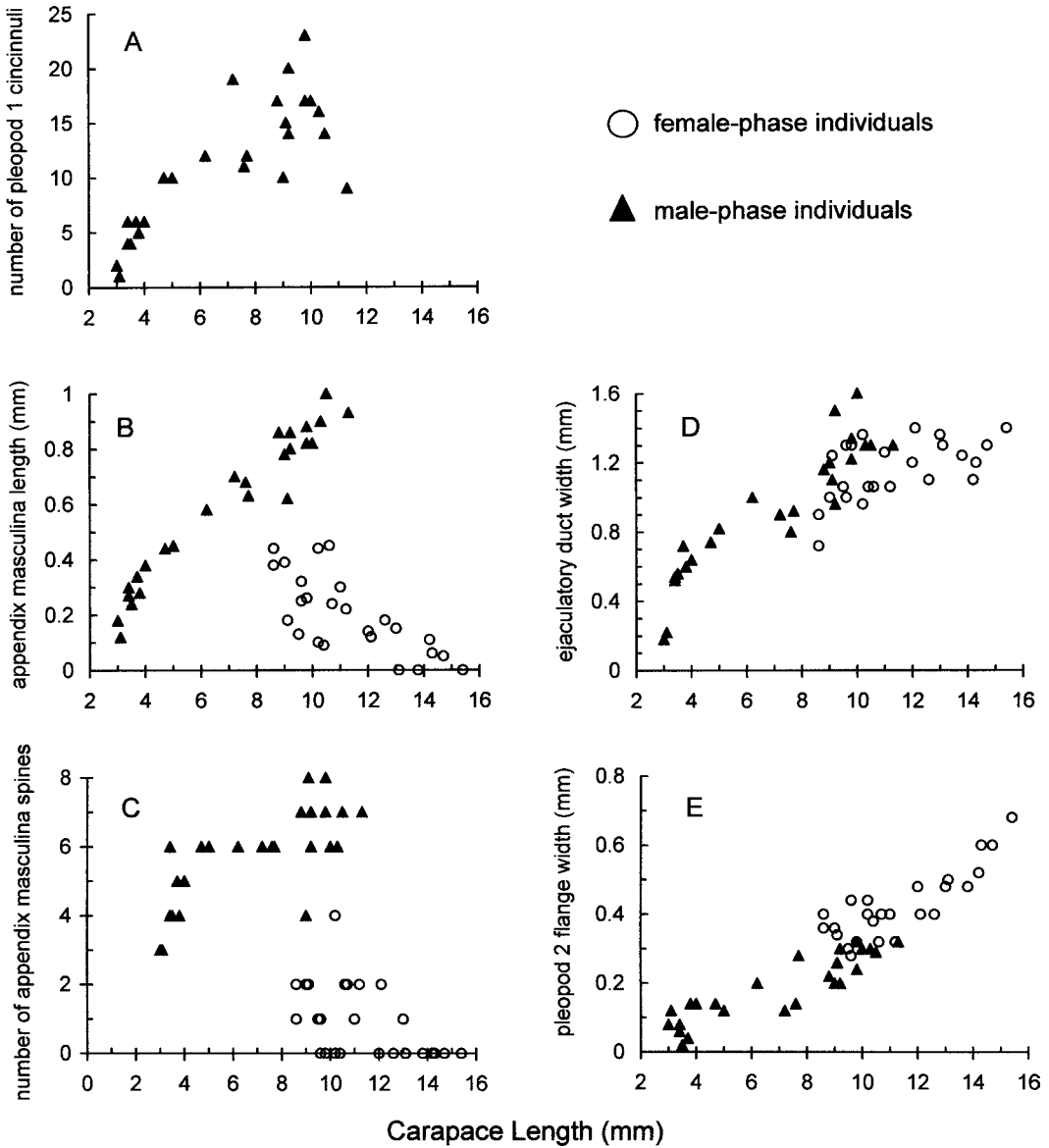


Fig. 3. Variation in sexual characteristics with increasing body size of *Lysmata californica* sexual morphs ($n = 25$ male-phase, 25 female-phase individuals). A, number of cincinnuli on endopod of pleopod 1; B, length of the appendix masculina (excluding spines) on endopod of pleopod 2; C, number of spines on the appendix masculina; D, maximum width of the ejaculatory duct; E, width of flange on the basipod of pleopod 2.

there are no juvenile females. Larger individuals spawn eggs and incubate embryos (female phase = FP) but retain male gonopores and ejaculatory ducts. Bauer (2000: fig. 2) illustrated the gonads from an MP and an FP of *L. californica*, showing them to be ovotestes. The FPs of *L. californica* are successive spawners during the warmer months of the year, simultaneously incubating a brood of embryos and filling the gonad with

vitellogenic oocytes for a new spawn at the next molt, as in *L. wurdemanni* (Bauer and Holt, 1998; Bauer, 2002a) and *L. amboinensis* (Fiedler, 1998). Our observations on spawning and brooding in FP pairs maintained in the laboratory indicated that FPs do mate as males and inseminate newly molted prespawning FPs. This was confirmed by time-lapse video observation of copulation in FP pairs. Isolated FPs did not

produce successful broods. Thus, as in *L. wurdemanni* (Bauer and Holt, 1998) and *L. amboinensis* (Fiedler, 1998), *L. californica* is an outcrossing simultaneous hermaphrodite in the female phase. It is likely that other *Lysmata* species in which male ejaculatory ducts have been observed in "females" have a similar sexual system (e.g., *L. seticaudata*, Spitschakoff, 1912; Berreur-Bonnenfant and Charmiaux-Cotton, 1965; *L. grabhami*, Wirtz, 1997; preliminary behavioral observations for *L. seticaudata* and *L. nilita* Dohrn and Holthuis, 1950, in Udekem D'Acoz, 2003).

Our observations on solitary FPs of *L. californica* show that they do not fertilize themselves. Like females of gonochoristic or purely protandric carideans, FPs of *L. wurdemanni* and *L. amboinensis* maintained alone will usually spawn after molting, discarding the unfertilized attached eggs within a few days (Bauer and Holt, 1998; Fiedler, 1998). However, Bauer and Holt (1998) reported that a few (3 of 17) isolated FPs of *L. wurdemanni* did not spawn after the prespawning molt. Instead, the retained vitellogenic oocytes underwent necrosis and/or reabsorption in the gonads. In *L. californica*, a single virgin FP observed through three molt cycles at the SIO laboratory followed the usual *L. wurdemanni* and *L. amboinensis* FP pattern of spawning unsuccessfully when maintained in isolation. On the other hand, ten prespawning FPs of *L. californica* maintained individually at the ULL laboratory followed the rarer pattern observed in *L. wurdemanni* in which the isolated FP does not spawn after the molt and the vitellogenic oocytes take on a necrotic appearance. This could be a laboratory artifact from unknown causes at the ULL setup, but FPs allowed to mate in ULL aquaria or in the video observations spawned and produced successful broods.

As in *Lysmata wurdemanni* (Bauer and Holt, 1998), individuals transitional between MP and FP were observed in *L. californica*. Transitional MPs show fully male pleopod characters, but the gonad is full of vitellogenic oocytes. Presumably, as in *L. wurdemanni*, these individuals change completely to FPs and spawn at the next molt. The large variation in size of these individuals reflects the variation in size of MP to FP change in *L. californica* as in *L. wurdemanni* (Lin and Zhang, 2001; Bauer, 2002b; Baldwin and Bauer, 2003).

In protandric pandalids, MPs lose male pleopod characters during several transitional

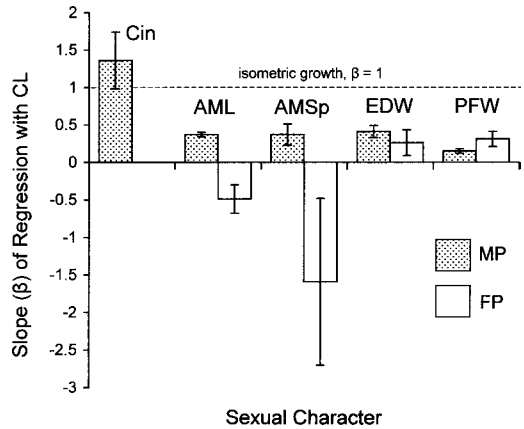


Fig. 4. Allometry of growth in sexual characters in *Lysmata californica*. Slopes (histogram bars) with 95% confidence intervals of regression lines calculated from measures of sexual characters on carapace length (size), with log transformation of both dependent variables and carapace length. AML, appendix masculina length; AMSp; number of appendix masculina spines; Cin, cincinnuli; EDW, ejaculatory duct width; FP, female-phase individual; MP, male-phase individual; PFW, width of basipod flange of pleopod 2.

molts to the female phase (Butler, 1980). However, in the protandric hippolytid *Chorismus antarcticus*, a somewhat reduced appendix masculina (male character) is often retained in the female phase. If such individuals are nongravid, female status can only be confirmed by the opening and the closure of the female and male gonopores, respectively (Mascetti *et al.*, 1997). In protandric individuals of the hippolytid *Thor manningi*, MPs gradually lose male characters (appendices masculinae, ejaculatory ducts, testicular part of gonads) and gain female characters (pleopod flange expansion, vitellogenesis in the gonads) with increasing size up to the complete change to FP. In MPs of *L. californica*, the increase in the number of cincinnuli on pleopod 1, an important male character in many caridean species, is positively allometric. The cincinnuli are completely lost in the single molt from MP to FP. On the other hand, in the presumably several MP growth molts, there is a decrease in the relative size (negative allometry) in the length and number of spines in the appendix masculina of MPs. In most FPs, there is some remnant of the appendix masculina, occasionally with spines, and these vestiges of MP history become smaller or disappear with increasing FP size. Unlike protandric hermaphrodites of *Thor manningi*, in which the ejaculatory duct becomes smaller

with increasing MP size, disappearing completely in the female phase, there is no significant difference in its relative size between MP and FPs of *L. californica*. This structure, which stores sperm from the testicular portion of the gonad prior to copulation, is as "male" in FPs as it is in MPs. The male gonopores are completely retained and open in FPs.

Finally, the pleopod flange is a structure associated with spawning of eggs and incubation of embryos. In reproductive females of many carideans, pleopod flanges and pleura of the anterior abdominal segments become expanded as part of the "breeding dress" (Höglund, 1943; Bauer and VanHoy, 1996). In *L. californica*, the relative growth of the pleopod flanges in FPs was statistically greater than that of MPs. Nonetheless, the expansion of the pleopod flanges (and abdominal pleura) of FPs is qualitatively much less than that of FP protandrites of *Thor manningi* (see Bauer, 1986) and females of many gonochoristic carideans (Höglund, 1943; Bauer and VanHoy, 1996).

The relative growth of all these male and female characters appears similar to that of MPs and FPs of *L. wurdemanni* from the Gulf of Mexico (Bauer and Holt, 1998; Bauer, 2000). Thus, in *Lysmata* species investigated, in addition to male mating capabilities, the FPs are somewhat masculine in reproductive morphology, in spite of the lack of the key male characters on the anterior pleopods.

The size-frequency distributions of the three population samples (SIO flume 2, SIO-BIC, and NMHLAC) from different locations and dates were highly biased towards one sexual phase or the other. In the first two samples, from La Jolla, California, there were few FPs. The lack of FPs in the SIO flume 2 sample might be explained by human activity, because shrimps are periodically collected there for fish food in a public aquarium. It might be presumed that collectors are biased for the larger individuals, which tend to be FPs. If the SIO-BIC museum sample (winter, 1916) is really representative of a population sample, the paucity of FPs is puzzling unless it is a seasonal phenomenon. On the other hand, the NMHLAC sample, taken in summer (August), 1970, is heavily biased towards FPs. However, all the *L. californica* samples, taken together, definitely show that individuals first develop in a male phase and change to the female (simultaneous hermaphrodite) phase later in life.

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