Reproduction and Population Dynamics of a Population of Grandidierella japonica (Stephensen) (Crustacea: Amphipoda) in Upper Newport Bay, California

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Abstract.—Patterns of reproduction, as measured by brood size and abundance, were studied for a population of the amphipod *Grandidierella japonica* (Amphipoda: Gammaridea) in Newport Bay, California during the period of July 1993 to June 1994. Weekly measurements of temperature, salinity and photoperiod were also made at the study site. *G. japonica* reproduced year-round at this site. However, both brood size and abundance declined during the winter months. Large females were found to have both a larger brood size and produced offspring of greater length. Physical factors, such as temperature and photoperiod, appear to play a role in the pattern of reproduction. However, biotic factors, such as food supply and predation, which were not measured in this study, appear to have an effect as well.

Grandidierella japonica (Amphipoda: Gammaridea) is a small (usually <10 mm), tube-dwelling amphipod that was introduced from Japan to California where it was first reported in San Francisco Bay in 1966 (Chapman and Dorman 1975) and in Newport Bay in 1979 (MBC and SCCWRP 1980). It currently occurs in intertidal and sub-tidal sediments of bays and estuaries of California from San Francisco to San Diego (Lamberson et al. 1994).

Little is known about the biology and life history of *Grandidierella japonica*. It inhabits U-shaped tubes in sediments ranging from coarse sand to clay (MBC and SCCWRP 1980). We have successfully cultured *G. japonica* in our laboratory at temperatures ranging from 15 to 23°C and have found the generation time to be about 30 d at 19°C, under laboratory conditions (Nipper et al. 1989). The eggs develop in the marsupium of the female and juveniles are released within 7 to 10 d after the first appearance of the eggs. In the lab, females are known to produce at least one more clutch of eggs (D. Greenstein, unpublished observations). The life span and number of broods of young produced are unknown. Some life history information is available on a related species, *Grandidierella bonnieri*, which inhabits coastal areas of India (Nayar 1956).

We have developed short-term (10 d) and long-term (28 d) sediment toxicity tests using *G. japonica* (Nipper et al. 1989) and the methods for the short-term tests were published by the American Society for Testing and Materials (ASTM 1991). The 28 d test has end points of survival and growth. We have also conducted longer term tests where fecundity has been used as an end point.

For the long-term tests, 3 to 7 d old juveniles are added to the sediment. The juveniles are obtained from gravid females collected in the field and held in separate petri dishes in the laboratory until the young are released. During pre-

vious experiments, females generally released 10 to 40 young (average about 25) (SCCWRP unpublished data). However, during an experiment in March 1992, females released as many as 150 offspring (average about 40). This prompted us to seek additional information on the natural variability of brood size and factors affecting brood size in the wild population of *G. japonica*. Among factors likely to influence fecundity are photoperiod (Segerstråle 1970; DeMarch 1977; Steele et al. 1977; Steele 1981; Williams 1985), temperature (Moore and Francis 1986; Morritt and Stevenson 1993) and biotic factors such as food supply (Wildish 1982).

The objectives of this study were to measure fluctuations in abundance and fecundity in a population of *Grandidierella japonica* in Newport Bay, California and to identify possible relationships between fecundity and environmental characteristics such as temperature, salinity and photoperiod.

Materials and Methods

Grandidierella japonica and water samples were collected between July 1993 and June 1994 from Upper Newport Bay (33°37′N, 117°53′W) on the south shore of Shellmaker Island, west of the Newport Dunes Aquatic Park boat launching ramp. A water sample was collected weekly from the bottom in approximately 1 m of water with a 3 L Van Dorn bottle. Water temperature was recorded and the water sample was taken to the laboratory where salinity was determined from conductivity measurements performed with an Orion 122 Conductivity Meter.

Population density was determined by taking three sediment cores monthly in approximately 0.5 m of water with a 78 mm diameter (48 cm²) stainless steel hand core. All core samples were taken within 2 h of low tides and were hap-hazardly distributed along approximately 50 m of shoreline. The cores were packaged separately and taken to the laboratory where they were screened through a 0.3 mm sieve within 24 h. *Grandidierella japonica* were counted and scored by eye as male, ovigerous female, or non-ovigerous female. Any individuals that could not be sexed by eye were scored as juveniles.

In order to obtain gravid females for the fecundity measurements, samples of surface sediments were collected monthly in approximately $0.5\,\mathrm{m}$ of water with a shovel and sieved through a 1 mm screen in the field. Material retained on the screen was taken to the laboratory. The first 65 gravid females encountered were removed from the animals collected on the screen. However, fewer than 65 gravid females were collected during some months. Each gravid female was placed in a separate $60 \times 15\,\mathrm{mm}$ petri dish filled with seawater. The dishes were kept at $20^{\circ}\mathrm{C}$ and checked daily until all juveniles were released (within 8 d). The offspring were then collected and counted. After releasing offspring, up to 19 females were preserved in alcohol for length measurements and all of the juveniles from up to five of these females were preserved for length measurements.

Amphipod length was measured by projecting a silhouette of their body on a Nikon Shadowgraph at a 10× magnification and tracing a line along the middle of the body that extended from the tip of the rostrum to the end of the telson. These tracings were made onto a clear plastic sheet. The drawings were then retraced on a digitizer board with the digitized values being converted to millimeters, using a computer program written in Basic language.

Descriptive statistics were calculated for all replicate data. Female size, juvenile

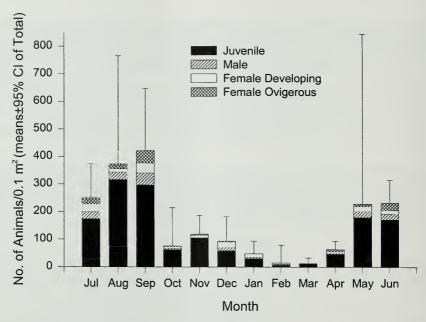


Fig. 1. Number of *Grandidierella japonica* collected in cores per 0.1 m^2 in Upper Newport Bay from July 1993 to June 1994 (N = 3; mean \pm 95% C.I. for total number).

size and proportion of each sex class of animals in the cores were tested for temporal variation by analysis of variance (ANOVA) and Student-Newman-Keuls multiple comparison test (Zar 1984). Proportion data were arcsine transformed before testing. Data that failed a test for normality were tested with Kruskal-Wallis ANOVA on ranks and Dunn's multiple comparison test (Zar 1984). The relationship between female length and brood size was tested by linear regression (Zar 1984). The relationships between juvenile length and female length or brood size were tested using Kendall's coefficient of rank correlation (Sokal and Rohlf 1995). Correlations between physical factors and biotic factors were tested by Pearson product moment correlation. Photoperiod data were generate as hours and minutes of daylight by a computer program called Sunny 2000 written by Lou Moccia.

Results

The mean total number of *Grandidierella japonica* in the cores differed by two orders of magnitude during the year (Fig. 1). The variability of the core data was high with the coefficient of variation ranging from 20% to over 100%, but a significant difference between months was detected (P < 0.05). The abundance decreased in October and remained low through April. Juveniles were found in the cores for each month and accounted for greater than 50% of the total (Fig. 2). The largest percentage of juveniles was found in November and the lowest in February. However, the difference between these months was not found to be significant (P > 0.05). There were significantly more developing females in January than in March. No significant differences between months were detected for males or ovigerous females.

Gravid females were found during all 12 months of the study. However, during

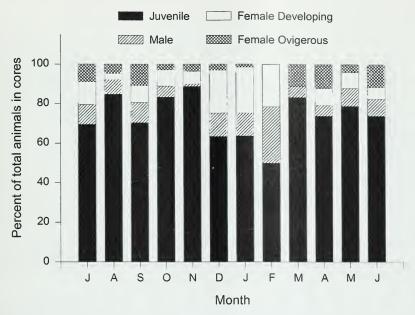


Fig. 2. Percent of each sex category of Grandidierella japonica collected in sediment cores.

December through February we were unable to obtain our target of 65 gravid females. The average number of juveniles released per female was lowest from October through January with a low of six in December (Fig. 3). Except for the peak of 29 juveniles released in August, numbers released were similar for February through September (Fig. 3). The brood sizes for October through January were significantly smaller than for all other months except September ($P \le 0.05$).

The number of young released was significantly related to female length (r =

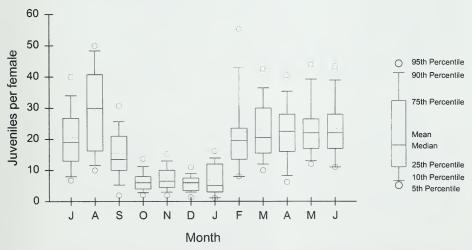


Fig. 3. Number of offspring released by female *Grandidierella japonica* collected in Upper Newport Bay from July 1993 to June 1994 ($16 \le N \le 72$ females per month).

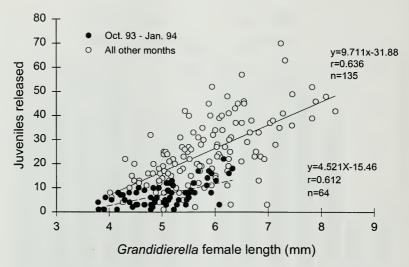


Fig. 4. Number of offspring released versus female length for *Grandidierella japonica* collected in Upper Newport Bay from July 1993 through June 1994.

0.69, P < 0.05, N = 199) (Fig. 4), with larger females producing more offspring. The slope was different for females collected from October through January compared to the other months, but larger females still produced larger broods. To minimize the effect of variations in female size, the brood size data were normalized before correlation analysis with the physical parameters. The normalization consisted of using the regression of female length versus brood size for each month to adjust the observed number of offspring per female to the value corresponding to a female of average size (5.58 mm).

The average length of the juveniles released was lowest in July, December, and January (Fig. 5). Animals released in January were significantly smaller than

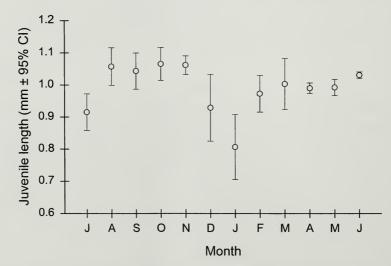


Fig. 5. Length of offspring released from *Grandidierella japonica* females collected in Upper Newport Bay from July 1993 through June 1994 (N = 4-7 females per month; mean \pm 95% C.I.).

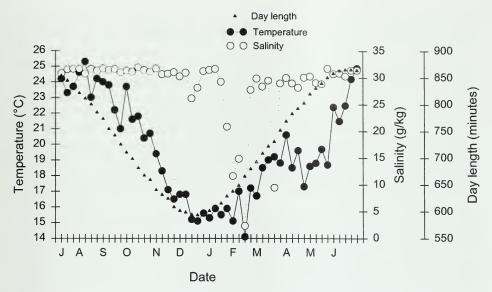


Fig. 6. Weekly bottom water temperature and salinity in Upper Newport Bay, and day length, from July 1993 to June 1994.

animals released in all other months except July (P < 0.05). A significant correlation was found between the length of the female and the average length of the offspring produced (P < 0.05). However, when offspring length was adjusted for female size (data not shown), the pattern for juvenile size by month remained the same. There was no significant relationship between the brood size and the length of the juveniles.

The bottom water temperature in Upper Newport Bay was highest from June through September and then declined to a low in December (Fig. 6). Day length showed a pattern similar to temperature. Salinity remained fairly constant at about 30 g/kg except for a few declines following periods of rain. A significant correlation was found between temperature and day length (r = 0.794, P < 0.05). However, mean brood size correlated with day length (r = 0.756, P < 0.05), but not with temperature or salinity. The total number of animals found in the cores correlated both with day length (r = 0.815, P < 0.05) and temperature (r = 0.650, P < 0.05), but not with salinity.

Discussion

The presence of juveniles and gravid females each month during the present study indicates that *Grandidierella japonica* reproduce throughout the year, at this site in Upper Newport Bay. Year-round breeding has been noted in other Gammaridea, especially among those in warm climates (Wildish 1982). If the generation times that we found in the laboratory hold true for the natural habitat, then the population of *G. japonica* may be capable of producing 10–12 generations per year.

The abundance of *Grandidierella japonica* in cores collected from Upper Newport Bay was high throughout the summer, declined in the fall to a low in winter, and recovered the following spring. A similar pattern was observed by MBC and

SCCWRP (1980). In that study, *G. japonica* were collected at most stations in November, December, and July, but were rarely collected in January and March. In our study, juveniles represented greater than 50% of the animals in all months, with their proportion being lowest during December through February, when fecundity was also low. The high variability within each month of the abundance data in the present study suggested that the animals had a patchy distribution. Power analysis on data at the start of the study indicated that about 20 cores per month were necessary to achieve an 80% chance of detecting a 50% change in the population. Unfortunately, time constraints prevented us from collecting and analyzing more than three cores per month. More cores might have allowed us to better distinguish differences amongst the developing and ovigerous female classes.

The annual pattern of decreases in abundance and fecundity in *Grandidierella japonica* parallel decreases of temperature and photoperiod in Upper Newport Bay. Unfortunately, there is no laboratory verification available for how these parameters affect reproduction of *G. japonica*. The initiation of reproduction in the beach flea, *Orchestia gammarellus*, is affected by temperature, but not by changes in photoperiod or salinity (Moore and Francis 1986; Morritt and Stevenson 1993). There is a large body of work indicating that reproduction in various amphipods is affected greatly by photoperiod (Segerstråle 1970; DeMarch 1977; Steele et al. 1977; Steele 1981; Williams 1985). In our study, photoperiod correlated both with fecundity and abundance. The decreases in fecundity and abundance began to occur as photoperiod was reduced, but before the temperature had started to drop. These factors indicate that photoperiod may have an effect on the reproduction of *Grandidierella japonica*.

While the seasonal brood size pattern observed for *Grandidierella japonica* is similar to other species of Gammaridea, the pattern of offspring size is opposite of what is expected. More northern Gammaridea species usually produce smaller clutches during the colder months, but this is associated with an increase in egg size, giving the offspring a better chance of surviving harsh conditions (Van Dolah and Bird 1980; Kolding and Fenchel 1981; Skadsheim 1984). During our study, *G. japonica* had reduced brood sizes in the winter, but this was coupled with a decrease in juvenile size. For the *G. japonica* population that we studied, temperature variations were relatively small and did not correlate with changes in brood size. Temperature may not play as large a role in determining offspring and clutch size for this species as it does for colder climate species.

Though it is possible that temperature and photoperiod could directly affect reproduction of *Grandidierella japonica*, the effect on the availability of food, such as algae, may also be important. The decrease in brood size during the winter, and the decrease in juvenile size in December and January, indicate that less energy was expended on reproduction, perhaps because of reduced food availability. While we have no quantitative data on food supply, it was noted that the cover of algae was lower during the winter months.

Although changes in fecundity should have an effect on population size, changes in mortality rate may have played an important role in affecting this *Grandidierella japonica* population. While the decrease in fecundity was about four-fold, the decrease in abundance was about 10-fold. A reduction in food supplies coupled with lower water temperature and reduced salinity (due to freshwater runoff from storms) could decrease juvenile production and increase adult and

juvenile mortality. The survival of *G. japonica* in the laboratory decreased by more than 10% at a salinity of 10 g/kg during a 10-d test (SCCWRP, unpublished data).

To what degree predation plays a role in controlling the population structure of *G. japonica* is unknown. The abundance of fish in the littoral zone in Newport Bay is quite high from summer through fall (Allen 1982) and many of these fishes prey on amphipods (Horn and Allen 1985). If larger amphipods are selectively removed by predation, then by the end of fall the smaller females, producing fewer offspring, would be left. In the spring, with fewer predators and more abundant food, the females may survive longer and grow larger producing greater brood sizes. Since we did not measure all of the females collected in our study, the data are not sufficient to determine if the average length of the females changes throughout the year.

The seemingly inefficient pattern of both brood size and juvenile size decreasing during the harsher winter months may be explained by a combination of many factors. Brood size and size of the offspring decreased during the winter. Brood size and juvenile size are positively correlated with female length. However, changes in brood size and juvenile size are not entirely accounted for by differences in female length. In explaining changes in brood size and juvenile size, not only factors that affect reproduction must be observed, but also factors that affect female size. Photoperiod may act as a cue to reduce reproduction, but factors such as reduced food supply or predation may cause the average female to be smaller, thus reducing both juvenile production and size.

Learning more about the life history of *Grandidierella japonica* is important, given its use in sediment toxicity tests. Laboratory studies are needed to better define the roles of temperature, food and photoperiod on reproduction. Other species of amphipod are known to change their breeding habits depending on latitude (Wildish 1982). A field study similar to ours on the more northern *G. japonica* population in San Francisco Bay might determine if it behaves in a like manner.

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