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SEX CHANGE AND POPULATION FLUCTUATIONS IN PANDALID SHRIMP

Sex-allocation theory applied to sex reversal generally predicts that the age and/or size at sex reversal should show variation linked to the underlying age and/or size *distribution of the breeding population* (Leigh et al. 1976; Charnov et al. 1978; Hoagland 1978; Charnov 1979, 1982). Spatial or temporal variation in the age and/or size distribution of breeding adults may result from any of a number of factors: biogeographic (large-scale, between-population) variation in growth and/or mortality; small-scale variation in growth, mortality, or social-group structure; or year-to-year variation in growth, mortality, or recruitment (e.g., Albers and Anderson 1985). All these forms of variation have been used to look at adaptive sex change and to review much of the current fish and invertebrate work (Charnov 1979, 1982). Of particular interest is the small-scale variation in sex change, a form of phenotypic plasticity whereby an individual alters its age and/or size at sex change to match current breeding opportunities. Sex-reversing organisms that live in stable social groups are known to show labile sex change, whereby an individual alters the time or size at which it changes sex according to the sex and size identity of its immediate neighbors (Charnov 1982; Shapiro 1987). Such labile sexuality is widespread in coral-reef fish (Fishelson 1970; Robertson 1972; Fricke and Fricke 1977; Warner 1984, 1988; Shapiro 1987) and invertebrates such as the limpet *Crepidula* (Hoagland 1978) and the polychaete *Ophryotrocha* (Bacci 1965).

Protandrous pandalid shrimp do not live in stable social groups; yet there is strong correlational evidence that individuals alter their age and/or size at sex change in the face of year-to-year fluctuations in population age (= size) structure (Charnov et al. 1978), caused mainly (but not entirely) by a variation in recruitment from the planktonic larval phase (Albers and Anderson 1985). This earlier evidence is for *Pandalus jordani* off the west coast of North America. At the study locations, the shrimp is short-lived (only two breeding age groups), and the age structure fluctuates greatly from year to year. This work plus several other forms of evidence strongly argued that pandalid shrimp, at a single location, have neither a fixed size nor a fixed age at sex change and that the age or size at sex change alters in response to year-to-year variation in the age and/or size distribution of breeding adults (review in Charnov 1982). In years when most of the breeders are larger, so is the size at sex change (Charnov et al. 1978).

We present here further correlational evidence in support of the notion that year-to-year fluctuations in the population size distribution are tracked by year-to-year variation in the size at sex change. Our data complement earlier work

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TABLE 1

NUMBER OF SHRIMP (N), CALCULATED MEAN SIZE ($\bar{x}$), AND OBSERVED SIZE ($x_{0.5}$)

Survey Year	N	$\bar{x}$	$x_{0.5}$*
1972	2243	17.00	19.75
1973	186	16.56	19.25
1974	1905	17.43	18.75
1975	2721	17.53	19.00
1976	2424	17.23	19.50
1977	3471	19.20	19.50
1978	5363	18.59	20.00
1979	2439	15.59	18.25
1980	2654	16.45	17.00
1981	2553	18.10	19.75
1982	4636	17.02	17.50
1983	4063	16.11	16.75
1984	3381	17.06	15.50
1985	5523	15.10	16.75
1986	8600	15.38	15.50
1987	3320	17.35	17.75

NOTE.—Data are for *Pandalus borealis* from Pavlof Bay, 1972–1987. Sizes in millimeters.

* Size at which 50% of the shrimp were identified as female.

(Charnov et al. 1978) in that the shrimp in our study, *Pandalus borealis*, is relatively long-lived at the study location, having a life span more than double that of the California species. Indeed, here we provide the analysis in terms of size, rather than age, because separate age groups cannot easily be recognized.

Pavlof Bay, on the southern side of the Alaska Peninsula, supported one of the world's largest pandalid shrimp fisheries until 1979, and about 70% of the catches consisted of the northern shrimp, *Pandalus borealis* (Anderson 1981, MS). Although the area was closed to fishing after the catches abruptly declined in the late 1970s, a scientific sampling program has been carried out by the U.S. government since 1972. Data collected from these surveys include carapace-length frequencies by sex and estimates of abundance during the late summer-fall breeding season. The shrimp breed only once a year and at this location have a life span of 8–10 yr; sex change takes place sometime between the third and sixth year of life. Sampling methods are detailed elsewhere (Anderson 1981). In all, the data span 16 yr, 1972 through 1987.

In order to ask whether the size at sex change altered from year to year, in concert with the prevailing population size distribution that year, we performed the following correlation analysis. The size at sex change was defined as the size at which 50% of the individuals were female ($x_{0.5}$). To summarize the position of the population size distribution, we simply used the average size of a breeding individual ($\bar{x}$). This measure for the position of the population size distribution is biased since the sampling gear underestimates the number of small shrimp; larger shrimp are much more vulnerable to the gear (Charnov et al. 1978; Anderson 1981,

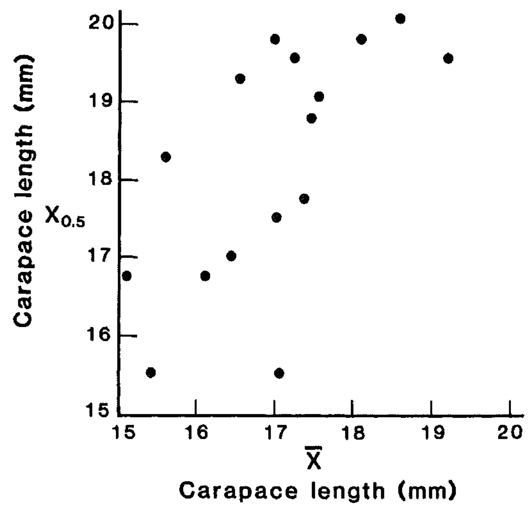

FIG. 1.—The size at which 50% of the individuals are female ($x_{0.5}$) correlates positively with the position of the overall size distribution of the breeding population, as indexed simply by the mean size of a breeder, $\bar{x}$ ($r = 0.65$, $P < 0.01$).

MS). However, we have no reason to believe that the bias alters from year to year in any consistent fashion. Table 1 summarizes the data; in all, about 55,000 shrimp were sampled over the 16-yr period. Figure 1 shows the plot of $x_{0.5}$ versus $\bar{x}$. The correlation is significant at the 1% level. We believe that the relation demonstrated here (fig. 1) suggests that the size at sex change tracks the population size distribution. Sampling limitations preclude a stronger statement, and pandalid shrimp are poor candidates for experimental manipulation.

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