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Eric Charnov

Robert Hannah

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Eric L. Charnov[1,2] and Robert W. Hannah[3]

[1]*Department of Biology, The University of New Mexico, Albuquerque, NM 87131 and*
[2]*Department of Zoology, Oregon State University, Corvallis, OR 97331 and* [3]*Oregon Department of Fish and Wildlife, 2040 S.E. Marine Science Drive, Newport, OR 97365, USA*

ABSTRACT

Long-term data sets that quantitatively confirm basic ecological theory are rare for field populations. Highly variable recruitment often causes wide temporal variation in population age distribution and basic theory for adaptive sex ratio often predicts 'sex ratio tracking' to match the fluctuating age distribution. Using sex-changing shrimp as a model system, we test this in a new data set of 20 years duration. The new data support the theory, despite intense fishery exploitation that itself has greatly altered the age distribution in recent years.

Keywords: evolutionarily stable strategy, fisheries, frequency dependence, protandry, recruitment variation.

INTRODUCTION

Twenty-four years ago, Charnov *et al.* (1978) first showed that the breeding sex ratio of commercially important sex-changing shrimp (*Pandalus jordani*) off the US west coast varied in response to year-to-year fluctuations in the population's age structure; here we extend the analysis to include the next 20 years, making our data set the longest ever used to test theory for adaptive sex ratio adjustment in a field population. Briefly, the data consisted of sex ratio each fall for each of two adult age groups and the proportion of the adult population (*P*) that was first versus older, mostly second, breeders; the life history is illustrated in Fig. 1. It is easy to separate first breeders from older breeders, since a first breeder is only about half the mass (weight) of an older breeder; gender is also easily determined morphologically within an age group. The analysis showed that the proportion of females $(1 - r_1)$ among the first breeders declined to zero with decreasing *P*; $1 - r_1$ was roughly 0.5 when strong first breeder recruitment (Hannah, 1993) pushed *P* to near 1. This response was predicted by theory for adaptive sex ratio (developed below). The data spanned the mid-1960s through 1975 ($\approx$12 years for each of three sampling areas). Data for these early years also showed that, when *P* was very small, some older breeding shrimp remained males, a result also predicted by theory. The data are summarized in Charnov (1982, ch. 10).
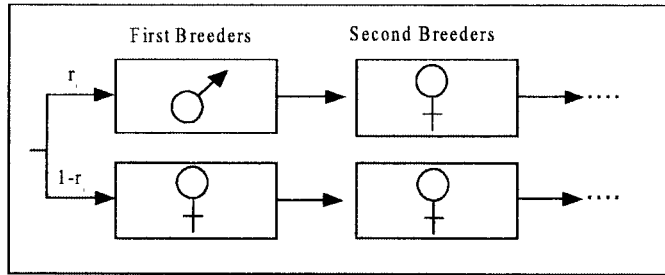

Fig. 1. Pandalid shrimp change sex from male to female (top path), but with only a few breeding age groups (here two), some first breeders mature as females (lower path). The shrimp breed once a year, in the fall, so second breeders are one year older than first breeders; a second breeder is about twice the weight of a first breeder. Theory predicts that the female proportion of first breeders $(1 - r_1)$ depends upon the ratio of older breeders to first breeders (see text). Sometimes some second breeders are predicted to remain female.

In this paper, we return to sex change in *P. jordani* off Oregon and ask if data for the rest of the century (i.e. 1980–2000) still support the theory for adaptive sex ratio tracking. Since our test of theory will be quantitative, the next section will develop the ESS (evolutionarily stable strategy) argument (Charnov *et al.*, 1978).

SEX RATIO THEORY

Consider the life history in Fig. 1 and assume two breeding-age (size) groups. Provided growth and survival are not dependent on gender, the best an individual can do is to maximize its reproductive gains while a first breeder and then again as a second breeder. So long as the ESS sex ratio among the second breeders does not require anyone to change back from female to male, the shrimp (which can change sex only once) can be modelled as follows. Let P equal the proportion of breeders that are small. Furthermore, let an individual that is big and reproducing as a female have an egg count of W_2 relative to a small individual as a female. Big individuals reproducing as males will be given a fertility of W_1 relative to a small individual as a male.

Consider a very large population (of size N) with the characteristics that the proportion r_1 of the small individuals reproduce as males, while the proportion r_2 of the big individuals are males. If we define fitness to be the probability that an individual passes its genes to a zygote formed during the current breeding season, the fitness of a small individual (W_s), which reproduces as a male with some other probability ($\hat{r}_1$, where $\hat{r}_1 \neq r_1$), may be written as:

$$W_s = \frac{P}{2 \cdot N} \left[\frac{\hat{r}_1}{Pr_1 + r_2 W_1(1 - P)} + \frac{1 - \hat{r}_1}{P(1 - r_1) + W_2(1 - P)(1 - r_2)} \right] \tag{1}$$

$$W_s = \frac{P}{2 \cdot N} \left(\frac{\hat{r}_1}{M} + \frac{1 - \hat{r}_1}{F} \right)$$

The fitness of a big individual (W_b) that alters the probability (with which it reproduces as a male) to $\hat{r}_2$ is similarly defined:

$$W_b = \frac{1-P}{2 \cdot N}\left(\frac{\hat{r}_2 W_1}{M} + \frac{W_2(1-\hat{r}_2)}{F}\right) \tag{2}$$

If the situation is to be evolutionarily stable, it must be that an individual cannot increase its own fitness by altering the probability with which it becomes a male (or a female) away from the respective population values (Maynard Smith, 1982) (that is, W_s and W_b do not increase as $\hat{r}_1$ and $\hat{r}_2$ are altered from r_1 and r_2). The task now becomes to find r_1 and r_2 that satisfy this condition; as in much of sex allocation theory (Charnov, 1982), the r_1 and r_2 we seek are those that maximize the product ($M \cdot F$).

The maximization of $M \cdot F$ by choice of r_1 and r_2 (provided $W_2 > W_1$) implies the following rules:

$$1 - r_1 \begin{cases} = \dfrac{1}{2}\left[1 - W_2\left(\dfrac{1-P}{P}\right)\right] & \text{if } W_2 < P/(1-P) \\[2ex] = 0 & \text{if } W_2 > P/(1-P) \end{cases} \tag{3}$$

and

$$r_2 \begin{cases} = \dfrac{1}{2}\left[1 - \dfrac{1}{W_1}\left(\dfrac{P}{1-P}\right)\right] & \text{if } W_1 > P/(1-P) \\[2ex] = 0 & \text{if } W_1 < P/(1-P) \end{cases} \tag{4}$$

This solution has the characteristics that: (1) sex ratio within a size class depends on the frequency distribution of size classes, but (2) more than 50% of the small shrimp should be males, while more than 50% of the big shrimp should be females, because females gain more reproductive success by being big than males do (that is, $W_2 > W_1$); indeed, $W_2 > W_1$ is required for male-to-female sex change itself to be stable (Charnov, 1982). Figure 2 is a graphical presentation of equations (3) and (4).

BIAS IN THE ESTIMATE OF P

Our data consist of shrimp sampled from the commercial catch during the fall breeding period; since the fishing gear changed in a major way at the end of 1970s, we analysed sex and size composition for the period 1980–2000. The fishing gear tends to select larger shrimp, so the *observed* $(1-P)/P$ will be inflated, reflecting the extent to which the respective size groups are caught. For example, suppose the true ratio of second (N_2) to first (N_1) breeders is N_2/N_1 [$=(1-P)/P$]; our *observed* ratio is thus $q_2 N_2/q_1 N_1$, where q_2/q_1 reflects the relative catchability of second versus first breeders. Call $q_2 N_2/q_1 N_1 \equiv (1-P)^*/P$; then $(1-P)/P = (q_1/q_2)(1-P)^*/P$.

So the ESS equation for the female proportion of first breeders $(1-r_1)$ (equation 3) can be written as:
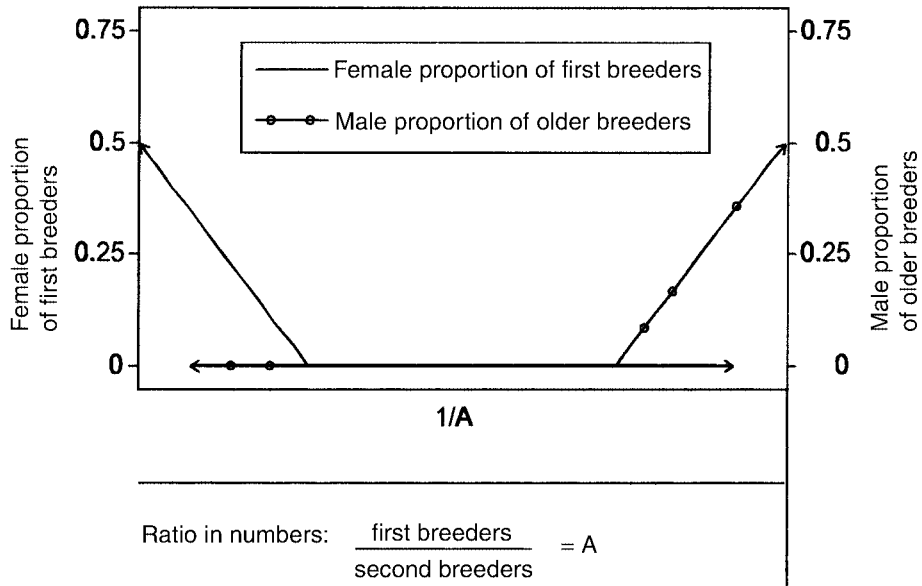
Fig. 2. Alteration in the time of sex reversal in response to fluctuating age distributions. We illustrate a population with only two breeding-age groups (first breeders, older breeders). Their ratio gives the age distribution, which is assumed to vary from year to year. If there are few older breeders ($1/A$ small), all the older breeders should be female, and some fraction of the first breeders should also be female (the rest, male). If there are few first breeders ($1/A$ large, or A small), all of the first breeders should be male, while some of the older breeders should also be male (the rest, female). As the age distribution varies from year to year, the cohorts are predicted to alter their sex ratios accordingly. Note that >50% of first breeders are male, while <50% of older breeders are male, thus the theory *never* requires an individual to sex reverse from female to male. [Original derivation and equations in Charnov *et al.* (1978). The reason for plotting one sex ratio versus A, and the other versus $1/A$, is to make the theoretical relations linear.]

$$1 - r_1 = \frac{1}{2}\left(1 - W_2\left(\frac{q_1}{q_2}\right)\left(\frac{1-P}{P}\right)^*\right) \tag{5}$$

W_2, the relative fecundity of second versus first breeders, is of a magnitude of about 2–3 (Hannah *et al.*, 1995), but q_1/q_2 is unknown, except <1 (perhaps ≪1).

The equation for the male proportion of second breeders (equation 3) will be rewritten:

$$r_2 = \frac{1}{2}\left(1 - \left(\frac{1}{W_1}\right)\left(\frac{q_2}{q_1}\right)\left(\frac{P}{1-P}\right)^*\right) \tag{6}$$

As can be seen, these ESS equations in terms of $(1-P)^*/P$ and $P^*/(1-P)$ simply change the slope of the predicted sex-ratio/age-ratio relation; for example; the slope is changed from $-W_2/2$ to $-(W_2/2)(q_1/q_2)$ for first breeder females.

SHRIMP SEX CHANGE: 1980–2000

The population age structure for *P. jordani* off the Oregon coast has been greatly changed since the 1970s because of intensification of the fishery (Hannah and Jones, 1991); for example, the proportion of first breeders in the commercial catch (which estimates *P*, with bias) has increased from ≈30% to ≈70%. As theoretically predicted (equation 3, or 5), this increase in *P* over time has been matched by a general increase in $1 - r_1$ (Hannah and Jones, 1991, fig. 9), particularly since 1979. But do the data support equations (5) and (6) for the 1980s and 1990s on a year-by-year basis? We have analysed P^* and $1 - r_1$ and r_2 by year for each of the seven areas (Fig. 3) sampled from the commercial catch during the fall breeding period. Figure 4 shows the results for $1 - r_1$ versus $(1 - P)^*/P$ for three representative areas spanning the geographic range studied; adaptive adjustment of the first breeder sex ratio still takes place on a year-by-year basis, now extending the test of equation (5) to more than 30 years, or roughly 15 generations, because there are only two breeding age classes. Since *P* is generally much larger in these recent years, failure in recruitment of first breeders should
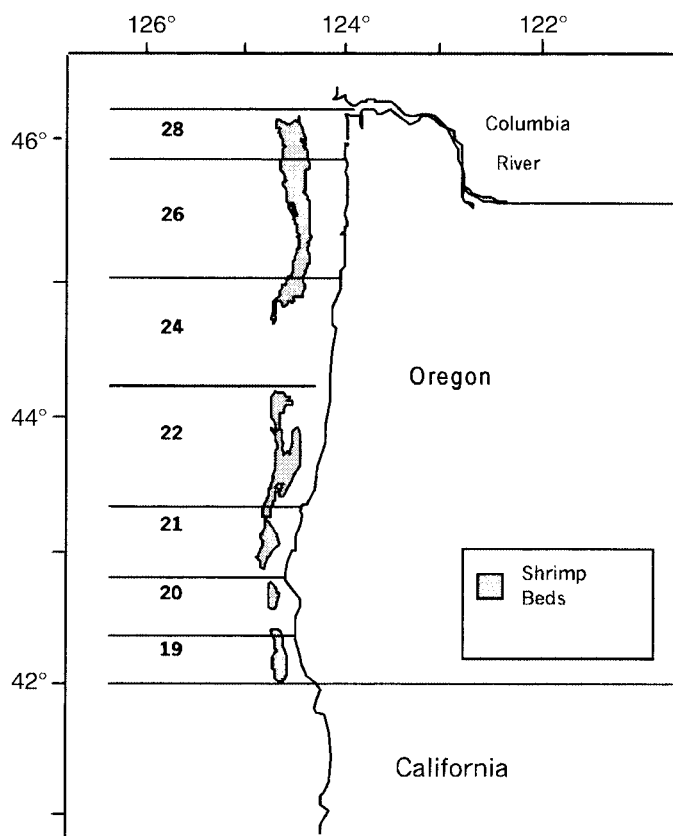

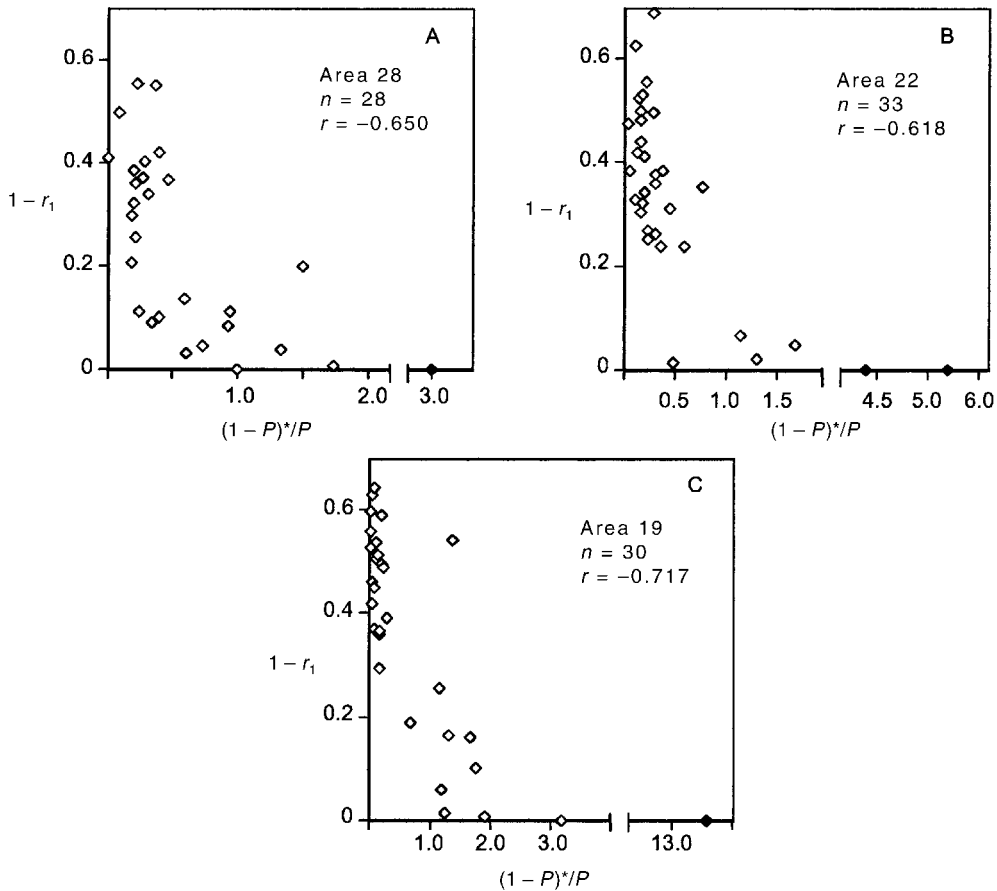**Fig. 3.** The fishery sampling areas on the US west coast.

Fig. 4. Proportion of female first breeders $(1 - r_1)$ versus the ratio of older breeders to first breeders $((1 - P)^*/P)$ from samples of the commercial catch of *P. jordani* from catch areas 19, 22 and 28 for the months of September and October, 1981–2000 (see Fig. 3). When available, we treated the two months each year as separate estimates, which is why $n > 20$. Transitional shrimp were considered to be functionally female, since they will breed as females that year. Shaded data points were omitted for calculation of the Spearman rank correlation coefficient (r). All correlations were significant at $p < 0.001$. If we accept the ($\approx$) quantitative test of theory implied by this figure, we can use it to give a rough estimate of the catchability ratio q_1/q_2. Let x^* be the intercept on the abscissa; then, equation (5) set equal to zero yields $W_2 \cdot x^* = q_2/q_1$. $W_2 \approx 2.5$ (Hannah *et al.*, 1995) and inspection of the above data puts $x^* \approx 1.5$; thus, $q_2/q_1 \approx 4$.

more rarely push P down to values small enough to favour some second breeders remaining males (equation 4); as expected, the r_2 are most often at or near zero and positive values of r_2 are only associated with very small P (= P^*) values. Since there are very few positive values of r_2, we have not fit correlations, but display the data in Fig. 5. The $P^*/(1 - P)$ axis is truncated at about 6 (and in each case there are many more zero r_2 at the larger abscissa; values not shown). Also, as expected, non-zero r_2 are much rarer in these latter years (contrast Fig. 5 here with figs 10.8 and 10.9 in Charnov, 1982).
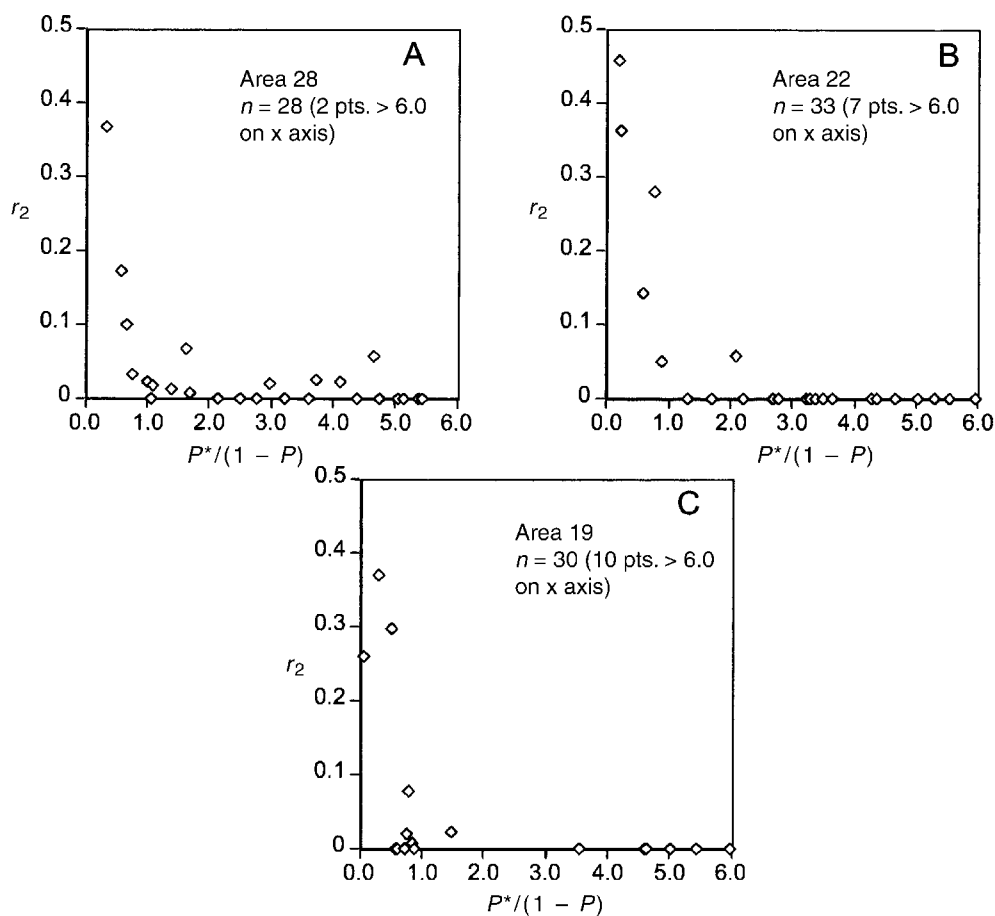
Fig. 5. Proportions of male second breeders (r_2) versus the ratio of first breeders to older breeders ($P*/(1 - P)$). There are many more $r_2 = 0$ points at ever higher abscissa values (>6), as noted on each panel.

CONCLUSION

We display data (Figs 4 and 5) for three of the seven fishery sampling areas (Fig. 3), three areas that more or less correspond to the sampling areas used in Charnov and co-workers' 1978 paper. Data for the four areas not displayed likewise support the theory. We still have no knowledge about the physiological or social mechanisms the shrimp use in 'their decision' to become male or female at the age of first breeding, or to remain males as second breeders. Hannah and Jones (1991) suggest that accelerated sex change (Fig. 4) under increasing P (i.e. increased exploitation) may buffer recruitment and thus somewhat protect the population from overharvesting; of course, facultative sex reversal would have exactly the opposite effect in exploited protogynous (i.e. female-to-male sex change) fishes (Charnov, 1982).

ACKNOWLEDGEMENTS

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