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Fluctuating age distributions and sex ratio tracking in a protandrous shrimp

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ABSTRACT

Question: Do recent sampling data (2001–2019) of the protandrous marine shrimp *Pandalus jordani* show that population sex ratios track population fluctuations [predicted by ESS (evolutionarily stable strategy) theory] as was shown for previous decades (1960s–2000)?

Methods: Oregon Department of Fish and Wildlife biologists sampled the commercial catch to estimate age distribution and sex ratio during each fall breeding period from 2001 through 2019. ESS modelling predicts sex ratio for each of the two breeding-age groups, first and second breeders. Geometric mean regression is used to fit the lines.

Conclusions: The sex ratios tracked population fluctuations during 2001–2019, just as in the previous decades. The theoretical predictions of adaptive (ESS) sex ratios are still strongly supported. The total data sets now cover ~ 50 years and the three locations studied span the entire Oregon coast.

Keywords: ESS, long-term data sets, Pandalid shrimp, recruitment variation, sex-change.

INTRODUCTION

Charnov and colleagues (1978) first showed that the breeding sex ratio of the protandrous shrimp *Pandalus jordani* off the US west coast varied in response to year-to-year fluctuations in the population's age structure for the period of the mid-1960s through 1975. Charnov and Hannah (2002) extended the analysis to the period 1981–2000. The shrimp's life history is abstracted in Fig. 1, which shows a typical protandrous sex changer with discrete age groups and once-yearly reproduction.

The data consist of the sex ratio in the fall breeding period for each of the two adult age groups and the proportion P of the adult population that are first (versus second) breeders. (There are very few third breeders, and these are pooled with the second breeders in our analysis.) The previous analyses showed that the proportion of females ($1 - r_1$) among the first breeders declined to zero with decreasing P ; $1 - r_1$ was ~ 0.5 when strong first breeder recruitment pushed P close to 1 (see also Hannah, 1993). This response was predicted by theory for adaptive

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(ESS) sex ratio (developed below). Data for these early years also showed that when P was small, some older breeding shrimp remained males, a result likewise predicted by theory.

In this paper, we return to sex change in *P. jordani* (off Oregon) and ask if data for the period 2001–2019 continues to support the theory for adaptive sex ratio tracking. Since our test of theory will be semi-quantitative, the next two sections will develop the formal ESS argument (from Charnov *et al.*, 1978; Charnov and Hannah, 2002). Box 1 defines the main parameters and variables used in this paper.

Box 1. Summary of main parameters and variables

- P = proportion of the breeders that are first breeders; also used in $P/(1 - P)$ and $(1 - P)/P$
- $[P/(1 - P)]^*$ or $[(1 - P)/P]^*$ = the P age ratios when used for the *observed* age ratios (eqns. 5 and 6)
- q_1/q_2 = relative catchability of first (q_1) vs. second (q_2) breeders, used in eqns. 5 and 6
- $1 - r_1$ = proportion of first breeders that are female
- r_2 = proportion of second breeders that are male
- W_1 = relative male fertility of second vs. first breeding shrimp
- W_2 = relative female fecundity of second vs. first breeding shrimp
- $W_2/W_1 > 1$ is required for protandrous sex change to be evolutionarily stable

ESS SEX RATIO THEORY

Consider the life history in Fig. 1 and assume two breeding-age (size) groups. Provided growth and survival do not depend upon gender, the best an individual can do is to maximize its reproductive gains when it is a first breeder, and then again when a second breeder. So long as the ESS (evolutionarily stable strategy) sex ratio among the second breeders does not require individuals to change back from female to male, we can model the shrimp (which can change sex only once) as follows.

First breeders are small, whereas second breeders are big. Let P equal the proportion of breeders that are small. Further, let an individual that is big and reproducing as a female have an egg count of W_2 relative to a small female. Big individuals reproducing as males will be given a fertility of W_1 relative to a small male. For male to female sex change (protandry) itself to be evolutionarily stable, we require $W_2 > W_1$.

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 do so. We define fitness as 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) that reproduces as a male with some other probability (\hat{r}_1 for mutant vs. r_1 for typical) may be written as:

$$W_s = \frac{1}{2 \cdot N} \left[\frac{\hat{r}_1}{Pr_1 + r_2W_1(1 - P)} + \frac{1 - \hat{r}_1}{P(1 - r_1) + W_2(1 - P)(1 - r_2)} \right] \tag{1}$$

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

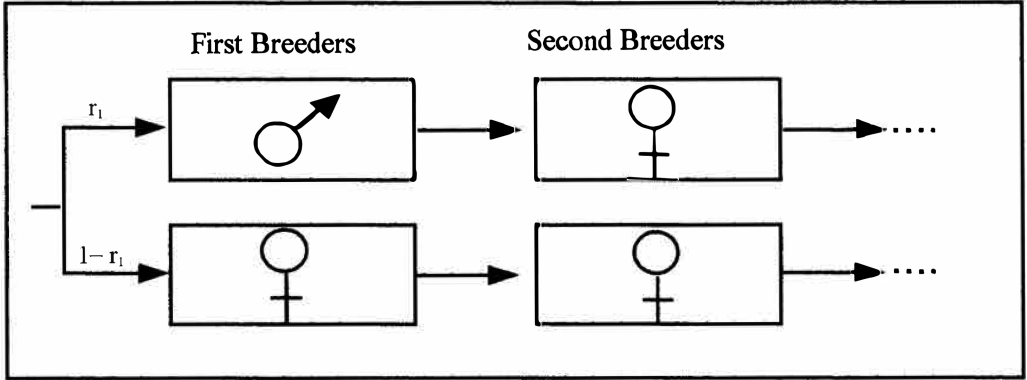


Fig. 1. Pandalid shrimp change sex from male to female as they age (top path), but with only a few breeding-age groups, some first breeders mature as females (lower path). Age structure in *P. jordani* is well approximated by two breeding-age groups. The shrimp breed once a year, in the fall, so second breeders are one year older and much larger than first breeders. ESS theory predicts that the proportion of first breeders that are female ($1 - r_1$) depends upon the ratio of second breeders to first breeders; sometimes some second breeders are predicted to remain male (see Fig. 2 for exact ESS predictions).

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:

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

If the situation is to be evolutionarily stable (at the ESS), it must be that the mutant individual cannot increase its own fitness by altering the probability with which it becomes a male 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 ESS condition; as in much of sex allocation theory (Charnov, 1982), we seek the r_1 and r_2 that maximize the product ($M \times F$).

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

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

and

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

This solution has the characteristics that the sex ratio within a size class depends on the frequency distribution of size classes (P), but more than 50% of the small shrimp should be males, whereas more than 50% of the big shrimp should be females. Figures 2A and 2B are plots of equations (3) and (4) for a typical case: $W_1 = 1$ and $W_2 = 2$. Figure 2C plots both ESS sex ratios as a function

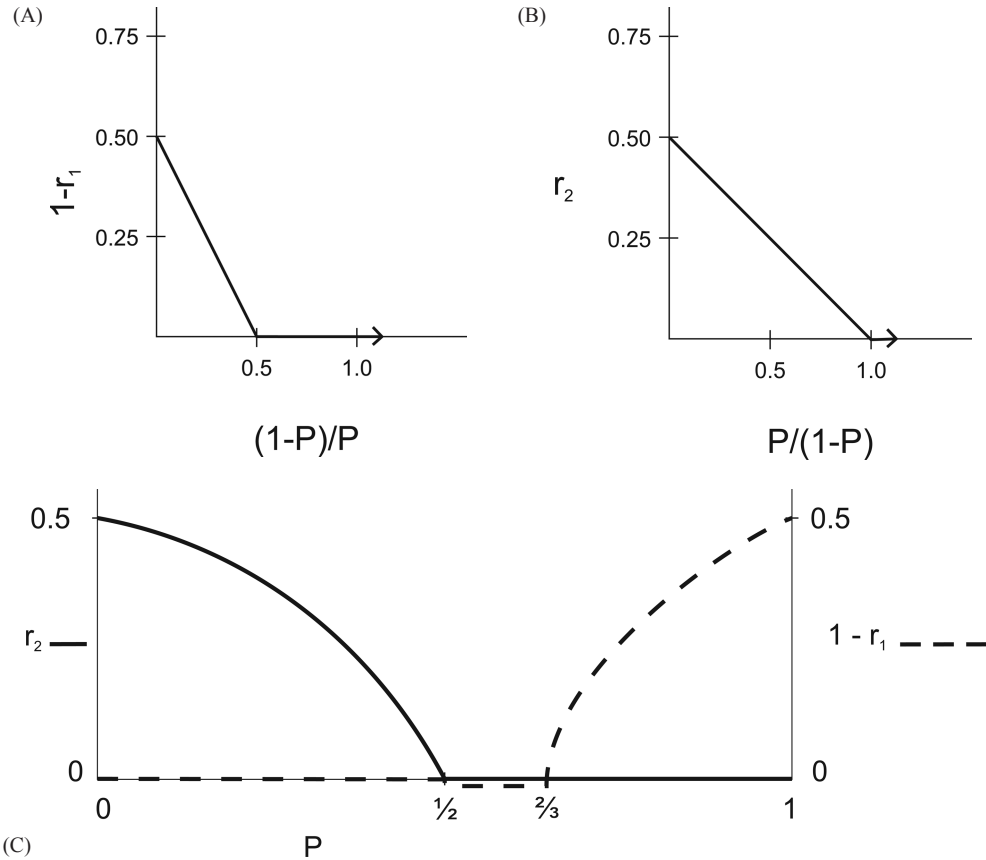


Fig. 2. ESS sex ratios within an age group ($1 - r_1$ and r_2) depend upon the ratio in numbers of the two breeding-age groups; $P =$ proportion that are first breeders. These three panels illustrate equations (3) and (4) from the text. The panels assume relative fertility ratios of $W_1 = 1$ and $W_2 = 2$ but the shape is general for any $W_2 > W_1$. (A) The proportion of first breeders that are female ($1 - r_1$) is near 0.5 when P is large, and declines to zero as P gets smaller; it is graphed against the $(1 - P)/P$ age ratio to make the prediction linear. It remains 0 after it hits the x-axis at $1/W_2$, which is $1/2$ in this illustration. (B) The proportion of second breeders that are male (r_2) is near 0.5 when P is small and declines to zero as P gets larger; it is graphed against $P/(1 - P)$ to make the prediction linear. It remains zero after it hits the x-axis at W_1 , which is 1 in this illustration. Panel (C) shows $1 - r_1$ and r_2 as a function of P . The functions are non-linear but somewhat easier to visualize compared to panels (A) and (B). Notice that one sex ratio can be positive (> 0) only if the other equals zero.

of P . The advantage of plots 2A and 2B for data analysis is their linearity. But plot 2C makes it easy to visualize how the sex ratios change as P sweeps from 0 to 1. The captions to Figs. 2A and 2B also discuss the numeric rules about where on their respective x-axes r_2 and $1 - r_1$ become 0.

One other theoretical relation is worth noting with reference to Fig. 2C. Positive values of $1 - r_1$ are predicted to be associated always with zero values of r_2 , and positive values of r_2 are associated always with zero values of $1 - r_1$. The positive sex ratios are bounded by 0.5. Both sex ratios will be zero over a range of intermediate P values.

BIAS IN THE ESTIMATE OF P

Our data consist of shrimp sampled from the commercial catch during the fall breeding seasons; we analysed sex and size/age composition for the period 2001–2019. 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. Define $q_2 N_2/q_1 N_1$ as $[(1 - P)/P]^*$, then $(1 - P)/P = (q_1/q_2) [(1 - P)/P]^*$. (The asterisk indicates the biased *observed* ratio.)

The ESS equation (eqn. 3) for the proportion of first breeders that are female ($1 - r_1$) can be rewritten as:

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

The relative fecundity of second versus first breeders (W_2) is about 2.5 (Hannah *et al.*, 1995) and $q_1/q_2 < 1$.

The equation for the proportion of second breeders that are male (eqn. 4) will be rewritten:

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

These new ESS equations in terms of $[(1 - P)/P]^*$ and $[P/(1 - P)]^*$ simply change the slope of the predicted sex-ratio/age-ratio relation; i.e. for females among the first breeders, the slope changes from $-W_2/2$ to $-(W_2/2)(q_1/q_2)$. Both lines still begin at $1/2$. So, the general forms shown in Figs. 2A and 2B apply here also. Thus to change from 2A or 2B, simply change the x-axes $[(1 - P)/P]^*$ and $[P/(1 - P)]^*$, respectively. Of course, both sex ratios remain zero after they reach their respective x-axes.

One other prediction is worth noting. Let X_1^* and X_2^* be the intercepts of the $1 - r_1$ and r_2 lines on their respective x-axes (i.e. solve eqns. 5 and 6 = 0); the theoretical product is $X_1^* X_2^* = W_1/W_2$, which does not depend upon the q_1/q_2 ratio. Since $W_1 < W_2$, an upper bound on the product is 1; thus $X_1^* X_2^*$ must be < 1 . If one intercept is > 1 , the other must be < 1 . For example, if one is 2, the other must be $< 1/2$. The W_1/W_2 ratio controls the relative positions of the descending $1 - r_1$ and r_2 lines; if one is shallow, the other must be steep because both begin at 0.50. We don't know the W_1/W_2 ratio for the shrimp, so $X_1^* X_2^* < 1$ is a qualitative prediction. It is worth testing whenever one intercept is much greater than 1; such a large value should be associated with a large displacement downward of the other line.

RESULTS

We test three aspects of the ESS sex ratios.

Prediction #1: We ask if r_2 and $1 - r_1$ show the expected descending (and zero) relations (eqns. 5 and 6; Figs. 2A and 2B) when plotted against their appropriate age ratios for the 2001–2019 time period. Then we pool the data with the former time period (1981–2000) to produce summary graphs of 39 years' duration. We do this for three separate locations off the Oregon coast.

Prediction #2: We ask if the r_2 and $1 - r_1$ descending relations (non-zero parts of eqns. 5 and 6) are appropriately positioned *with respect to each other*: do their intercepts on the respective x-axes (X_2^* and X_1^*) satisfy the $X_1^*X_2^* < 1$ rule, at least qualitatively?

Prediction #3: We ask if a plot of $1 - r_1$ and r_2 satisfies the prediction (Fig. 2C) that one is positive *only* when the other is zero. (Both can be zero at the same time.)

Shrimp sex change 2001–2019 compared with 1981–2000 (test of prediction #1, eqns. 5 and 6)

Figure 3 shows the Oregon coast sampling areas. We analysed the same three areas (28, 22, and 18/19) that were sampled previously (in 1981–2000). Our data are from the fall spawning period (September/October) and come from the commercial catch.

Figure 4 shows the data for females among the first breeders ($1 - r_1$) versus the age ratio second-breeders/first-breeders, $[(1 - P)/P]^*$. In all three cases, the female proportion declines from near $\frac{1}{2}$ to zero. In each case, there are a few zero data points at even higher age ratios (indicated on graphs as not plotted). Since there is error on both the x- and y-axes, we show

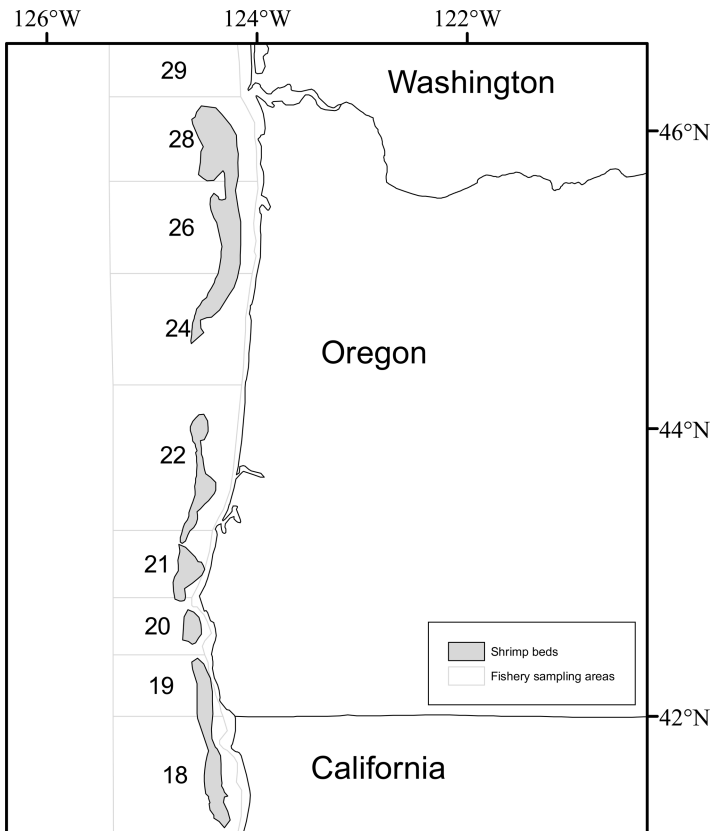


Fig. 3. The fishery sampling areas on the US west coast.

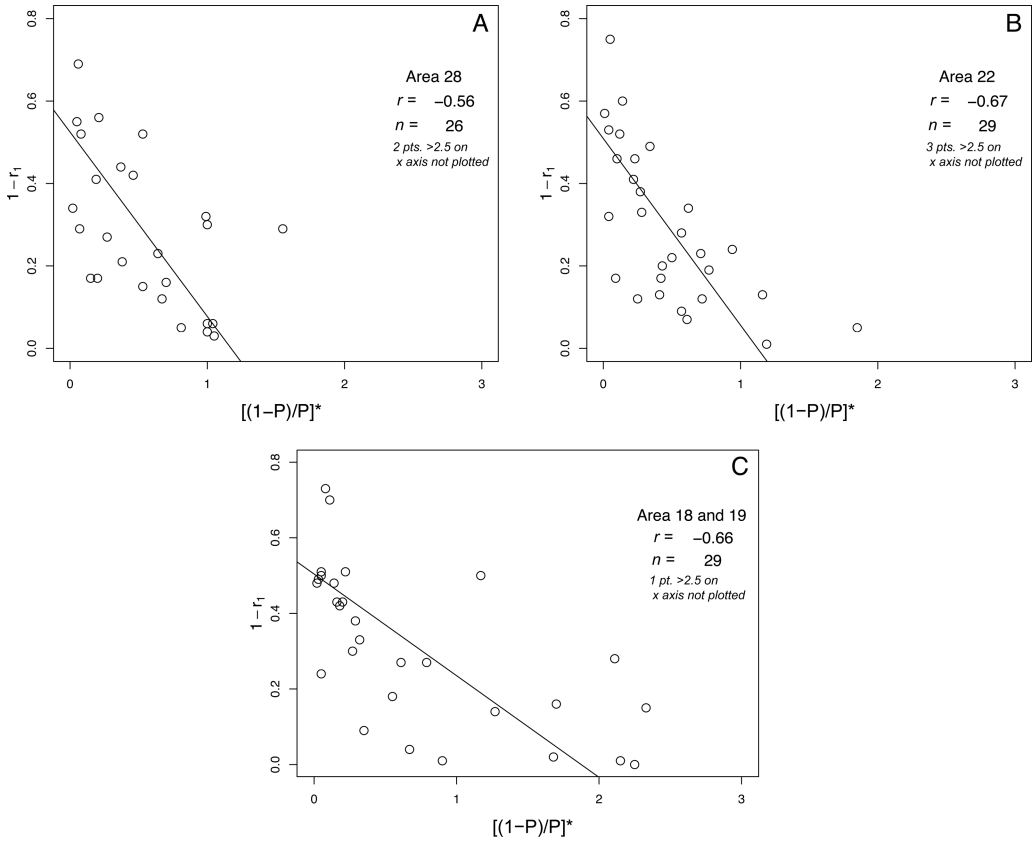


Fig. 4. The proportion of first breeders that are female ($1 - r_1$) versus the ratio of older breeders to first breeders from samples of the commercial catch of *P. jordani* from areas 18/19, 22, and 28 for the months of September and October, 2001–2019 (see Fig. 3 for catch areas). When available, we treated the two months each year as separate estimates, which is why $N > 19$. Transitional shrimp were considered to be functionally female, since they will breed as females that year. A few zero points at $X > 2.5$ are not plotted, nor included in regression (the number is indicated on each panel). The lines were fitted with geometric mean [also called reduced major axis or standard major axis (Ricker, 1973)] regressions, because there is error on both axes. All correlations were significant at probabilities < 0.001 . The 95% confidence intervals for the Y -intercepts always include 0.50. See text for discussion of these plots *vis-à-vis* theory. These plots test equation (5), prediction #1 from the Results section.

the geometric mean [also called reduced major axis or standard major axis (Ricker, 1973)] regression lines for the range of positive Y -values (i.e. $X < 2.5$). All are highly significant (prob. < 0.001) and the 95% confidence intervals for the X -intercepts include 0.50. In Fig. 5 we have added the earlier data [1981–2000 (Charnov and Hannah, 2002)] to the 2001–2019 data; the fitted lines are almost identical to those of Fig. 4 and the correlations are slightly larger (because the sample size is double). These plots are the form predicted by equation (5).

Figure 6 shows the three area plots of males among the second breeders (r_2) versus the age ratio of first to second breeders, $[P/(1 - P)]^*$, for the 2001–2019 time period. The x -axis is truncated at 6, and there are many zero points above 6 not shown (see panels for counts). We

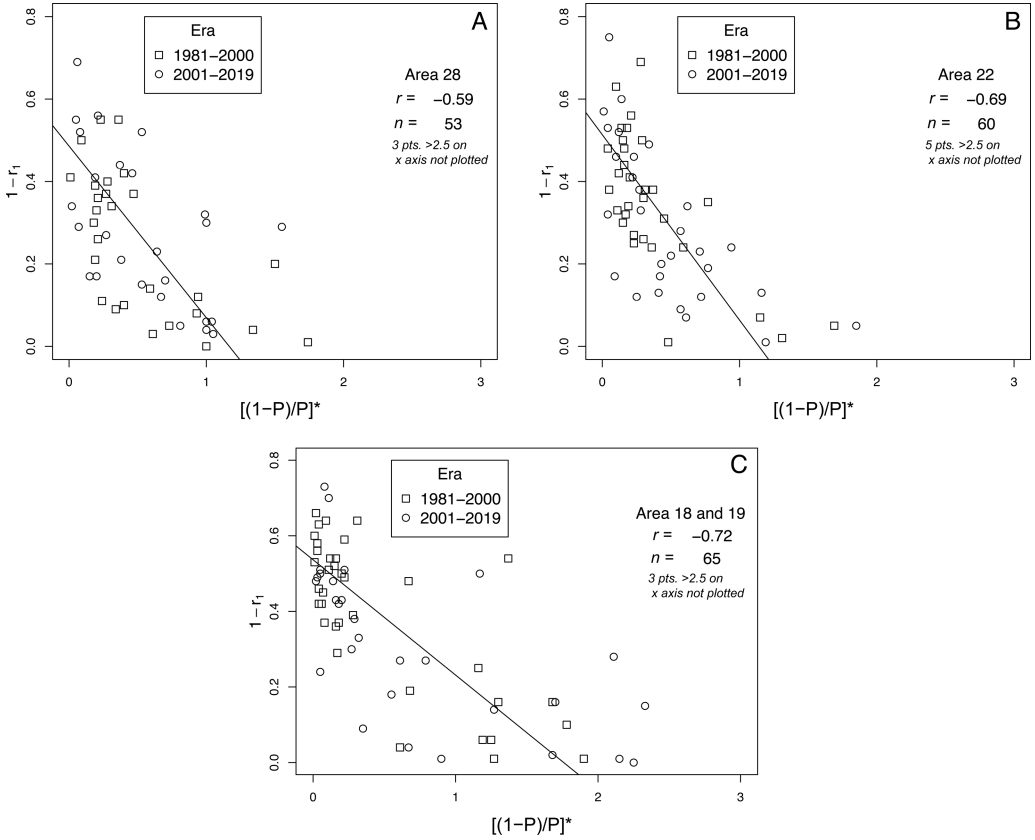


Fig. 5. The earlier data (1981–2000) for the proportion of first breeders that were female is added to the data from Fig. 4. The results are the same as Fig. 4, with double the sample size.

did not fit lines to these data because clearly the non-zero r_2 -values are associated with small X -values and larger X -values give only zeros. The small number of non-zero points provides little confidence in any fitted line. This pattern of positive values at small X and zero values at larger X is exactly the same as shown by data from the earlier time periods.

In Fig. 7 we add the 1981–2000 data to provide a summary of the entire 39 years for each of the three areas. A majority of r_2 -values are zero. Only about 15% of the r_2 -values are > 0.10, and about 5% are above 0.30. Males among the second breeders are rare or absent in most years. These plots follow the form predicted by equation (6).

Are the $1 - r_1$ and r_2 descending relations in the correct places with respect to each other? (test of prediction #2)

Recall the theoretical rule: the product of the respective X -intercepts of the descending sex ratio lines will be < 1. Since we only fit lines to the $1 - r_1$ data, we focus on the three areas in Fig. 5. Two of the three intercepts are near 1 and thus the corresponding r_2 data are not necessarily predicted to be displaced downward very much from the $1 - r_1$ data. Area 18/19 is different in that

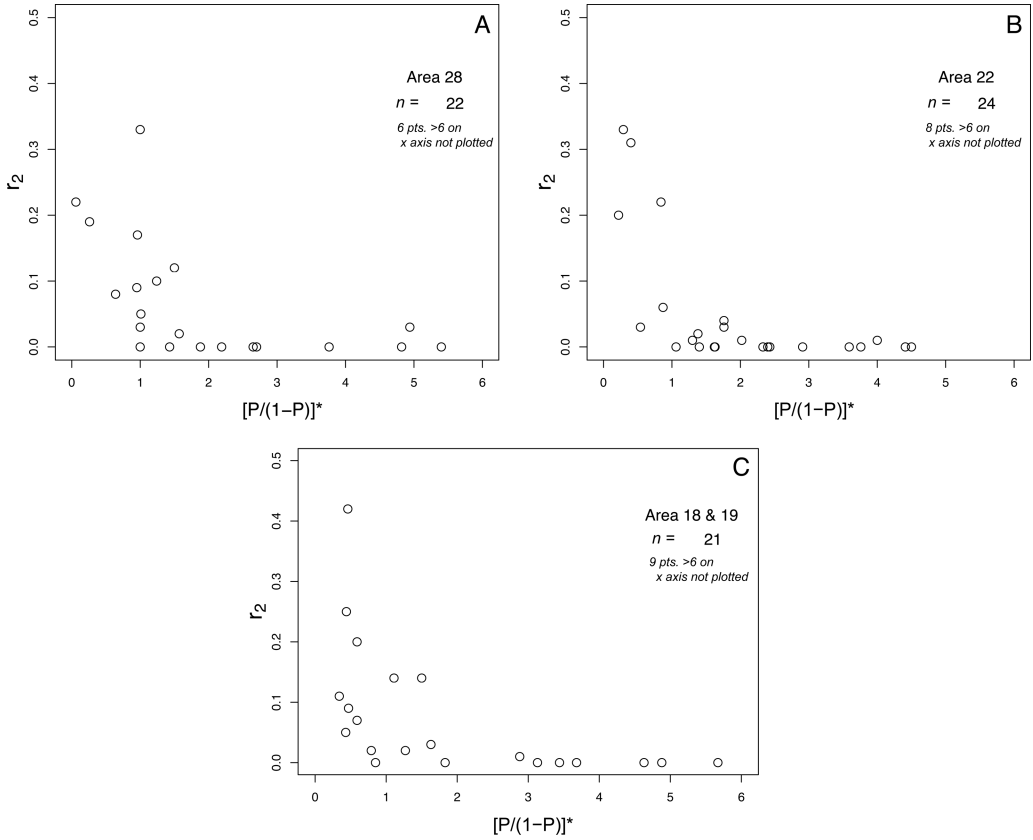


Fig. 6. The proportion of second breeders that are male (r_2) versus the ratio of first breeders to older breeders for the three sampling areas, for the period 2001–2019. There are many more $r_2 = 0$ points at even higher X -values (> 6), as noted on each panel. See text for discussion of these plots *vis-à-vis* theory. These plots test equation (6), prediction #1 from the Results section.

the $1 - r_1$ X -intercept is near 1.8, so that the r_2 intercept should be $< 1/1.8 \sim 0.55$. Thus, for area 18/19 the r_2 data are predicted to lie below the $1 - r_1$ data if the two sex ratios are plotted with respect to *their appropriate age ratios on the same graph*. Figure 8 shows such a plot. It is clear that at any fixed age ratio (x -axis value), most of the $1 - r_1$ data points lie above the r_2 data points, and r_2 becomes zero at much smaller age ratios. This is qualitatively what the $X_1^* X_2^* < 1$ rule predicts.

1 - r_1 versus r_2 ? (test of prediction #3)

There is one other informative way to view the sex ratio data. A plot of $1 - r_1$ versus r_2 is predicted to have all the positive $1 - r_1$ values associated with $r_2 = 0$, and all the positive r_2 values associated with $1 - r_1 = 0$ (Fig. 2C). It is perhaps unrealistic to require that the estimated sex ratios be exactly zero, but they should be very small if theory is correct. Figure 9 shows our result plotted for all data where $r_2 > 0$. (In Fig. 9 we omitted data where r_2 exactly equals 0. These are a majority of the data points and simply span the entire range of $1 - r_1$ values, so they support theory but are

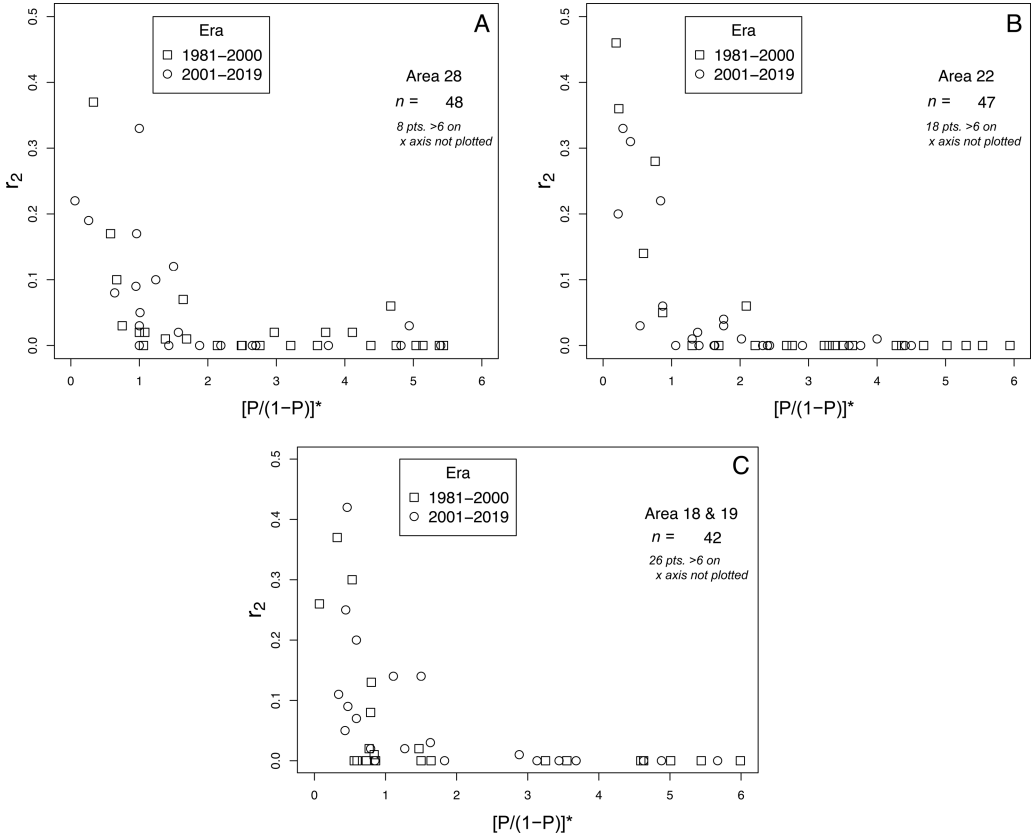


Fig. 7. Proportion of second breeders that are male versus the ratio of first breeders to older breeders for the periods 1981–2000 and 1981–2019 combined.

relatively uninformative.) Our interest is whether large positive sex ratios ever occur together, the result forbidden by theory. The dotted lines are sex ratios of 0.05, and we take a sex ratio < 0.05 as effectively zero. The theory is strongly supported, as almost all the data fall inside the two 0.05 bounds. Notice particularly that all the higher r_2 points are on (or very near) the $1 - r_1 = 0$ line.

SUMMARY AND DISCUSSION

General theoretical themes (and do we know how the shrimp do it?)

The recent and extended data sets strongly support adaptive sex ratio theory [for general overviews of adaptive sex ratios, see Charnov (1982) and West (2010)]. The sex ratios appear driven by the fluctuating age distribution, measured by P . The general theoretical predictions are illustrated in Fig. 2C. Age-specific sex ratio plots versus the appropriate age ratios are the right form (eqns. 5 and 6 tested in Figs. 4–7). We test the predicted relative position of the two descending sex ratio curves in one data set, area 18/19, and find that they correspond to theory, at least qualitatively (Fig. 8). Finally, the age-specific sex ratios are correct when plotted against each other, under the assumption that sex ratios < 0.05 are effectively zero (theoretical Fig. 2C, tested in Fig. 9).

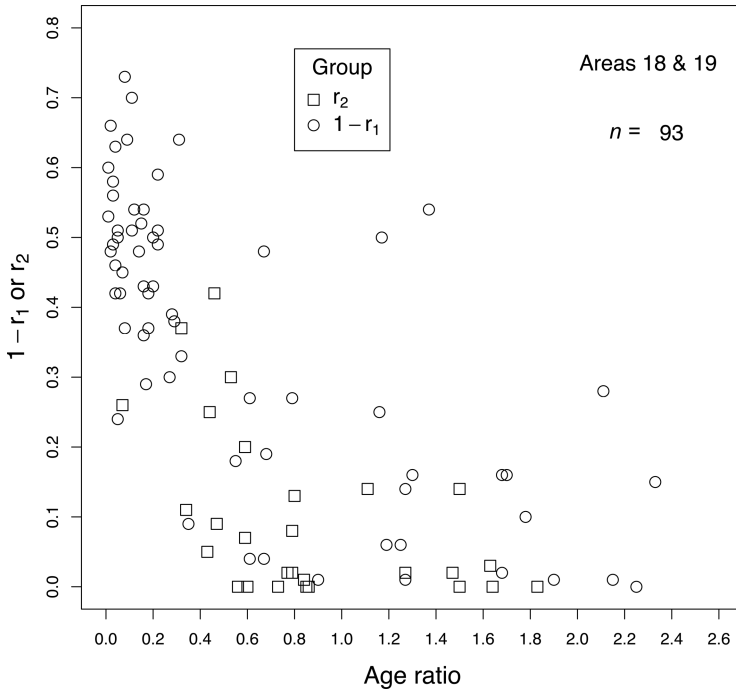


Fig. 8. We plot r_2 and $1 - r_1$ versus their appropriate age ratios for area 18/19. See text for theory and argument for why the $1 - r_1$ data should fall above the r_2 data for this particular location. This plot tests prediction #2 from the Results section.

The data from the still earlier period [mid 1960s–1975 (Charnov *et al.*, 1978)] also support the predictions of Figs. 2A and 2B, transformed into equations (5) and (6). We have not added them to our summary graphs, however, because the fishing gear and (some) sampling methods changed from this earlier era.

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 male as second breeders. Our analysis is at a very large spatial scale because the samples come from the commercial catch, and it seems likely that the scale for decision-making by the shrimp is much smaller. Thus, we are lumping over many smaller units; perhaps this is why small positive sex ratios are sometimes observed when zero is predicted for the aggregated age ratio? It is clearly very difficult to study the details of the mating system and local age structure of a marine shrimp in deeper waters. One shallow water Pandalid has been studied intensively and shows experimental evidence for a plastic sex change response to fluctuating age structure, among other effects (Chiba *et al.*, 2013). For an overview of life history and mating systems in Caridean shrimp, including sex change, see Bauer (2004), whose own work provides fine-scale studies of several other shallow water species. A general overview of plasticity of sex in sex-changing animals is Munday *et al.* (2006).

Practical applications

There are clear population dynamic implications for this adaptive response. Hannah and Jones (1991) suggest that accelerated sex change (Figs. 4 and 5) under increasing P (driven by increased

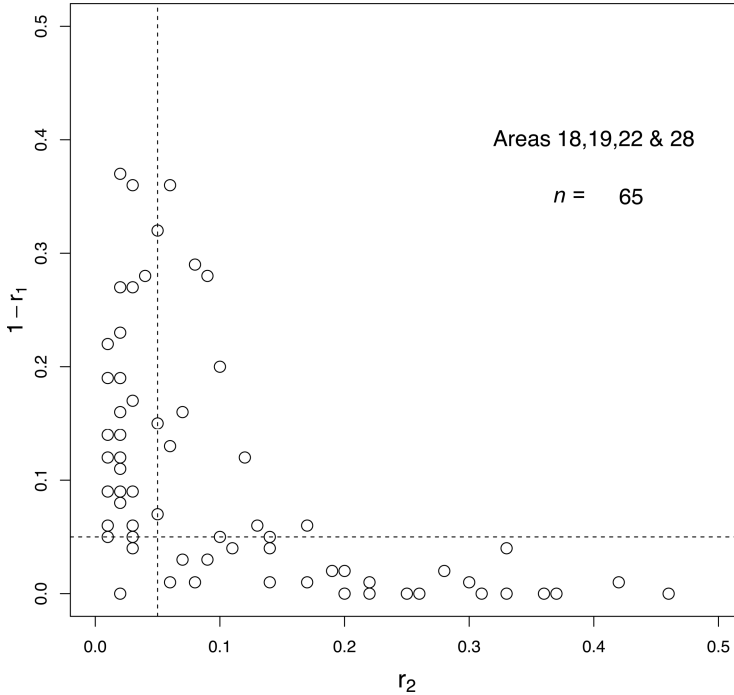


Fig. 9. The proportion of first breeders that are female ($1 - r_1$) versus the proportion of second breeders that are male (r_2) for years where $r_2 > 0$. (Recall that most $r_2 = 0$.) The dotted lines are where the sex ratios are 0.05, and we consider a sex ratio < 0.05 as effectively zero. Theory predicts that all sex ratios should fall inside the 0.05 lines. (See text and Fig. 2C for theory development.) This plot tests prediction #3 from the Results section.

exploitation) may buffer recruitment, and thus somewhat protect the population from overharvesting. And the population age structure for *P. jordani* off the Oregon coast has 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 has increased from $\sim 30\%$ to $\sim 70\%$. As theoretically predicted (eqn. 5, or Fig. 2C), this increase in P over time has been matched by a general increase in the proportion of females among the first breeders, particularly since 1979 [see, for example, figure 9 of Hannah and Jones (1991)]. It is intriguing that the shrimp treat the presence of more first breeders caused by increased fishing pressure similarly to the natural fluctuations in age structure which sometimes result in more first breeders. Groth and Hannah (2018) provide a detailed discussion of the effects of fishing and the environment on the population structure and recruitment for Oregon *P. jordani* through 2017.

Oregon's *P. jordani* is managed as a sustainable fishery and was the world's first shrimp fishery to be certified 'sustainable' by the Marine Stewardship Council (MSC) in 2005, and has been recertified twice since (see MSC, 2015). The Oregon Department of Fish and Wildlife maintains a website devoted to *P. jordani*, its biology and fishery (see ODFW, n.d.).

DATA ACCESSIBILITY

The data and r scripts that made the figures used in this paper are available at the Oregon Department of Fish and Wildlife Data Clearinghouse: <https://nrmp.dfw.state.or.us/DataClearinghouse/default.aspx?p=202&XMLname=41866.xml>

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Jim Bull read and improved the paper. The desktop publishing and editing skills of Anne Rice made this paper possible, and E.L.C. thanks her for collaboration over the last 22 years. Finally, Julia Laylander's keen editorial eye fixed, well, almost everything in the text.

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