Consequences of Sex Change for Effective Population Size

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short title: Sex change and N_e

November 2018

Abstract

Sequential hermaphroditism, where males change to females (protandry) or the reverse (protogyny), is widespread in animals and plants and can be an Evolutionarily Stable Strategy (ESS) if fecundity rises faster with age in the second sex. Sequential hermaphrodites also generally have sex ratios skewed toward the initial sex, and standard theory based on fixed sexes indicates that this should reduce effective population size (N_e) and increase deleterious effects of genetic drift. We show that despite having skewed sex ratios, populations that change sex at the ESS age do not have reduced N_e compared to fixed-sex populations with an even sex ratio. This implies that the ability of individuals to operate as both male and female allows the population to avoid some evolutionary constraints imposed by fixed sexes. Furthermore, N_e would be maximized if sex change occurred at a different (generally earlier) age than is selected for at the individual level, which suggests a potential conflict between individual and group selection. We also develop a novel method to quantify the strength of selection for sex reversal.

Introduction

Sequential hermaphroditism, a reproductive strategy in which individuals operate first as males and later as females (protandry) or the reverse (protogyny), is widespread in nature. Sex reversal is found in over a dozen invertebrate phyla, including corals, sponges, molluscs, annelids, echinoderms, and (alone among arthropods) crustaceans; in plants, simultaneous hermaphrodites are more common, but species that change sex occur in all major groups (*1*-*3*). Among vertebrates, this strategy is restricted to teleost fishes, but within that group it occurs in at least 27 families (*4*-*8*).

What causes species to adopt this strategy? Most explanations involve some form of the size-advantage model: sex-reversal can be favored when an individual can reproduce more effectively as one sex when small and the other sex when large (*9*, *10*). Regular sex reversal has only been reported in species with indeterminate growth (*1*), so size and age are positively correlated. Therefore, a general requirement for sequential hermaphroditism to evolve is that age-specific fecundity patterns of males and females must differ, with the direction of change being toward the sex for which fecundity increases faster with age. For any given set of age- and sex-specific vital rates that satisfy this condition, it is possible to identify an age at sex change (τ) that represents an Evolutionarily Stable Strategy (ESS), in the sense that no individual would have a selective advantage by changing sex at a different age (*11, 12*). At the ESS age (τ), an individual is indifferent regarding which sex it reproduces as.

Although sequential hermaphroditism occurs in many diverse taxa, it is not as common as might be expected based on species' life histories. Physiological and behavioral costs can reduce or negate potential selective advantages in some species (*1*, *13*), but these costs alone do not appear to be strong enough to provide a general explanation for why more species do not change sex (*14*). An additional potential cost of sex reversal exists at the population level: sequential hermaphrodites typically have sex ratios skewed toward the initial sex, sometimes exceeding 10:1 (*4, 11, 15*). A well-known consequence of skewed sex ratio is reduction of effective population size, N_e (*16*), which in turn reduces the effectiveness of natural selection and leads to higher rates of genetic drift, inbreeding, and loss of genetic variability (*17*). Although some potential consequences of sex reversal for N_e have been noted (*7, 18, 19*), costs have not been evaluated quantitatively in the ESS context. Is it possible that evolutionary drag, in terms of increased genetic drift, has limited the number of species that can support viable sex-changing populations? Wright's (*16*) sex-ratio adjustment for N_e assumed discrete generations and fixed sexes (gonochorism). This theory cannot be applied directly to sequential hermaphrodites, because it is necessary to account for 1) effects of iteroparity and overlapping generations, and 2) the fact that individuals can reproduce as both sexes.

Here, we apply a recently-developed (*20*) eco-evolutionary model to synthetic and empirical data for sequential hermaphrodites to address the following questions:

1. If a population changes sex at the ESS age (τ), is N_e reduced compared to a species that has the same vital rates but does not change sex? If so, it implies an evolutionary cost to populations that adopt sex-change strategies that has not been formally accounted for.
2. Could the population achieve a higher N_e by changing sex at a different age than τ?
3. Can these results be predicted based on the population's vital rates?

Results

Datasets. We constructed 10 hypothetical "species" having different pairs of male-female fecundity schedules (Tables 1-2). In each pairwise comparison, fecundity rises faster with age in the second sex, which would be expected to promote sex change (Table 2). We supplemented the synthetic datasets with empirical data for 8 marine fish species—four protandrous and four protogynous hermaphrodites (Table 3). In these species, female fecundity increases roughly linearly with age (Fig. 1A,B). Because empirical data for males are lacking, we chose generic male fecundity patterns such that fecundity increases faster with age in males for protogyny (Fig. 1C) and fecundity increases more slowly with age in males for protandry (Fig. 1D).

An Index of Selection. Paired equations describing the relative age-specific fitness of males and females are called fitness sets and involve functions of survival and fecundity and the age-specific sex ratios (see Methods for details). Let R_1 (R_2) represent expected fitness of an individual operating as the first sex (second sex). For each potential age at sex change T, the pair of values $R_{1(\mathrm{T})}$, $R_{2(\mathrm{T})}$ represents expected lifetime reproductive success from operating as the first and second sex, respectively. Each pair of values describes a point in Cartesian space, and the series of points generated by considering a range of values of T describes a curve as illustrated in Fig. 2. The dotted line for $R_1+R_2=1$ represents a zone of indifference, in which there is no net gain or loss from changing sex. Charnov (*11, 21*) showed that sex reversal is favored by natural selection only if the plot forms a convex curve, as illustrated in Fig. 2.

The architecture of Fig. 2 suggests a novel index of the strength of selection for sex reversal, which is favored to the extent that the curve bulges out from the $R_1+R_2=1$ line. This can be quantified as the area X that lies under the curve defined by the fitness sets and above the line of indifference. Because of the 0-1 standardization (see Methods), neither R_1 nor R_2 can exceed unity, so the maximum possible value for X is one-half of a 1x1 square, or 0.5 units. It follows that $I=X/0.5=2X$ is an index of the relative strength of selection for sex reversal. This is analogous to the Gini Index used in conjunction with the Lorenz Curve to quantify the extent of income inequality (*22*).

Sex Change and Effective Population Size. Selection indices for the 10 comparisons involving hypothetical data ranged from I=0.07 for comparison GA to 0.53 for comparison AE (Table 2; Fig. 2B). The latter comparison is probably extreme as it assumes that fecundity increases with the square of age in the second sex. ESS ages at sex change ranged from τ=3.5 to 6.5, or about 1/3 to a bit over half of the maximum lifespan. Later ages at sex change produced more skewed adult sex ratios (78% initial sex for scenarios CE and CD, for which τ=6.5). For three scenarios (AF, BC, FC), effective population size at the ESS age at sex change (N_{eESS}) was within 1% of what it would be for a gonochoristic population with equal sex ratio (N_{eG}), and for the remaining scenarios N_{eESS} was 2-9% higher than it would have been without sex change (Table 2). In every scenario, the maximum N_e possible with sex change (N_{eMax}) occurred at an earlier age than τ, which means that N_{eESS} was less than it could have been if sex change had occurred at an earlier age. This effect was rather modest in the synthetic datasets, ranging from less than 1% reduction for 5 scenarios to 4% reduction for scenarios CE and CD.

Using empirical data, selection indices were all lower (0.060-0.087) for the protandrous marine fishes than for the protogynous species, where they ranged from 0.158 (black seabream) to 0.290 (sheephead). ESS ages at sex change occurred at roughly half (range 41-64%) of the maximum lifespan (Table 3). In all 8 species, the mean age at sex change reported in the literature (T) was essentially equal to or less than the ESS age; the ratio T/τ ranged from 0.84 to 1.02 for the protandrous species and from 0.71 to 0.91 for the protogynous species.

Consequences for effective size in the marine fishes were qualitatively similar to those for the synthetic datasets, but effects were generally larger in magnitude (Table 3). Sex change had almost no effect on N_e in the protandrous species compared to what it would have been with fixed sexes (range of N_{eESS}/N_{eG}=0.99-1.02); in the protogynous species, sex change at the ESS age increased N_e by 1% (black seabream) to 4% (sheephead). The most striking difference compared to the synthetic datasets involved the relationship between N_{eESS} and maximum possible effective size. N_{eESS}/N_{eMax} was never lower than 0.96 in the synthetic datasets, but in 5 of the 8 marine fishes it was below 0.9, including 0.75 in pandora and 0.70 in sheephead. This means that N_e in sheephead could be increased by more than 40% above N_{eESS} if sex change occurred earlier; in pandora, the increase could be over 30%. Age at sex change that would produce the maximum N_e (A) was 8.8 years earlier than τ for sheephead (Fig. 3) and 6.9 years earlier for pandora, but only 1.4 years earlier in the slinger and gilt-headed seabream.

Assuming sex change at age τ, adult sex ratios would be heavily skewed toward the initial sex in all species (from almost 2:1 in gilt-headed seabream to 9:1 in sheephead and pandora; Table 3). In spite of these uneven sex ratios, N_e for populations that change sex at age τ are consistently as high or higher than they would be for populations with an equal sex ratio that do not change sex. This effect can be quantified by comparing N_{eESS} to what N_e would be in a gonochoristic population that has an adult sex ratio equal to that in the sex-changing population; we denote this effective size as N_{eG^*}. We calculated (*20*) N_{eG^*} assuming that sex ratio at birth for the gonorchoristic population was as specified in Table 3. If a sheephead population changes sex at age τ=15.7 years, the adult sex ratio would be 90% female, but N_{eESS} would still be 3.6% higher than for a gonochoristic population with equal sex ratio. If the gonochoristic population had a similarly-skewed sex ratio, its effective size (N_{eG^*}) would only be 30% that of the even-sex-ratio population (Fig. 3). Thus, N_{eESS} in sheephead is 1.036/0.3=3.45 times as high as would occur in a gonochoristic population with a similarly-skewed sex ratio. This is termed the "N_e bonus" in Tables 2 and 3. For the protandrous barramundi (SI Appendix Fig. S6), the bonus is smaller but still not trivial: N_{eESS}/N_{eG^*}=1.27, representing a 27% N_e bonus from sex change. Except for the slinger, the N_e bonus is higher in the protogynous species.

Across all 18 synthetic and real species, the ratio N_{eESS}/N_{eG} was positively and highly-significantly correlated with the selection index (Fig. 4; r=0.87; two-tailed P<0.001), indicating that species with higher selection indices experienced larger increases in N_e compared to gonochoristic species having the same vital rates. In contrast, the ratio N_{eESS}/N_{eMax}, which quantifies the degree to which changing sex at the ESS age sacrifices what could be even higher N_e by changing sex earlier, is negatively correlated with the adult sex ratio (r=-0.79, two-tailed P<0.001; SI Appendix Fig. S7). Across the eight marine fishes, we found a nearly 1:1 relationship ($r = 0.94$; $P < 0.001$) between the age at sex change that produces maximum N_e (N_{eMax}) and the age at sex change that produces an equal adult sex ratio (Fig. S8).

Sensitivity analyses (see SI Appendix for details) produced the following results: a) if some individuals begin life as the terminal sex and/or others reach maximum age without changing sex, adult sex ratio is less skewed, I declines, and the ratios N_{eESS}/N_{eG} and N_{eESS}/N_{eMax} both converge toward 1.0 (SI Appendix Fig. S3); b) if longevity is allowed to increase while maintaining the functional relationship between male and female fecundity, adult sex ratio becomes more skewed, I increases, and N_{eESS}/N_{eMax} declines, but there is little effect on N_{eESS}/N_{eG} (SI Appendix Fig. S4); c) if individuals of the same age and sex have overdispersed variance in reproductive success, there is little effect on N_{eESS}/N_{eG}, but maximum N_e is reduced so N_{eESS}/N_{eMax} converges on 1.0 (SI Appendix Fig. S5); d) if survival rates are different for males and females, higher survival in the second sex increases the evolutionary pressure for sex change, while lower survival in the second sex reduces or eliminates the selective advantage of sex change (SI Appendix Table S1).

Discussion

Three major themes emerge from consideration of the above results. First, contrary to expectations based on standard evolutionary theory, sex change does not have to incur an evolutionary cost in terms of increased genetic drift, even when it leads to highly skewed adult sex ratios. In each of the synthetic or real "species," effective population size at the ESS age at sex change was essentially the same or a bit larger than would occur in a non-sex-changing population having the same vital rates and an equal sex ratio. The strong positive correlation between N_{eESS}/N_{eG} and I (Fig. 4) suggests that the latter can be useful for predicting the consequences of sex change for N_e. Furthermore, we demonstrate that sex change confers a "N_e bonus" on a population by allowing effective size to be larger that it would be in a gonochoristic population that has the same degree of sex-ratio skew. This effect can be substantial (Fig. 3): in 3 of 4 protogynous species, N_e at ESS age at sex change was more than twice what it would be in a population that does not change sex and has the same skewed sex ratio.

How can sequential hermaphrodites escape some of the best-known evolutionary consequences of a biased sex ratio? In all diploid species, half the genes in offspring must come from male parents and half from female parents. If the adult sex ratio is skewed, an inevitable consequence is that members of the less numerous sex produce more offspring per parent. For example, with female sheephead making up almost 90% of the adult population, in every reproductive season the average male will produce about 9 times as many offspring as the average female. Under Wright's (*16*) model, which assumes that generations are discrete and sexes are fixed, the relatively few members of the less-numerous sex can be thought of as a bottleneck through which half the genes for the next generation must pass, and this bottleneck is what reduces N_e. But in sequential hermaphrodites, members of the less-numerous (generally terminal) sex do not represent a small, fixed number of individuals; instead, they all have already had an opportunity to reproduce as the initial sex in previous years. Furthermore, many members of the terminal sex will only recently have changed sex, and none will have had an entire lifetime performing as the rare sex. These factors considerably constrain the ability of a small number of individuals to persistently dominate reproduction, and they tend to equalize lifetime reproductive success among individuals in the population. This "N_e bonus," which our analyses show can be quite substantial, represents an under-appreciated evolutionary consequence of sex reversal.

A second theme is that although sex change at the ESS age is optimal from the perspective of individual fitness, it is not optimal at the population level because genetic drift could be reduced even further if sex reversal occurred at a different age. In the synthetic and real species the age that produces N_{eMax} was always earlier than τ, but sensitivity analyses showed that in some scenarios with $\phi>1$, the age that produces N_{eMax} could be later than τ. The effect involving N_{eMax} is not trivial: a population with vital rates like sheephead as modeled here could increase N_e by over 40% by changing sex earlier than the ESS age. This increase can be accomplished because changing sex at an earlier age produces a more even adult sex ratio (Fig. S8). Thus, although the N_e bonus allows sex-changing species to avoid some of the evolutionary costs of skewed sex ratios that gonochoristic populations experience, uneven sex ratios nevertheless do generally reduce N_e somewhat compared to what it could be if adult sex ratio were 1:1.

This result implies a general opportunity cost to sex-changing populations in terms of foregone benefits that could have been achieved by changing sex at a different age. This in turn implies a potential conflict between selection at the individual level and population level favoring different reproductive strategies. For 6 of the 8 marine fishes, the empirical estimate of mean age at sex change is earlier than the ESS age (Table 3), which is in the direction that should increase N_e. Thus there appears to be an opportunity for the operation of group or multi-level selection (*23, 24*). A general requirement for group selection to be important is that intergroup differences be large compared to differences within groups (*25, 26*). In this context, Cowen (*27*) documented large differences in vital rates among different populations of sheephead. However, whether the conditions exist in nature to facilitate multi-level selection involving genetic drift and N_e is not clear. Because of the non-linear relationship between N_e and genetic drift, if group selection does exert pressure toward earlier sex change, it is most likely to be important in small populations; once N_e reaches 500-1000, additional increases confer relatively little benefit.

The third major theme is that, although ESS equations for protandry and protogyny are entirely symmetrical, in real species expression of these strategies is heavily determined by age-specific fecundity of females. If female fecundity is roughly proportional to age (as in Fig. 1), opportunities for protogyny (which require that male fecundity rise faster with age) are rather open-ended. In contrast, protandry is expected to evolve only if male fecundity increases more slowly with age. Unless males suffer from substantial reproductive senescence (as in schedules F and G in Table 1), male fecundity for protandrous marine fishes must follow something like a hockey-stick pattern similar to schedule B. This produces relatively weak selection for sex reversal and explains why we found generally larger effects on the protogynous species in this study. This result is consistent with the general observation that protogyny is more common than protandry in sequential hermaphrodites (*6, 8*).

Some caveats are in order. Although the results for the marine fishes are based on empirical data, vital rates and environmental conditions can vary widely among populations within a species ((*27-29*)). For example, many sheephead populations have much shorter lifespans than the one we modeled (*27*). Furthermore, empirical data for male fecundity are extremely rare, so we had to make some educated guesses about how male fecundity changes with age. Therefore, even though the qualitative patterns are robust across both empirical and synthetic dataset, results presented here might not apply quantitatively to any particular population. We don't have comparable empirical data for other plant and animal species that are sequential hermaphrodites, but the range of scenarios considered here suggests that results should be qualitatively similar. We adopted fairly simple behavioral models to scale relative male and female fecundity in the marine fishes. Realized reproductive success in the wild can be more complex, and this complexity can be accommodated in the framework used here, provided that their effects on age-specific fecundity can be quantified (*14*). Finally, our analyses made some simplifying assumptions. Sensitivity analyses indicate that the general themes described above are qualitatively robust to these assumptions, but the magnitude of the effects could differ depending on particular datasets.

Methods

ESS Theory. Although evolutionary theory for sex reversal was originally developed for species with continuous reproduction (*11, 12*), most species in nature (and all those considered here) have seasonal reproduction that better fits the discrete-time, birth-pulse model (*30*), in which births are assumed to occur at integer parental ages. After reproducing at age x, an individual survives to age x+1 with probability s_x. Maximum attainable age is ω, cumulative survival through age x is $L_x = \prod_{i=0}^{i=x-1} s_i$ (with L_0=1), and a single L_x function applies to both sexes.

Now consider a sex-change species that has relative fecundity at age x of q_x for the initial sex and b_x for the terminal sex. All individuals begin life as the initial sex, and at a certain age T all surviving individuals switch to the terminal sex for the rest of their lives. For such a population, there exists an optimal age for sex change that represents an evolutionarily stable strategy (ESS) (*11, 12*).

The ESS age can be solved analytically by dividing age-specific fecundities for each sex by the value that pertains to a specific age y: $B_x=b_x/b_y$ and $Q_x=q_x/q_y$. Choice of y is arbitrary, but it must be the same for both sexes. Total expected lifetime genetic contribution of an individual of the initial sex is thus

$$R_1 = \sum_0^T L_x Q_x \quad , \tag{1A}$$

and for an individual of the terminal sex it is

$$R_2 = \sum_T^{\omega} L_x B_x \ . \tag{1B}$$

Expressions in equation 1 can be thought of as fitness sets (*31*) for the two sexes. The ESS age is the value of T that maximizes the product R_1R_2 (*11, 12*); it can be found iteratively by substituting potential values of τ in equation 2 until the product is maximized. This ESS framework is identical regardless the direction of sex change.

The above model assumes a single, knife-edge age at which all surviving individuals change sex. In real populations, the distribution of sex ratio over time is typically sigmoidal (*7*):

$$f_x=f_0+(f_\infty-f_0)/(1+e(^{T-x})) \quad , \qquad (2A)$$

where f_x is the fraction of individuals of age x that are the terminal sex, f_0 and f_∞ are the fractions of the terminal sex at birth and at an arbitrarily old age, and T is the inflection point. Sex change is assumed to occur after reproduction at age x but before reproduction at age $x+1$; therefore, T can take fractional values between integers. Empirical estimates of f_0 and f_∞ are rare, so except as noted we assumed that $f_0=0$ and $f_\infty=1$, in which case equation 2A simplifies to

$$f_x = 1/(1+e^{T-x}). \qquad (2B)$$

Using f_x values as weights, fitness sets in equation 1 can be rewritten as

$$R_1 = \sum_0^\omega (1-f_x)L_xQ_x \;; \qquad (3A)$$

$$R_2 = \sum_0^\omega f_xL_xB_x \;, \qquad (3B)$$

with the summations computed across all ages. This weighting method is similar to that used for marine fish (*4*) and for pandalid shrimp (*21*).

The summations of fecundity×survivorship terms in equation 3 can be thought of as indices of population replacement rate. If the relative fecundities are standardized as follows, they are converted into absolute fecundities required to produce a population of constant size: $Q'_x=Q_x/\sum_0^\omega(1-f_x)L_xq_x$ and $B_x'=B_x/\sum_0^\omega L_xb_x$. These standardized fecundities can be used to rescale the fitness sets as follows:

$$R_1 = \sum_0^\omega(1-f_x)L_xQ'_x \qquad \text{and} \qquad (4A)$$

$$R_2 = \sum_0^\omega f_xL_xB'_x \;. \qquad (4B)$$

Following these transformations, expected lifetime reproductive success of individuals of the initial and terminal sexes, respectively, are $\sum_0^\omega(1-f_x)L_xQ'_x=\sum_0^\omega f_xL_xB'_x=1$.

Expressions in equation 4 can be used to illustrate conditions under which sex reversal is favored by natural selection. Consider the following scenario, in which fecundity is constant with age in the first sex and increases linearly with age in the second sex (schedules A and C in Table 1). The filled circles and solid line in Fig. 2 are paired R_1, R_2 values for each integer age at sex change. The curve intersects the axes at points [0,1] and [1,0], indicating that individuals who function their entire life as a single sex have expected reproductive success=1. The dotted line represents all points that satisfy the condition that $R_1+R_2=1$, which occurs when vital rates are identical in both sexes. If the fitness set lies along this line, there is no evolutionary pressure to change sex; that only occurs when the fitness sets describe a convex curve (*11, 21*).

Population sex ratio. Equation 2 specifies the sex ratio for each age. It is also of interest to quantify the sex ratio in both the population as a whole and the adult population (all individuals that have reached the age at maturity, α). In the total population, relative numbers of the initial and terminal sexes are $\sum_0^\omega(1-f_x)L_x$ and $\sum_0^\omega f_xL_x$. Let Z be the fraction of individuals of the terminal sex, then

$$Z_{\text{Total}} = \sum_0^\omega f_xL_x/\Sigma L_x \qquad (5)$$

$$Z_{\text{Adult}} = \sum_\alpha^\omega f_xL_x/\Sigma L_x \;,$$

with the summation computed from age 0 for the total population and age α for adults.

Effective population size. The most general model for calculating effective size in species with overlapping generations is (*32*):

$$N_e \approx \frac{4N_1G}{V_{k\bullet}+2}, \tag{6}$$

where N_1 is the number of offspring in each cohort, $G=\Sigma xL_xb_x/\Sigma L_xb_x$ is generation length (average age of parents), and $V_{k\bullet}$ is the lifetime variance in reproductive success across all members of a cohort. This model assumes stable age structure, constant population size, and independence of survival and fecundity across time periods (*32, 33*).

For sex-changing species, the program AgeNe (*20*) computes $V_{k\bullet}$ T, and hence N_e using Equation 6 from sex- and age-specific vital rates: survival and fecundity (as noted above), the age-specific sex ratio (f_x), and a fourth parameter, $\phi_x=V_x/b_x$, which is the ratio of the variance to mean reproductive success by individuals of the same age and sex. As a default, we assumed that $\phi_x=1$ and evaluated sensitivity in the SI Appendix.

Generic life tables. Following Warner (*4*), we constructed synthetic life tables for hypothetical species that mature at age $\alpha=1$ and have maximum longevity of $\omega=11$ years. Each of these fecundity schedules has analogues in published life tables for diverse taxa (*34-36*). Except as noted, survivorship was constant at $s_x=0.8$/year in both sexes. For each of 10 modeled scenarios, we calculated f_x for potential ages at sex change from $T=1.5$ to 10.5, and we calculated τ (to the nearest 0.1 year) by maximizing the product R_1R_2 from equation 3. Then, we used AgeNe to calculate N_e, G, and adult sex ratio for a range of values of T. As a point of reference, we also calculated N_e (N_{eG}) for a gonochoristic population having the same vital rates and an equal primary sex ratio. We are interested in relative changes to effective size, so we used a single, fixed value (N_1=10,000) for the total number of offspring produced per year in every scenario. This ensured adequate numbers of individuals in older age classes for long-lived species.

In sensitivity analyses, we evaluated scenarios in which annual survival differed for males and females; longevity was increased up to $\omega=30$ years; pure-sex individuals occurred ($f_0>0$ and/or $f_\infty<1$); and variance in reproductive success of same-age, same-sex individuals was overdispersed ($\phi>1$) (see SI Appendix for details).

Empirical life tables. Vital rates for the marine fishes are based on published data (*7*) and appear in Table S1. As in the hypothetical scenarios, we assumed $f_0=0$ and $f_\infty=1$ to estimate f_x. Empirical data on age-specific male fecundity are lacking. For the protogynous species with harems (sheephead, slinger, and black seabream), we adopted Warner's (*4*) "female choice" model in which females will only mate with a male as large (old) or larger (older) than they are. In this model, relative fecundity of males is the sum of relative fecundities of females the same age and younger. In the synthetic datasets, the scenario using fecundity schedule C for the initial sex and schedule D for the second sex follows this model. For the pandora, which is a broadcast spawner, we accounted for sperm competition (*37*) by reducing the benefits of a harem by 50%. For male fecundity in the four protandrous species, we mimicked the hockey-stick fecundity schedule B in Table 1 by setting male and female fecundities equal at age at maturity ($q_\alpha=b_\alpha$) and constraining asymptotic male fecundity to be one-half of the fecundity of the oldest females ($q_{max}=0.5b_\omega$). Then, we used a Lotka-Volterra function to describe relative male fecundity at the intervening ages:

$$q_{x+1}= q_x[1+ r(1- q_x/q_{max})],$$

with $r=0.6$ for the three short-lived species and $r=0.4$ for the barramundi.

Acknowledgments

We thank Spencer Barrett, Eric Charnov, Robert Warner, David Sloan Wilson, and an anonymous reviewer for useful comments and discussions. We acknowledge financial support from Science Foundation Ireland and the Irish Research Council.

Author contributions

RW and SM planned and designed research; CB compiled the life history data; RW analyzed the data; RW wrote the paper and RW, SM, and CB edited the paper.

Data availability

No new data were generated in this study; the empirical data for marine fishes have been previously published.

References

1. D. Policansky, Sex change in plants and animals. *Annual Review of Ecology and Systematics* **13**, 471-495 (1982).
2. J. P. Sinclair, J. Emlen, D. C. Freeman, Biased sex ratios in plants: Theory and trends. *The Botanical Review* **78**, 63-86 (2011).
3. R. Vega-Frutis, R. Macías-Ordóñez, R. Guevara, L. Fromhage, Sex change in plants and animals: a unified perspective. *Journal of Evolutionary Biology* **27**, 667-675 (2014).
4. R. R. Warner, The adaptive significance of sequential hermaphroditism in animals. *The American Naturalist* **109**, 61-82 (1975).
5. D. Y. Shapiro, Differentiation and evolution of sex change in fishes. *BioScience* **37**, 490-497 (1987).
6. J. C. Avise, J. E. Mank, Evolutionary perspectives on hermaphroditism in fishes. *Sexual Development* **3**, 152-163 (2009).
7. C. Benvenuto, I. Coscia, J. Chopelet, M. Sala-Bozano, S. Mariani, Ecological and evolutionary consequences of alternative sex-change pathways in fish. *Scientific Reports* **7**, 9084 (2017).
8. Y. S. de Mitcheson, M. Liu, Functional hermaphroditism in teleosts. *Fish and Fisheries* **9**, 1-43 (2008).
9. M. T. Ghiselin, The evolution of hermaphroditism among animals. *The Quarterly Review of Biology* **44**, 189-208 (1969).
10. R. R. Warner, Sex change and the size-advantage model. *Trends in Ecology & Evolution* **3**, 133-136 (1988).
11. E. L. Charnov, *The theory of sex allocation.*, (Princeton, NJ Princeton University Press., 1982).
12. E. L. Charnov, *Life History Invariants: Some Explorations of Symmetry in Evolutionary Ecology*. (Oxford University Press, Oxford UK, 1993).
13. P. Munday, B. Molony, The energetic cost of protogynous versus protandrous sex change in the bi-directional sex-changing fish *Gobiodon histrio*. *Marine Biology* **141**, 1011-1017 (2002).
14. E. Kazancioglu, Suzanne H. Alonzo, Costs of changing sex do not explain why sequential hermaphroditism is rare. *The American Naturalist* **173**, 327-336 (2009).
15. E. L. Charnov, J. J. Bull, Non-fisherian sex ratios with sex change and environmental sex determination. *Nature* **338**, 148-150 (1989).
16. S. Wright, Size of population and breeding structure in relation to evolution. *Science* **87**, 430-431 (1938).
17. B. Charlesworth, Effective population size and patterns of molecular evolution and variation. *Nature Reviews Genetics* **10**, 195-205 (2009).
18. J. Chopelet, R. S. Waples, S. Mariani, Sex change and the genetic structure of marine fish populations. *Fish and Fisheries* **10**, 329-343 (2009).
19. I. Coscia, J. Chopelet, R. S. Waples, B. Q. Mann, S. Mariani, Sex change and effective population size: implications for population genetic studies in marine fish. *Heredity* **117**, 251-258 (2016).
20. R. S. Waples, C. Do, J. Chopelet, Calculating Ne and Ne/N in age-structured populations: a hybrid Felsenstein-Hill approach. *Ecology* **92**, 1513-1522 (2011).

21. E. L. Charnov, Natural selection and sex change in pandalid shrimp: Test of a life-history theory. *The American Naturalist* **113**, 715-734 (1979).
22. J. L. Gastwirth, The estimation of the Lorenz Curve and Gini Index. *The Review of Economics and Statistics* **54**, 306 (1972).
23. D. S. Wilson, Altruism and organism: Disentangling the themes of multilevel selection theory. . *The American Naturalist* **150**, s122-S134 (1997).
24. B. Simon, J. A. Fletcher, M. Doebeli, Towards a general theory of group selection. *Evolution* **67**, 1561-1572 (2012).
25. J. Mitteldorf, D. S. Wilson, Population viscosity and the evolution of altruism. *Journal of Theoretical Biology* **204**, 481-496 (2000).
26. J. N. Pruitt, C. J. Goodnight, Site-specific group selection drives locally adapted group compositions. *Nature* **514**, 359-362 (2014).
27. R. K. Cowen, Sex change and life history patterns of the labrid, semicossyphus pulcher, across an environmental gradient. *Copeia* **1990**, 787 (1990).
28. J. E. Caselle, Hamilton, S. L., Schroeder, D.M., Love, M.S., Standish,J.D., Rosales-Casián,JA, Sosa-Nishizaki. O. , Geographic variation in density, demography, and life history traits of a harvested, sex-changing, temperate reef fish. *Canadian Journal of Fisheries and Aquatic Sciences* **68**, 288–303. (2011).
29. S. L. Hamilton, J. R. Wilson, T. Ben-Horin, J. E. Caselle, Utilizing spatial demographic and life history variation to optimize sustainable yield of a temperate sex-changing fish. . *PloS one* **6**, e 24580 (2011).
30. H. Caswell, *Matrix population models. 2nd edition.*, (Sinauer, Sunderland MA, 2001).
31. R. Levins, *Evolution in changing envrionments*. (Princeton University Press, 1968).
32. W. G. Hill, Effective size of populations with overlapping generations. *Theoretical Population Biology* **3**, 278-289 (1972).
33. J. Felsenstein, Inbreeding and variance effective numbers in populations with overlapping generations. *Genetics* **68**, 581–597 (1971).
34. H. C. Fung, R. S. Waples, Performance of IUCN proxies for generation length. *Conservation Biology* **31**, 883-893 (2017).
35. R. S. Waples, Life-history traits and effective population size in species with overlapping generations revisited: the importance of adult mortality. *Heredity* **117**, 241-250 (2016).
36. R. S. Waples, G. Luikart, J. R. Faulkner, D. A. Tallmon, Simple life-history traits explain key effective population size ratios across diverse taxa. *Proceedings of the Royal Society B: Biological Sciences* **280**, 20131339-20131339 (2013).
37. R. C. Muñoz, R. R. Warner, A new version of the size-advantage hypothesis for sex change: incorporating sperm competition and size-fecundity skew. *The American Naturalist* **161**, 749-761 (2003).

Table 1. Hypothetical relative fecundity schedules used in the modeling exercise.

Age	A	B	C	D	E	F	G
1	1	1	1	1	1	1	6
2	1	2	2	3	4	2	6
3	1	3	3	6	9	3	6
4	1	4	4	10	16	4	6
5	1	5	5	15	25	5	6
6	1	6	6	21	36	6	6
7	1	6	7	28	49	5	5
8	1	6	8	36	64	4	4
9	1	6	9	45	81	3	3
10	1	6	10	55	100	2	2
11	1	6	11	66	121	1	1

A: constant; B: upward hockey stick; C: linear increase; D: male with harem, where female fecundity follows schedule C; E: quadratic increase; F: dome-shaped; G: downward hockey stick

Table 2. Results for 10 modeled scenarios using hypothetical fecundity schedules shown in Table 1.

Pair	τ	S_1	N_{eESS} $/N_{eG}$	N_{eESS} $/N_{eMax}$	N_e bonus	I
AC	4.5	0.61	1.03	1.00	1.14	0.32
AE	5.5	0.71	1.09	0.98	1.51	0.53
AB	4.3	0.59	1.02	1.00	1.09	0.25
AF	3.8	0.53	1.00	1.00	1.01	0.16
BC	5.6	0.71	1.00	0.98	1.25	0.08
CE	6.5	0.78	1.03	0.96	1.36	0.24
CD	6.5	0.78	1.02	0.96	1.37	0.21
FC	5.5	0.71	1.00	0.98	1.27	0.19
GA	3.5	0.50	1.02	1.00	1.02	0.07
GC	4.5	0.61	1.05	1.00	1.17	0.40

'Pair' gives fecundity schedules used in each scenario, with the schedule for the initial sex shown first. All comparisons assumed constant survival at 0.8/yr in both sexes. τ = ESS age at sex change; S_1 is the fraction of adults that are the initial sex, assuming sex change at age τ; N_{eESS} is effective size if sex change occurs at age τ; N_{eMax} is maximum N_e for any age at sex change; N_{eG} is effective size of a gonochoristic population with equal sex ratio; N_{eG*} is effective size of a gonochoristic population with a sex ratio skewed as indicated for each comparison; N_e bonus = N_{eESS}/N_{eG*}. I is the index of selection described in Fig. 2.

Table 3. Data for eight marine fish species that are sequential hermaphrodites.

Species	α	ω	T	τ	τ/ω	T/τ	A	S_1	N_{eESS} $/N_{eG}$	N_{eESS} $/N_{eMax}$	N_e bonus	I
Protandry												
Diplodus sargus (white seabream)	3	12	6	7.0	0.58	0.86	4.5	0.77	1.02	0.87	1.49	0.06
Lates calcarifer (barramundi)	4	23	8	9.5	0.41	0.84	5.7	0.72	0.99	0.84	1.27	0.09
Lithognathus mormyrus (striped seabream)	3	11	6	5.9	0.54	1.02	4.2	0.69	1.00	0.91	1.21	0.08
Sparus aurata (gilt-head seabream)	3	12	6	5.9	0.49	1.02	4.5	0.65	1.01	0.94	1.12	0.09
Protogyny												
Chrysoblephus puniceus (slinger seabream)	3	10	5	5.5	0.55	0.91	4.1	0.67	1.03	0.94	1.25	0.21
Pagellus erythrinus (pandora)	3	21	9	12.6	0.60	0.71	5.7	0.89	1.03	0.75	3.18	0.23
Spondyliosoma cantharus (black seabream)	2	10	5	6.4	0.64	0.78	3.8	0.85	1.01	0.86	2.24	0.16
Semicossyphus pulcher (sheephead)	4	29	13	15.7	0.54	0.83	6.9	0.90	1.04	0.70	3.45	0.29

α = age at maturity; ω = maximum age; T = empirical age at sex change (from Benvenuto et al. 2017); A = age at sex change that produces N_{eMax}; other variables as defined in Table 2.

Figure Legends

Figure 1. Patterns of age-specific fecundity in some sequential hermaphrodite marine fishes. Left panels: protogyny (A) and protandry (B). Fecundity is relative to the maximum within each species. Right panels: differences between male and female fecundity in a protogynous species (sheephead, C) and a protandrous species (barramundi. D). Fecundity (expressed as number of offspring that survive to age 1) is scaled to that required to produce a stable population, given the annual survival rates shown in Table S1.

Figure 2. Plots of fitness sets depicting reproductive success of individuals operating as the first sex (R_1) and the second sex (R_2). Fecundities are scaled so that pure-sex individuals have R=1. Each datapoint represents a pair of R_1, R_2 values for a specific age at sex change. (A) Ages at sex change are above each datapoint. The dashed line for $R_1+R_2=1$ describes a zone in which there is no advantage to changing sex; sex change is selectively favored only when the fitness sets describe a convex curve. The area X quantifies the degree of concavity. The total area $X+Y=0.5$ is the maximum possible area above the dashed line encompassed by fitness sets, so $I = X/0.5=2X$ is an index of the intensity of selection for sex change. (B) Fitness sets for four of the comparisons shown in Table 2. The dashed line for CC falls on the $R_1+R_2=1$ line and illustrates what happens if both sexes have the same vital rates.

Figure 3. Influence of age at sex change on relative effective population size in the protogynous sheephead. Values on the Y axis are the ratio of realized N_e to N_e in a gonochoristic population that does not change sex and has an even sex ratio (N_{eG}). Vertical dashed line indicates ESS age at sex change (15.7 years for sheephead). Red circles show relative N_e under sex change (N_e/N_{eG}); blue triangles indicate what relative N_e would be (N_{eG*}/N_{eG}) in a gonochoristic population with the same adult sex ratios found in the sex-changing population. The green arrow indicates the magnitude of increase in N_e attributable to sex change (the "N_e bonus").

Figure 4. Association between the index of selection for sex change (I) and relative effective population size in sex-changing populations. The Y axis plots the ratio of N_e at the ESS age at sex change (N_{eESS}) to N_e in a gonochoristic population with an even sex ratio (N_{eG}). Blue circles are for synthetic datasets; red Xs are for 8 marine fishes; dotted line at 1.0 is provided for reference.