Consequences of Sex Change for Effective Population Size

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Supporting Information

Sensitivity Analyses

The core analyses adopted some simplifying assumptions, sensitivity to which is evaluated below.

Pure-sex individuals. The analyses in the main text assumed that no pure-sex individuals occurred (that is, in Eq. 2A, $f_0 = 0$ and $f_\infty = 1$). For an 11-year lifespan with constant survival in both sexes at 0.8/yr (as assumed for the synthetic life tables), the resulting age-specific sex ratios for sex change at ages $T = 4$, 7, and 9 are shown in Fig. S1A. This is realistic for many sex-changing species (e.g., see Cowen 1990 and Fig. S2) but not all. Unfortunately, although the existence of young members of the terminal sex (primary males and primary females in diandric and digynic populations) and/or very old members of the initial sex has been reported in a number of sex-changing populations (Erisman et al., 2013; C. Benvenuto, personal communication), quantitative estimates of $f_0 > 0$ and $f_\infty < 1$ are seldom available. Accordingly, we evaluated the consequences of assuming different values for f_0 and f_∞. Some variations of the age-specific sex ratio are shown in figure S1B.

In addition, we considered three different scenarios ($f_0 = 0.3, f_\infty = 1$; $f_0 = 0, f_\infty = 0.7$; and $f_0 = 0.3, f_\infty = 0.7$) and evaluated consequences of the resulting sex ratios for one protandrous species (barramundi) and one protogynous species (pandora), selected because they have similar adult lifespans. We tracked four indices related to sex change (Fig. S3). In the pandora, assuming that either $f_0 > 0$ or $f_\infty < 1$ has the following effects: the index of selection (I) declines; the overall skew in sex ratio becomes less pronounced; and the ratios N_{eESS}/N_{eG} and N_{eESS}/N_{eMax} both converge on 1.0. Results were qualitatively similar but less pronounced for the barramundi, for which I was largely unaffected. Overall, presence of very young members of the terminal sex or very old members of the initial sex dampens the consequences of sex change but does not change the qualitative patterns described in the main text.

Survival differences between males and females. The core analyses followed Charnov (1982, 1993) in assuming equal survival rates in males and females. Because the fitness sets are affected by survivorship as well as fecundity (Eqs 3-4), we also evaluated scenarios in which annual survival rates differed for the initial and terminal sexes. In the first set of scenarios, both initial and terminal sexes had the same fecundity schedule (C from Table 1; linear increase with age) but different survival rates (constant survival at $s_x = 0.7$/yr, 0.8/yr, or 0.9/yr). In the second set of scenarios, the initial sex had fecundity schedule C and the terminal sex fecundity schedule D, which corresponds to Warner's (1975) female choice model. We considered two variations: 1) $s_x = 0.7$/yr in the first sex and $s_x = 0.8$/yr in the second sex; 2) $s_x = 0.8$/yr in the first sex and $s_x = 0.7$/yr in the second sex.

When vital rates are the same in both sexes (Scenario 1 in Table S2), there is no evolutionary pressure for sex change ($I = 0$). If fecundity schedules are equal but survival differs

between the sexes, sex change is evolutionarily advantageous only if survival rates are higher in the terminal sex (Scenarios 2 and 3), and selection is stronger when survival differences are larger (Scenario 4; $I = 0.341$ when survival is 0.9/yr in the terminal sex and 0.7/yr in the first sex). Under the female choice model, relatively higher survival in the terminal sex (males) enhances the selective advantage of sex change ($I = 0.382$ for Scenario 6 compared to $I = 0.206$ for Scenario 5 with equal survivals), while selective pressure for sex change is reduced if the terminal sex has lower survival ($I = 0.036$ Scenario 7).

Longevity. The synthetic lifetables followed Warner (1975) in stipulating a fixed 11-year lifespan. In real species, choice of what value to use for maximum age (ω) is often somewhat arbitrary. In the discrete-time demographic model, it is assumed that after reaching age ω, survival suddenly drops to zero. Conversely, if s_x remains > 0 for all ages, then there is a non-zero probability that at least some individuals will survive to an arbitrarily old age. Selection of ω therefore generally requires one to pick an age beyond which older individuals are expected to be rare enough that they can be safely ignored. To formalize this process, we identified a quantitative criterion (adopted from Waples et al. 2013) that could be consistently applied to compute maximum age: ω is the oldest age for which the ratio L_ω/L_α is greater than 0.05—that is, the life tables were truncated at the oldest age for which cumulative survivorship from age at maturity (α) was at least 5%. We modeled "species" that matured at age 1 and had maximum lifespans of $\omega = 5\text{-}30$ years, and we chose constant survival rates in both sexes such that L_ω/L_α was close to 0.05. We modeled one mock protogynous species (with female fecundity increasingly linearly with age, as in Schedule C, and male fecundity following Schedule D) and one mock protandrous species (with a linear increase for females and a hockey-stick fecundity schedule similar to B for males).

Results were qualitatively similar for both directions of sex change (Fig. S4): increasing the lifespan increased the index of selection, increased the skew of the adult sex ratio, and increased the disparity between N_{eESS} and N_{eMax}, but longevity had little effect on N_{eESS}/N_{eG}.

Overdispersed variance in reproductive success. The parameter ϕ is the ratio of the variance to mean offspring number for individuals of the same age and sex. The analyses in the main text assumed that $\phi = 1$, which is equivalent to assuming that individuals of the same age and sex have random variation in reproductive success among themselves. For one of the synthetic "species" comparisons (CD, which models the female choice model), we considered how τ changed with larger fixed values of ϕ (overdispersed variance in reproductive success), or with ϕ values that increased with age. Assumptions about ϕ do not change the other vital rates and hence do not affect the ESS age at sex change, but they do affect N_e.

None of the alternative values for ϕ had an appreciable effect on N_{eESS}, which remained close to what it would have been without sex change (N_{eG}), but ϕ can have a substantial influence on N_e for other ages at sex change (Fig. S5), so it affects the ratio N_{eESS}/N_{eMax}. In general, for $\phi > 1$, effective size is reduced for ages earlier than τ and increased for ages later than τ.

Erisman, B. E., C. W. Petersen, P. A. Hastings, and R. R. Warner. 2013. Phylogenetic perspectives on the evolution of functional hermaphroditism in teleost fishes. Integrative and Comparative Biology 53:736-754.

Table S1. See separate Excel file for vital rates for the 8 marine fish species.

Table S2. Effects of different survival rates in the two sexes on results for synthetic species. Fecundity schedules are from Table 1; annual survival rates are constant. τ = ESS age at sex change; I = index of selection for sex change.

| | Fecundity | | Survival | | | |
Scenario	Sex1	Sex2	Sex1	Sex2	τ	I
1[a]	C	C	0.8	0.8	-[b]	0
2	C	C	0.8	0.7	-[b]	-0.181
3	C	C	0.7	0.8	5.3	0.181
4	C	C	0.7	0.9	5.7	0.341
5[c]	C	D	0.8	0.8	6.5	0.206
6	C	D	0.7	0.8	5.7	0.382
7	C	D	0.8	0.7	5.7	0.036

[a] This scenario generated the dotted line in Figure 2B
[b] ESS age is not defined for scenarios that don't select for sex change
[c] This scenario is from Table 2 and is provided here for reference
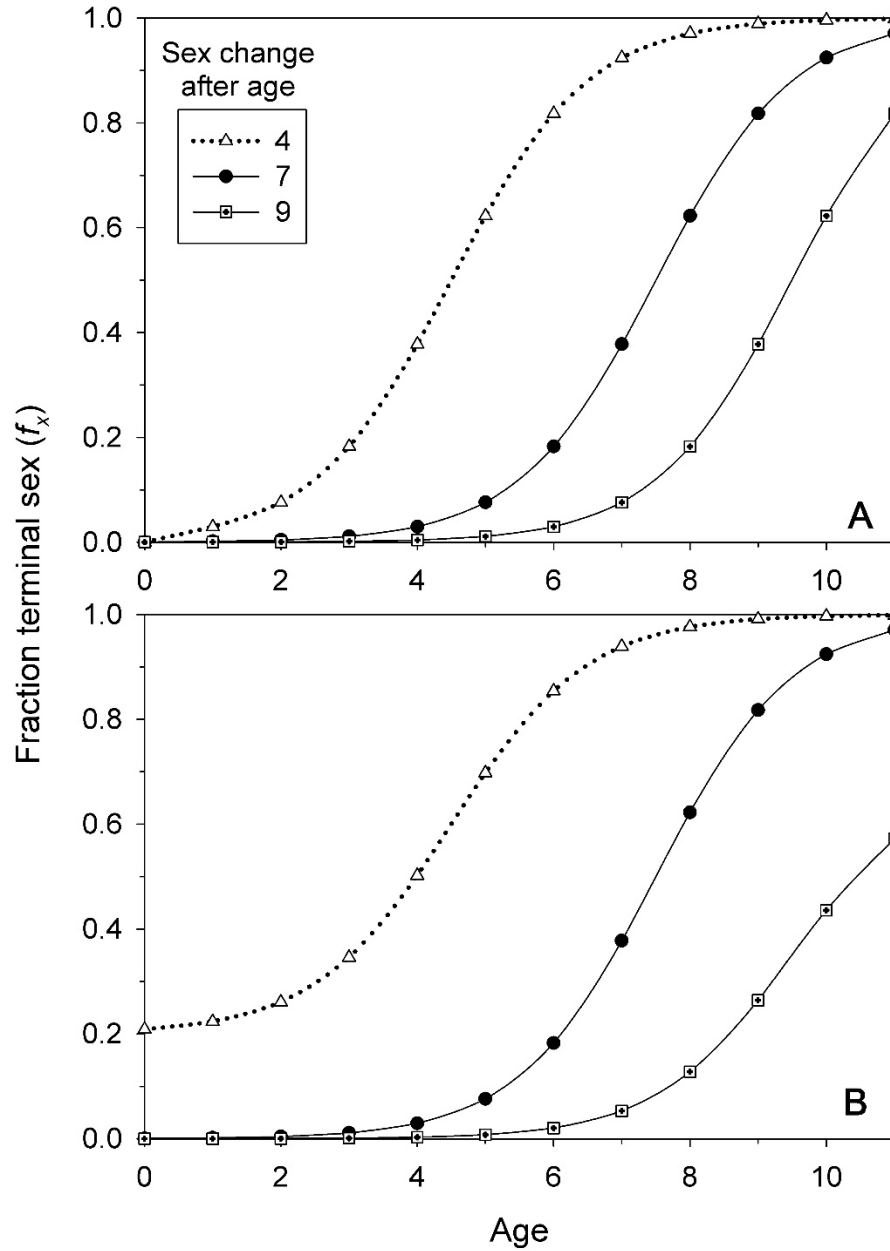
Figure S1. Examples of using Eq. 2A (main text) to calculate the age-specific sex ratio: $f_x = f_0 + (f_\infty - f_0)/(1+e^{T-x})$, where f_x is the fraction of individuals of age x that are the terminal sex, f_0 and f_∞ are the fractions of the terminal sex at birth and at an arbitrarily old age, and T = the inflection point = age at which sex ratio is equal. These examples assume an 11-year lifespan with constant survival at 0.8/yr in both sexes. **A**: Results for $T = 4, 7, 9$ when $f_0 = 0$ and $f_\infty = 1$. **B**: the curve for $T = 4$ used $f_0 = 0.2$ (20% of individuals are born as the terminal sex) and $f_\infty = 1$; the curve for $T = 7$ used $f_0 = 0$ and $f_\infty = 1$; and the curve for $T = 9$ used $f_0 = 0$ and $f_\infty = 0.7$ (30% of individuals that survive to maximum age are still the initial sex).
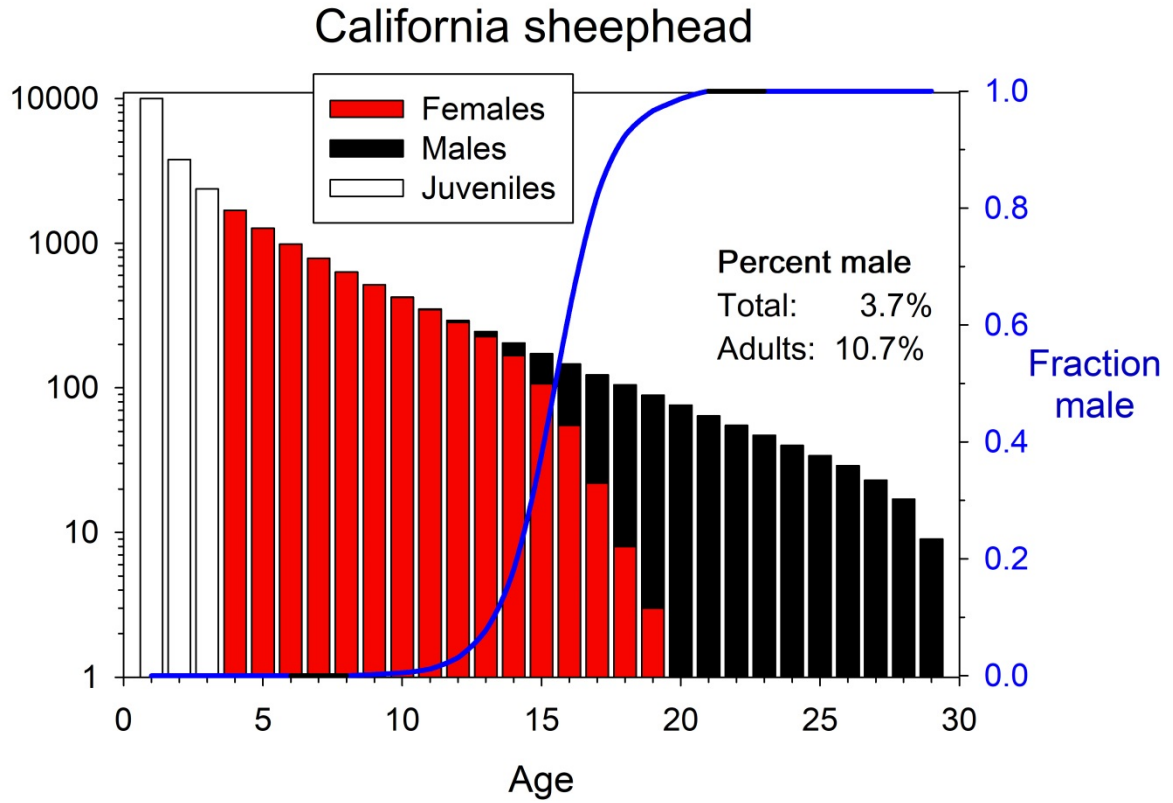
Figure S2. Example of using Eq. 2A (main text) to calculate the age-specific sex ratio in the California sheephead. These results use age-specific survivorships from Benevuto et al. (2017) (see Table S1) and assume $f_0 = 0$ (no primary males) and $f_\infty = 1$ (no females in oldest age class), both of which are consistent with data from Cowen (1990). The left Y axis (note log scale) shows the number of individuals in each age class, assuming a cohort of 10,000 that reach age 1.
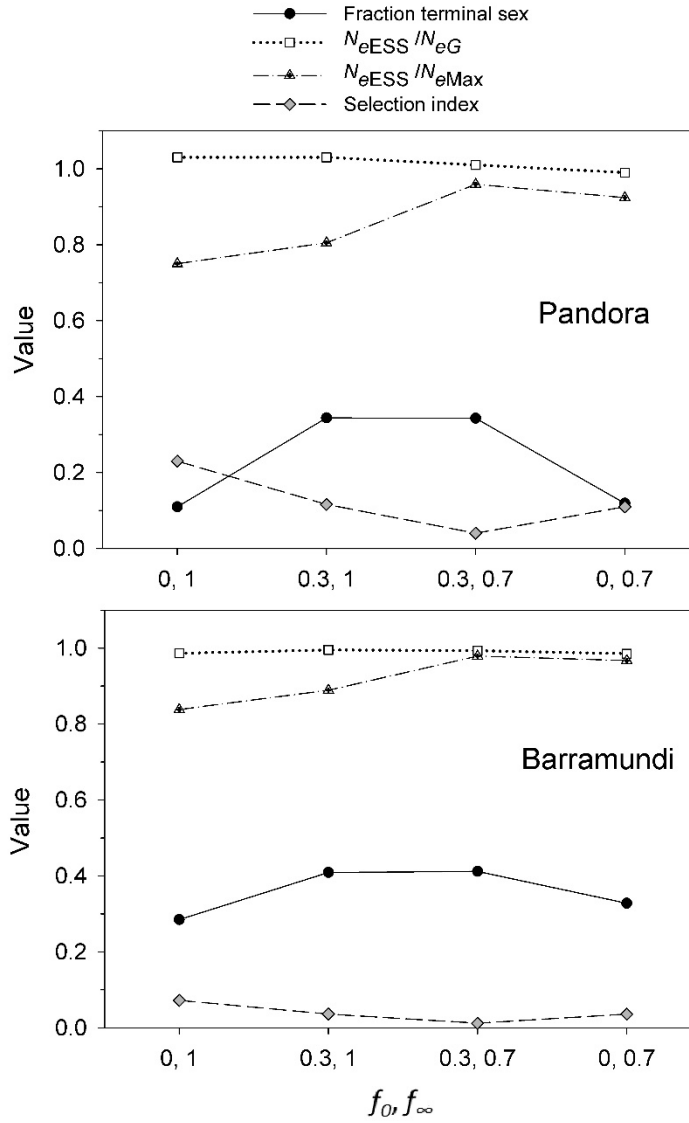
Figure S3. Effects of assumptions about initial and terminal sex ratios. Results for $(f_0, f_\infty) =$ (0,1) (no individuals are born as the terminal sex, no members of the initial sex survive to the oldest age class) are for the core analyses reported the in main text; other pairs of values used in the sensitivity analyses are as shown. Results are shown for one protogynous species (pandora) and one protandrous species (barramundi). Four indices are tracked: fraction of the terminal sex in the adult population (Z_{Adult} from Eq. 5); the selection index, I; the ratio of N_e at the ESS age at sex change to N_e in a gonochoristic population without sex change (N_{eESS}/N_{eG}); and the ratio of N_e at the ESS age at sex change to the maximum N_e for any age at sex change (N_{eESS}/N_{eMax}).
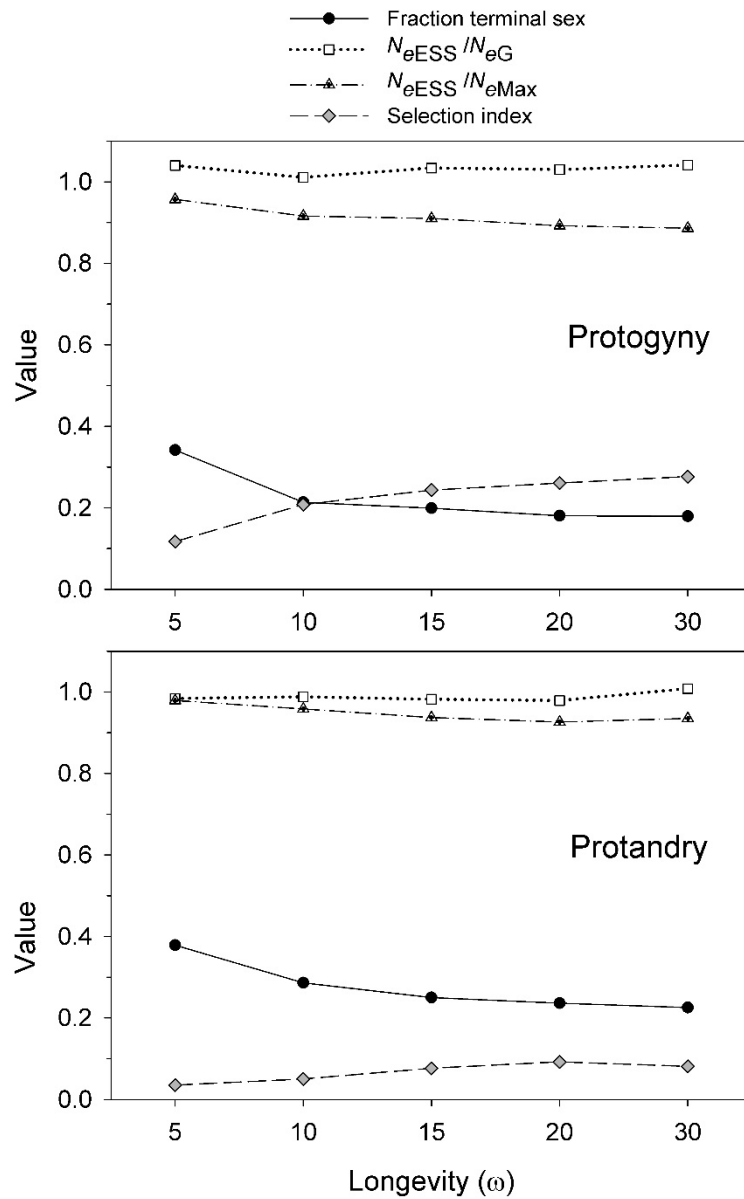
Figure S4. Effects of longevity. Results are shown for one mock-protogynous species, using fecundity schedule C (Table 1) for the first sex (~female) and schedule D for the second sex (~male), and one mock protandrous species, using fecundity schedule B for the first sex (~male) and schedule C for the second sex (~female). The same indices were tracked as in Figure S3.
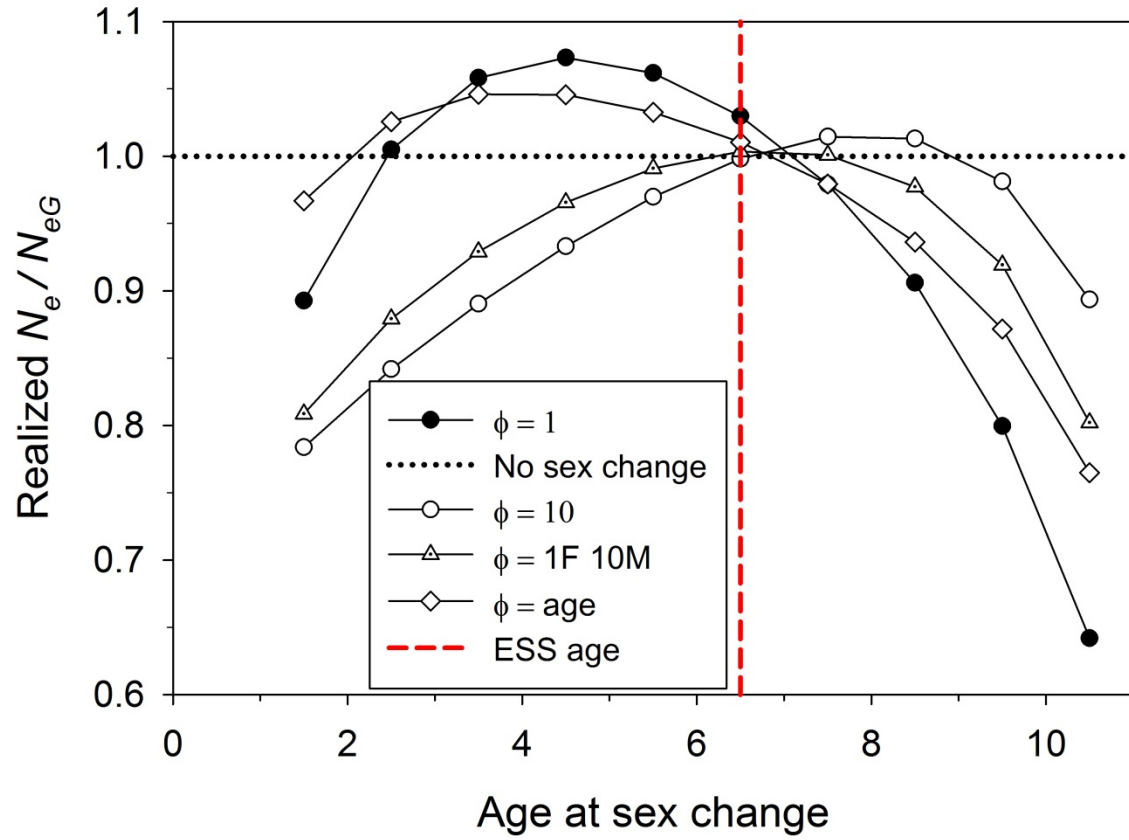
Figure S5. Effects of assumptions about ϕ on the relationship between N_e and ESS age at sex change (τ). ϕ is the ratio of the variance to mean reproductive success of individuals of the same age and sex; it does not affect τ but it does affect N_e. This scenario uses the female choice model in which females will only mate with males as old or older than they are (comparison CD in Table 1). The '$\phi = 1$' scenario replicates results for the CD comparison in Table 2. In the other scenarios, ϕ was either fixed at 10 for all ages in both sexes ('$\phi = 10$'), fixed at 1 for females and 10 for males ('$\phi = 1F\ 10M$'), or took the same value as age in both sexes ('$\phi = $age').
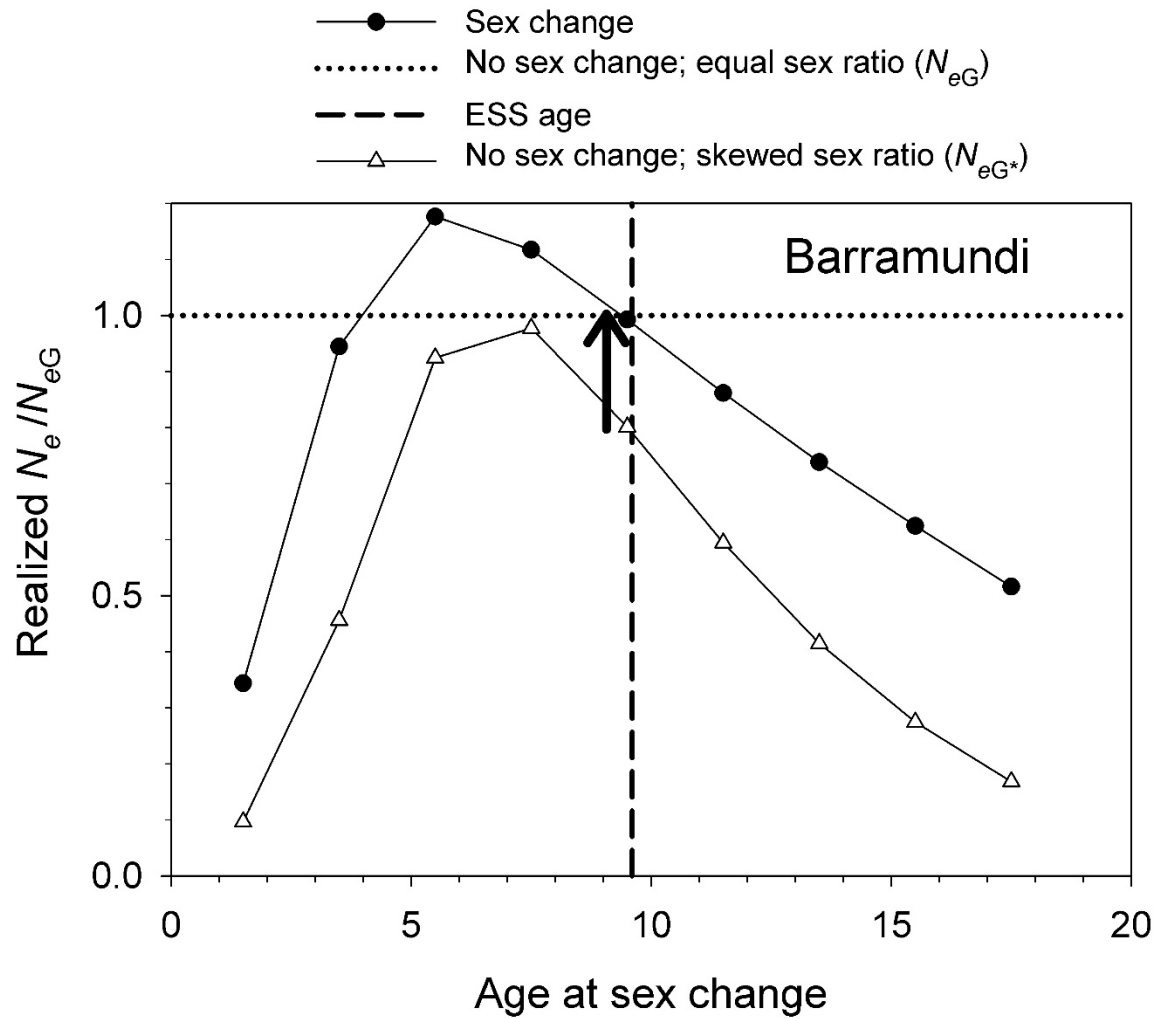
Figure S6. As in Fig 3, main text, but for the barramundi, a protandrous species. Values on the Y axis are the ratio of realized N_e to N_e in a gonochoristic population that does not change sex and has an even sex ratio (N_{eG}). Vertical dashed line indicates ESS age at sex change (9.5 years for the barramundi; Table 3). Filled circles show relative N_e under sex change (N_e/N_{eG}); open triangles indicate what relative N_e would be (N_{eG*}/N_{eG}) in a gonochoristic population with the same adult sex ratios found in the sex-changing population. Vertical arrow indicates the magnitude of increase in N_e attributable to sex change (the "N_e bonus").
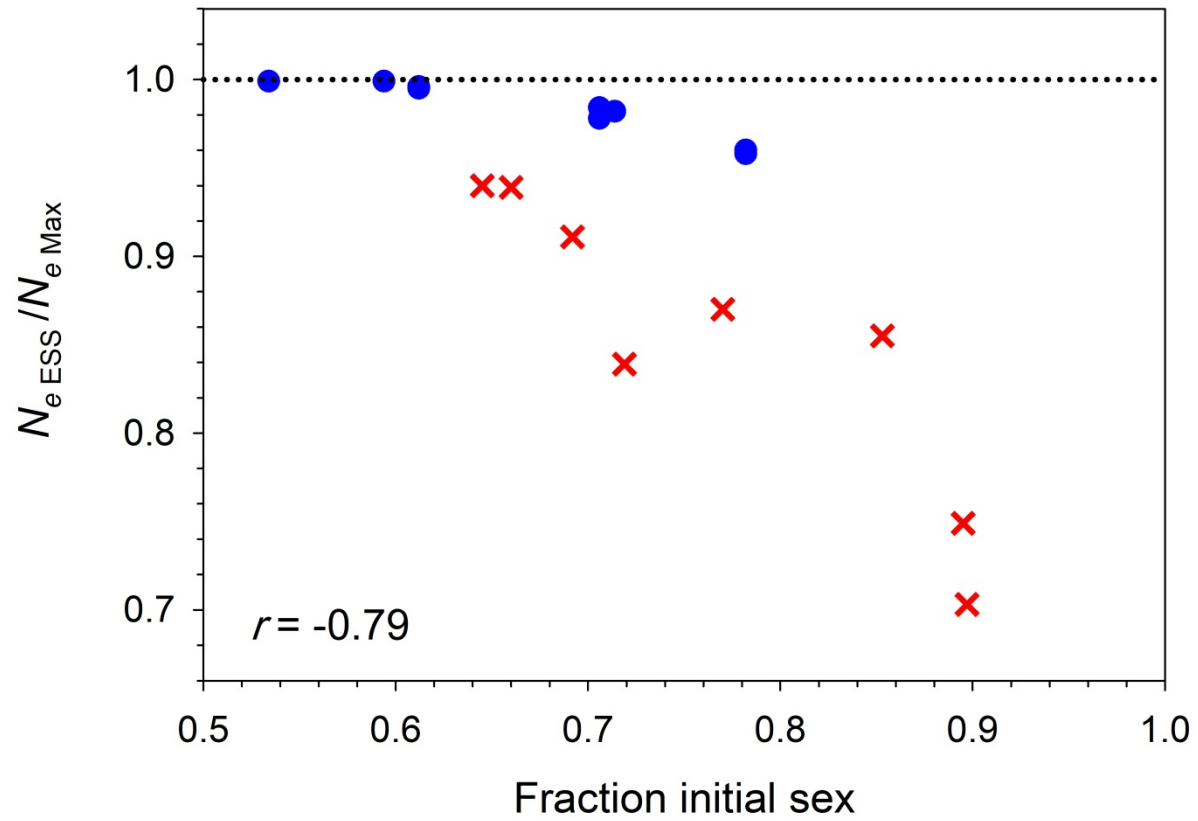
Figure S7. Relationship between adult sex ratio (indexed as the fraction of the initial sex in the adult population) and the ratio N_{eESS}/N_{eMax}. Blue circles are for synthetic datasets; red Xs are for 8 marine fishes; dotted line at 1.0 is provided for reference. The negative correlation is highly significant ($P < 0.001$).
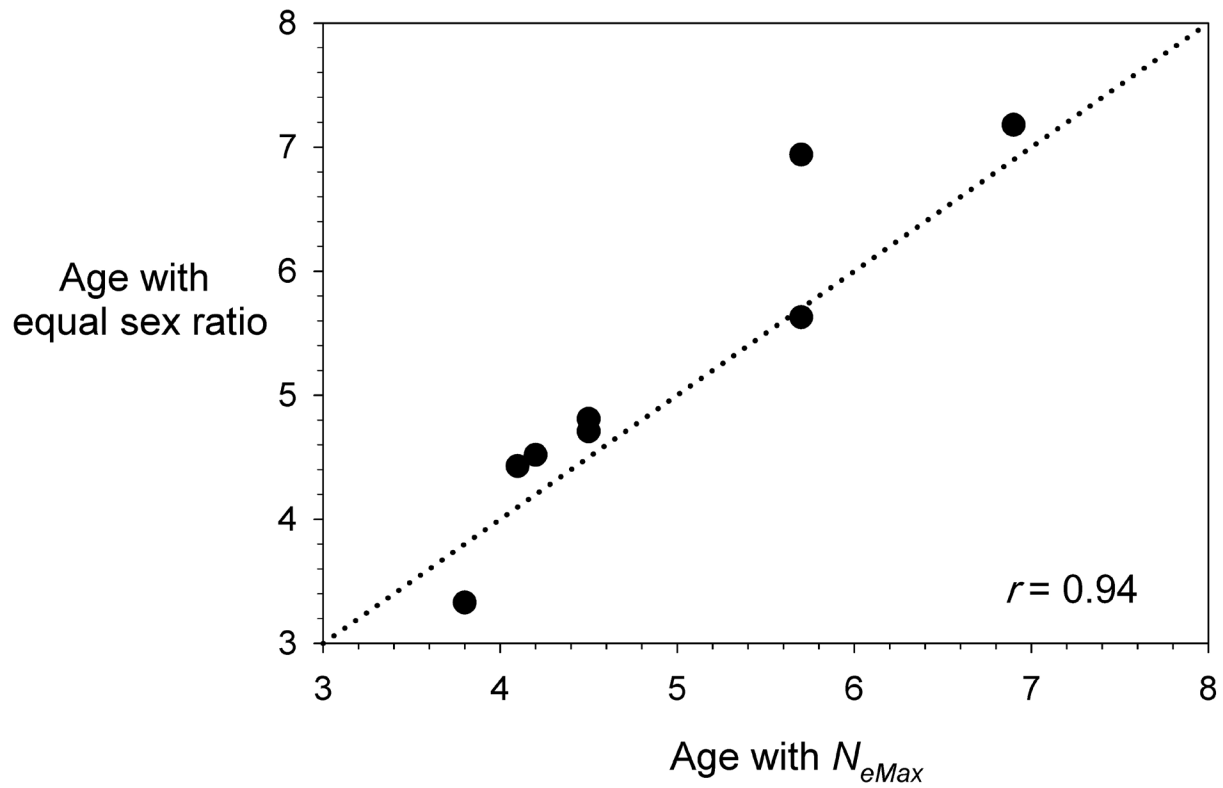
Figure S8. Relationship between the age at sex change (*A* from Table 3) that produces maximum N_e (N_{eMax}) and the age at sex change that produces an equal adult sex ratio. Results shown are for the eight marine fish species. The positive correlation is highly significant ($P < 0.001$). The 10 synthetic "species" all have identical lifespans and survival rates, so they also have identical ages that produce an equal adult sex ratio. Therefore, data for those "species" do not provide a test of the association of these two variables.