



Sex-specific mortality explains non-sex-change by large female *Sparisoma radians*

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The Caribbean parrotfish, *Sparisoma radians*, shows a remarkable pattern of demography. Like many other labroid fish, *S. radians* undergo female-to-male sex change (i.e. protogyny) within a largely harem mating system (Robertson & Warner 1978; Farm 1993; Muñoz & Warner 2004). The largest individuals of this species are, however, non-sex-changed females that occur in habitats ranging from open sea grass (their primary habitat; Robertson & Warner 1978; Randall 1983; Farm 1993) to patch reefs (Muñoz & Warner 2004). This observation challenges a fundamental prediction of Ghiselin's (1969) widely accepted size-advantage model of sex change; with protogyny, the largest individuals are expected to be male.

In a recent attempt to explain this inconsistency, Muñoz & Warner (2003a) moved beyond the general perception that sex change in harems is mediated by male dominance (e.g. Fishelson 1970; Fricke & Fricke 1977; Ross et al. 1990; Lutnesky 1994; Sakai 1997) to propose that social conditions may not always favour sex change by large harem females in the absence of a dominant male. Building from the premise that female fecundity scales nonlinearly with length (creating 'size-fecundity skew' within social units), the 'expected reproductive success threshold' (ERST) model predicts that a very large female, constrained to her immediate groupmates as potential future mating partners, should forgo sex change if her current reproductive rate as a female exceeds her potential reproductive rate as a male (Muñoz & Warner 2003a). The male rate is modelled as the collective fecundity of remaining females within a group, discounted by sperm competition from intruding males. In its

formulation, the model assumes: (1) equal rates of growth and mortality between the sexes; and (2) a mating system in which males defend and mate only with the females living inside their territories. Under appropriate social conditions (defined primarily by the number and size of females living within a male's territory), size-fecundity skew and sperm competition are deemed sufficient to explain non-sex-change by large females, and thus, the persistence of such fish within a protogynous population (Muñoz & Warner 2003a). The results of 22 male-removal experiments using *S. radians*, in which sex change by a resident female occurred just seven times (and only once by the largest female in a group), are offered in support of the model (Muñoz & Warner 2004). We disagree with this interpretation.

Drawing from our own studies of *S. radians*, as well as other published data, we find little support for the contention that female fecundity scales sufficiently with size to meaningfully influence the timing of sex change in this species, even when the effects of sperm competition are considered. We suggest, instead, that well-documented differences in sex-specific rates of mortality (assumed to be constant in the ERST model) offer an alternative explanation for the persistence of larger-than-male females within protogynous populations. Below, we describe the evidence that led us to this conclusion and use this effort to provide a broader assessment of the factors that influence the timing of sex change in species such as *S. radians*.

Size-fecundity Skew and the Timing of Sex Change

The contribution of size-fecundity skew to the timing of sex change ultimately depends upon three factors: the number of individuals in the potential mating pool, the size of those individuals, and the way that fecundity scales with size. Identifying the true nature of the size/fecundity

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relationship is a critical feature of any empirical test of a model that includes this variable, as lower rates of scaling will reduce reproductive variance among group members and thus constrain the set of social conditions (i.e. group size and composition) that would allow size-fecundity skew to affect the timing of sex change.

Estimating size-fecundity skew for *S. radians*

Various factors can influence female fecundity. Individual size, resource levels, and aspects of the social environment are especially relevant to the fecundity of harem-living fish. At an upper limit, we expect a linear relationship between fish mass and fecundity as body size constrains the capacity to hold eggs (Bagenal 1978). Variables like food availability and dominance may limit reproductive output beyond this initial constraint (e.g. Taborsky 1985; Clifton 1989, 1995; Buston 2003), as might seasonal or lunar cycles of reproduction (e.g. Robertson et al. 1990; Petersen & Hess 1991), although such temporal cycling may be less relevant for organisms such as *S. radians* that reproduce daily.

Muñoz & Warner (2004) estimated the relationship between body size and fecundity for *S. radians* by fitting an exponential curve ($m = 0.263e^{0.103(TL)}$) to data on clutch volume and fish size. This equation is also cited elsewhere (Muñoz & Warner 2003a), however, we find that estimates of fecundity generated by this equation (Table 1) do not match with the values given for the hypothetical harem (Muñoz & Warner 2003a), nor do they appear to correspond with the data used to generate the fitted curve (Figure 1b in Muñoz & Warner 2004).

To investigate this discrepancy, we extracted the plotted data from Figure 1b in Muñoz & Warner (2004) and fit nonlinear regression curves for fecundity versus length. Exponential and power functions both provided good fits to the data over the range (Fig. 1), with estimates of fecundity using the exponential equation (Table 1) matching well with values published by Muñoz & Warner (2003a). (Our equation also closely matches the predicted fecundity of an uncaptured 30.1-cm female: 196.6 ml of eggs versus the given estimate of 200 ml). From this, we infer that Muñoz & Warner (2003a) estimated fecundity from length using an exponential function with

coefficients very close to the values that we derived (Table 1, equation (3)).

Using this exponential function to estimate fecundities for the ERST model, Muñoz & Warner (2003a) predicted that very large females within certain size-structured groups (e.g. their hypothetical harem) could retain higher reproductive success by not changing sex based solely upon a size-fecundity skew argument (i.e. no sperm competition). We see no flaw in the basic logic of such an exercise. We note, however, that estimates of *S. radians* fecundity based on an exponential function, rather than a power function, drastically increases the potential for size-fecundity skew (Table 1) predicted for very large females (see Fig. 1).

A review of the literature on length/fecundity relationships reveals scant justification for the use of such an exponential function (ae^{bx}). Length-based estimates of fish fecundity are almost universally expressed as a power function (ax^b), with data from a variety of taxa and locations suggesting a scaling coefficient of $b \approx 3$ (e.g. Bagenal 1978; Pitcher & Hart 1982; Wootton 1992). The scaling coefficient we derived from fitting a power function to Muñoz & Warner's (2004) data ($b = 3.47$) matches well with this expectation and corresponds closely to relationships between both gonad mass and length ($b = 3.2$) and overall body mass and length ($b = 3.3$) that we have found for *S. radians* (Fig. 2). Farm's (1993) report of a linear relationship between cube-root of egg number and fish length for *S. radians* also agrees with this approach. While an exponential function may suffice for predicting the fecundity of smaller *S. radians*, predictions for larger individuals are likely to deviate from reality (e.g. the 200 ml of eggs ($\sim 6 \text{ cm}^3$) predicted for a 30-cm fish; Muñoz & Warner 2004).

Using a power rather than an exponential function for estimating fecundity from length for *S. radians* reduces estimates of size-fecundity skew within a group whenever the largest female's size exceeds 18 cm (Fig. 1a). This has important implications for the potential for size-fecundity skew to influence the life-history tactics of large female *S. radians*. Calculations of fecundity using the derived power function indicate that, based purely on size-fecundity skew arguments, the largest female in every harem, hypothetical or real,

Table 1. Predicted fecundity of female *Sparisoma radians* in a hypothetical harem of five females (size range 14–27 cm) using four different equations to describe the relationship between total length (cm) and clutch volume (ml)

Total length (cm)	(1) Given fecundity $m=0.0177e^{0.31(TL)}$	(2) Cited exponential $m=0.263e^{0.103(TL)}$	(3) Fitted exponential $m=0.025e^{0.298(TL)}$	(4) Fitted power $m=2.2 \times 10^{-4}$ $(TL)^{3.47}$
27	76	4.2*	78.0	20.4*
26.5	65*	4.0	67.2*	19.1
16	3	1.4	2.9	3.3
15	2	1.2	2.2	2.7
14	1	1.1	1.6	2.1

*Equation (1) is a fitted exponential curve to the data on length and fecundity in Table 1 of Muñoz & Warner (2003a). Equation (2) is the equation given by Muñoz & Warner (2004) to describe the relationship between length and fecundity. Equation (3) is the fitted exponential curve that we derived from extracted data (using GraphClick 2.9, Arizona Software, San Francisco, CA, U.S.A.) from Figure 1 in Muñoz & Warner (2004). Equation (4) is the fitted power curve from the same data used to derive equation (3). Asterisks denote the expected sex-changer within this harem based solely upon application of size-fecundity skew effects within an ERST model (see text and Muñoz & Warner 2004 for details). Note that the power curve (4) predicts no deferral of sex change by the largest female (i.e. the cumulative fecundity of harem-mates exceeds her own fecundity).

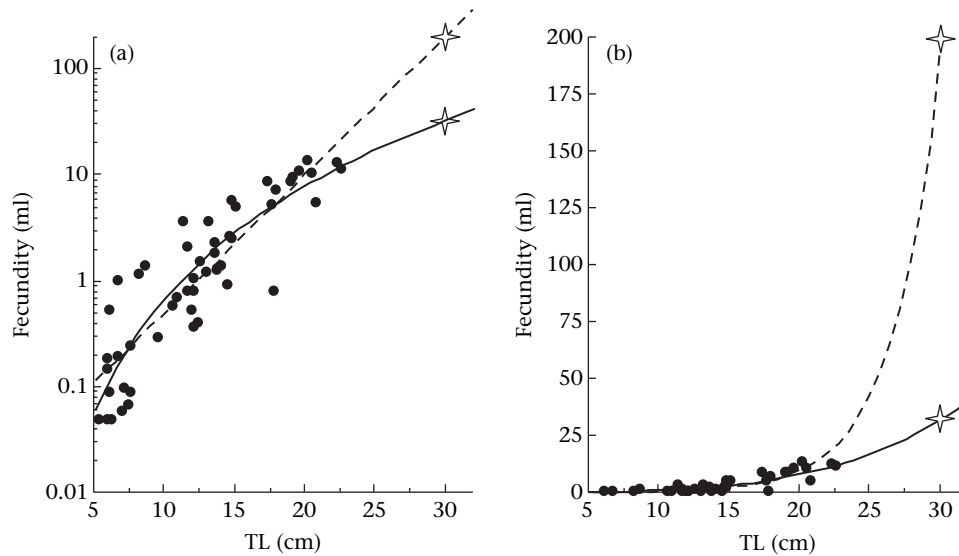


Figure 1. Regressions of total length (TL) versus fecundity for 51 female *Sparisoma radians* plotted with (a) a \log_{10} and (b) an untransformed Y axis from Figure 1 in Muñoz & Warner (2004) (data extracted with GraphClick v. 2.9, Arizona Software, San Francisco, CA, U.S.A.; 1 ml \approx 9600 eggs). Y axes represent virtually identical ranges of fecundity. Fitted curves are from exponential (dashed line; $Y = 0.025e^{0.298(x)}$; $r^2 = 0.78$) and power (plain line; $Y = 2.2 \times 10^{-4}(x)^{3.47}$; $r^2 = 0.80$) regressions. Stars highlight the nearly 10-fold difference in predicted fecundity for a 30.1-cm fish using the two different functions.

described by Muñoz & Warner (2003a, 2004) would have increased her reproductive success by changing sex in the absence of a male (i.e. non-sex-change is never predicted; lower curve, Fig. 3). While the observation that the largest female changed sex only once in 22 male-removal experiments (Muñoz & Warner 2004) reinforces the notion that *S. radians* deviate from the predictions of classical sex-change theory, it also indicates that size-fecundity skew alone does not account for non-sex-change in the species. Such effects could, none the less, be important if, in concert with sperm competition, they sufficiently reduce a female's expectation of reproductive success as a sex-changed male (Muñoz & Warner 2003a).

Sperm Competition and the Timing of Sex Change

Along with estimates of female fecundity, calculations of male reproductive success are a preeminent feature of any model of sex change. In the ERST model, potential reproductive gains to a sex-changing female (i.e. increased mating opportunities within the harem) are discounted by the potential for lost paternity arising from sperm competition from intruding males (Muñoz & Warner 2003a). The recognition that sufficiently high levels of mating interference might influence the timing of sex change represents a potentially important contribution to our understanding of the dynamics of protogyny.

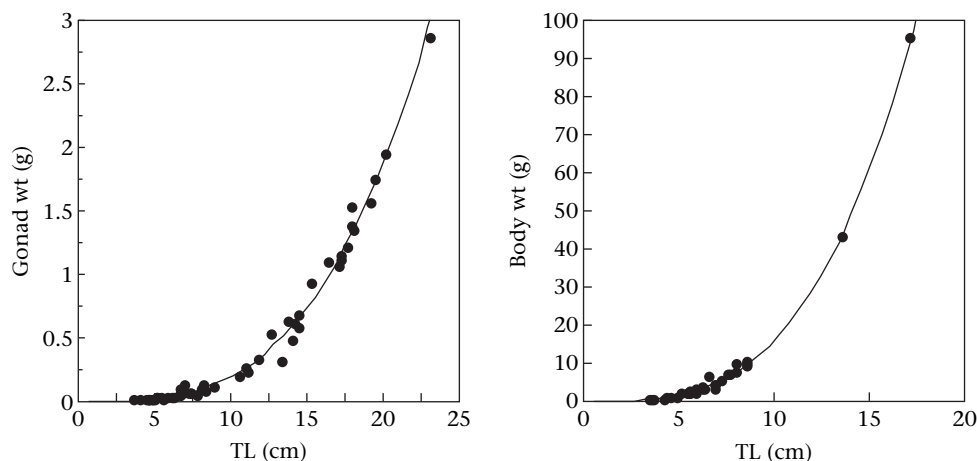


Figure 2. Mass versus total length (TL) relationships for (a) gonad size and (b) total fish mass for female *Sparisoma radians* (blotted wet weights). Fitted curves using Statview 5.0 (SAS Institute, Cary, NC, U.S.A.) from power regressions: (a) $Y = 0.00013(x)^{3.2}$, $P < 0.0001$, $N = 55$, $r^2 = 0.97$; (b) $Y = 0.008(x)^{3.3}$; $P < 0.0001$; $N = 35$, $r^2 = 0.99$. All fish were collected by trawl in sea grass habitat of San Blas, Panama in May 1992.

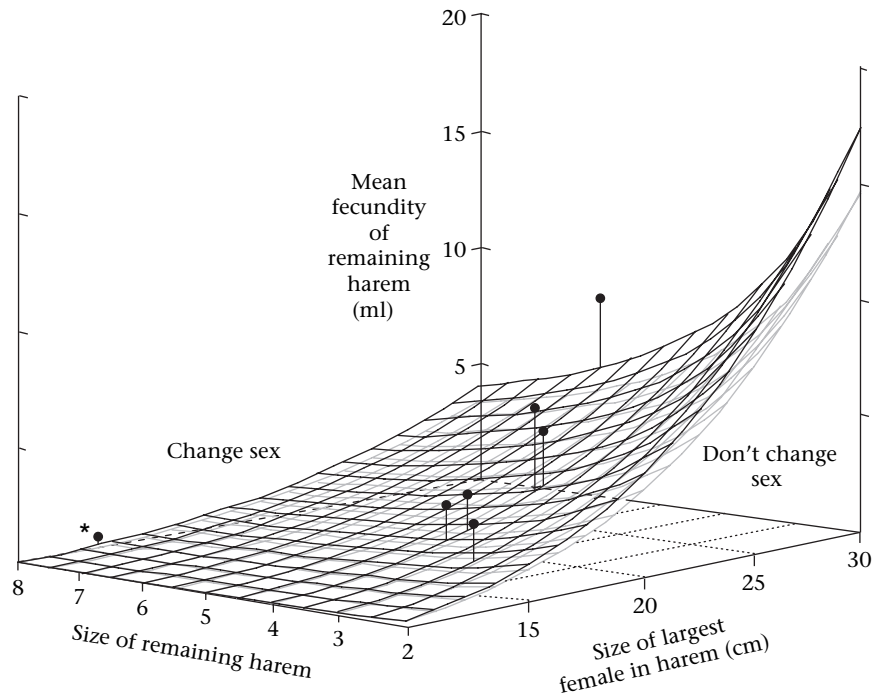


Figure 3. Phase diagram of change-sex/don't-change-sex space calculated from the ERST model (Muñoz & Warner 2003a) for the largest female in a *Sparisoma radians* harem as a function of the female's size, the size of the remaining harem (i.e. without the largest female) and the mean fecundity of fish in the remaining harem. No sex change is predicted by the model for all points that lie below the plotted equilibrium surface (i.e. where the fecundity of the largest female within a harem exceeds the expected reproductive success that she would accrue as a male following sex change). The lower of the two surfaces (grey lines) was generated solely from size-fecundity skew arguments (i.e. no sperm competition), using the power function ($m_x = 2.2 \times 10^{-4}(\text{TL})^{3.47}$). The upper surface (dark lines) incorporates sperm competition, based on observations of a 30% rate of male interference on patch reefs ($P = 0.3$) and a 50% paternity retention when interference occurs ($Z = 0.5$), generating an overall rate of 15% loss of paternity (Muñoz & Warner 2004). Black dots are plotted for the largest female in each of seven territories on patch reefs where sex change by any fish was observed following male-removal experiments (Muñoz & Warner 2004). Note that the ERST model, using a power function to estimate fecundity, predicts sex change by the largest fish (i.e. dots lie 1.6–2.7 times above the fecundity value at change-sex/don't-change-sex surface) in all cases. Sex change by the largest fish was observed only once, however (*; a 13-cm female in a group of nine females). The relationship between harem fecundity (Z axis) and the size of the largest female (Y axis) reveals the extent of size-fecundity skew within a particular harem.

Sperm competition is clearly an important component of *S. radians* social behaviour and life history, with notably high levels of mating interference reported for the species throughout its range (Robertson & Warner 1978; Farm 1993; Muñoz & Warner 2003b, 2004). The question remains, however, whether even the apparently high rates of sperm competition associated with *S. radians* mating behaviour are sufficient to explain non-sex-change using the ERST model? Combining estimates of fecundity (above) with estimates of paternity loss for territorial males on patch reefs (Muñoz & Warner 2003a), we find that social conditions (i.e. harem size and membership) that would predict non-sex-change by large female *S. radians* using the ERST have yet to be described (Fig. 3).

Estimating loss of paternity from observations of sex change

Perhaps the lack of correspondence between the predictions of ERST and observed patterns of sex change by *S. radians* (Fig. 3) arise because rates of male interference (and associated loss in paternity) are actually higher than 30% (the value obtained from observations of 66

matings on patch reefs; Muñoz & Warner 2003b). Mating interference rates for *S. radians* in sea grass habitats range from 46% (in St Croix, USVI; Muñoz & Warner 2003b) to 56% (in Panama; Robertson & Warner 1978). In addition, rates of paternity retention during contested spawns may be lower for *S. radians* than the 50% inferred from work on the bluehead wrasse, *Thalassoma bifasciatum* (the best data available on paternity retention for reef-fish matings with interference; see Wooninck et al. 2000).

We explored these possibilities by calculating the amount of paternity loss needed to explain observed patterns of non-sex-change by larger females following the removal of a territorial male (i.e. the six (of 22) harems of *S. radians* in which a subordinate female changed sex; Muñoz & Warner 2004). First, we estimated the fecundities of all females in those groups based on their lengths using the power function, $m_x = 2.2 \times 10^{-4}(\text{TL})^{3.47}$. We then used the ERST equation for modelling within-harem sperm competition,

$$\text{RS}_{\text{maleSC}} = \left[\left(\sum_{a=1}^H m_a \right) - m_i \right] \times [(1 - P) + (Z \times P)], \quad (1)$$

to calculate the expected reproductive success of the i th female available to that fish as a sex-changed male (where m_x = female fecundity, H = the size of the harem, P = the proportion of matings with interference; Z = the proportion of paternity retained when interference occurs; see Muñoz & Warner 2003b). We compared this value to the current fecundity of the i th female and calculated the overall paternity loss ($P \times Z$) needed to explain observed patterns of sex change (Table 2). We also calculated, for progressively lower values of paternity retention (i.e. $Z = 0.5, 0.25, 0.1, 0.01$), the range of interference rates (P) for which ERST correctly predicted the identity of the sex-changing fish (Table 2).

Our analysis indicates that unprecedented levels of paternity loss are needed to explain non-sex-change by *S. radians* using the ERST model (Table 2). In the six cases where subordinate sex-change occurred, the minimum amount of overall paternity loss needed to explain the identity of the sex-changer exceeded 50% (mean \pm SE = $69.3 \pm 6.0\%$). This general result cannot be reconciled with observed rates of mating interference for the species (Robertson & Warner 1978; Muñoz & Warner 2003b, 2004), even with dramatically lowered expectations of paternity retention during contested spawns (i.e. very small Z). Only under a condition of $Z = 0.01$ were we able to find a single instance (harem 13B; see Table 2) where the calculated rate of interference ($P = 53$ – 66%) bracketed the highest reported rate of mating interference for the species (56%; Robertson & Warner 1978). In fact, even this may be insufficient, as paternity loss within harems is presumably offset by the extraharem mating of territorial males (not modelled by ERST; as high as 23.7% of spawns in Panama sea grass: Robertson & Warner 1978; $\sim 10\%$ in Puerto Rico: Farm 1993; behaviour noted but not quantified in St Croix: Muñoz & Warner 2003b, 2004). On the cumulative basis of this information and our various calculations, we reject the argument that sperm competition and size-fecundity skew, as formulated in the ERST model, explain patterns of sex-change by *S. radians*.

An Alternative Explanation for Non-sex-change by Large Females

Observations of larger-than-male females (Fig. 4) and the results of male-removal experiments (Farm 1993; Muñoz & Warner 2004) clearly indicate that large female *S. radians* consistently do not change sex, even following the disappearance of a local male. We have shown, however, that levels of size-fecundity skew and sperm competition are insufficient in this species to predict non-sex-change using the ERST model; the expected reproductive success available to male *S. radians* is simply too great given natural patterns of fecundity scaling and harem membership, combined with reasonable estimates of sperm competition. We believe the inability of the ERST model to accurately predict the life-history tactics of *S. radians* relates to an important aspect of *S. radians* biology that was excluded from evaluation using ERST: sex-specific differences in mortality (acknowledged as a potentially important aspect of sex-change behaviour, but assumed to be equal in ERST; Muñoz & Warner 2003a).

Sex-specific mortality and the timing of sex change

While observations of larger-than-male females within a protogynous population specify non-sex-change by some females, they also strongly suggest that these females live longer and/or grow faster than males. Although variable patterns of juvenile recruitment into a population (a common feature of coral reef fish populations; e.g. Doherty 2002) might occasionally generate such a demographic pattern (i.e. in the absence of sex-specific differences in mortality and/or growth), variable recruitment is very unlikely to produce the consistent demographic pattern of larger-than-male females found for *S. radians* across different habitats and years (Fig. 4).

Declines in abundance within successive size classes ($n_{\text{size class}}$) can, with a few assumptions, give an estimate of survivorship. We calculated the sex-specific rate of mortality (μ_{sex}) for *S. radians* by fitting the exponential function

Table 2. Overall levels of paternity loss and rates of male interference that are needed to explain observed patterns of forgone female sex-change in six male-removal experiments in which subordinate sex-change occurred (Muñoz & Warner 2004) using the power function ($m = 2.2 \times 10^{-4}(\text{TL})^{3.47}$) to estimate fecundity based on size

Harem*	Group size	Rank (and size) of sex-changer†	Range of total paternity loss‡	Range of male interference rates (P)§			
				Z=0.5	=0.25	=0.1	=0.01
15C	7	5 (16.2 cm)	0.937–0.954	NP	NP	NP	0.94–0.96
13B	5	2 (20.0 cm)	0.519–0.654	NP	0.70–0.87	0.58–0.72	0.53–0.66
13A	5	2 (16.2 cm)	0.598–0.680	NP	0.80–0.90	0.67–0.75	0.61–0.68
8A	4	3 (14.5 cm)	0.650–0.700	NP	0.87–0.93	0.73–0.77	0.66–0.70
8B	5	3 (19.4 cm)	0.677–0.748	NP	0.91–0.99	0.75–0.83	0.69–0.75
2	5	4 (15.3 cm)	0.779–0.790	NP	NP	0.87–0.88	0.79–0.80

Ranges were calculated using the ERST equation for modelling within-harem sperm competition (equation (1)) both as: (1) total paternity loss ($P \times Z$); and as (2) a function of mating interference rate (P) given four different values of increasingly lower paternity retention (Z) when interference occurs. 'NP' = not possible; denoting cases where observed patterns of sex change would require an interference rate (P) > 1.0 for the given value of Z .

*From Table 3 in Muñoz & Warner 2004.

†Largest fish rank = 1, second largest = 2, etc.

‡Reported as the proportion of total paternity loss ($P \times Z$) for a territorial male due to mating interference.

§Reported as the proportion of spawns by a territorial male that include interference by an intruding male (P).

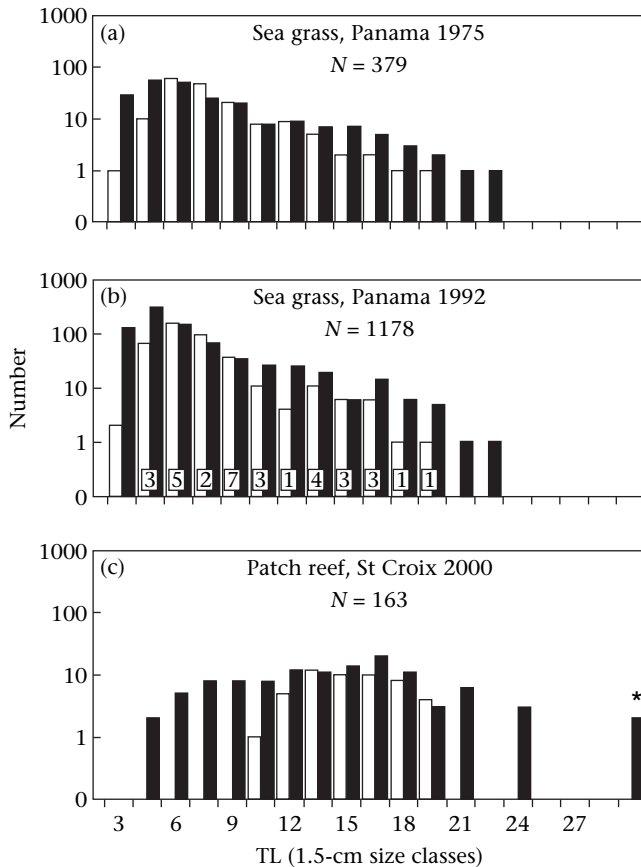


Figure 4. Size distributions of terminal phase (TP) male (□) and female (■) *Sparisoma radians* (log scale improves visualization of very large fish). (a) From trawls of sea grass habitat in San Blas, Panama (Robertson & Warner 1978; length converted from standard length (SL) to total length (TL) using the equation $TL = 1.22(SL) + 0.113$ from regression of dual measurements of *S. radians* collected by the authors during sea grass trawls in 1992; size range 3.6–21.9 cm TL, $N = 98$, $r^2 = 0.998$). Data from 1-cm size classes were fitted to 1.5-cm size classes using interpolation. (b) From trawls in the same location as (a) in 1992 (described in Clifton & Robertson 1993). The number of additional transitional fish (in the process of sex change) is boxed within each size class. (c) From visual census of patch reefs in St Croix (Muñoz & Warner 2004). Small males are notably absent from patch-reef populations. *Size of two very large *S. radians* females (visually estimated at 30.1 cm) extends the maximum size previously reported for the species by ~25% based on collections of measured fish (e.g. Randall 1983; panels a, b).

$n_{\text{sizeclass}} = ae^{(\mu_{\text{sex}})}$ to size-frequency data for males and females within 1.5-cm size classes from three surveys of *S. radians* (Table 3). We used data only from the most abundant size class (i.e. the mode) to the largest observed size class for each sex, and assumed that lower counts for the smaller (pre-mode) size classes reflected either reduced detection of smaller fish or nonlinear growth. Assuming no gender-related differences in growth for larger fish and normally distributed temporal patterns of recruitment, this approach generates a conservative estimate of sex-specific differences in mortality for monandric (all males derived from females) hermaphrodites such as *S. radians* (i.e. some loss of females in larger size classes will reflect sex change rather than mortality, while conversely, the

Table 3. Sex-specific mortality rates (μ) for territorial (TP) male and female *S. radians* estimated from fitted exponential curves to size-frequency data from three different population surveys (Fig. 4; see text for details)

Sex	N	Mortality (μ)	Relative risk ($\mu_{\text{male}}/\mu_{\text{female}}$)	Study
Female	222	-0.222	—	Robertson & Warner 1978
TP male	157	-0.324	1.46	
Female	781	-0.284	—	Clifton & Robertson 1993*
TP male	397	-0.352	1.24†	
Female	113	-0.148	—	Muñoz & Warner 2004
TP male	50	-0.161	1.10	

*See Fig. 4.

†Counts of 32 transitional (in the process of sex change) *S. radians* from the 1992 sea grass trawls (size range 5.2–20.2 cm; see Fig. 4) provide an estimate of size-specific probabilities of changing sex and suggest that TP males in sea grass actually die ~1.6 times (i.e. 60%) faster than females.

addition of males to the population via sex change will mask male mortality).

Our analysis of size/frequency data for larger *S. radians* suggests that territorial (TP) males die faster than females in both sea grass and patch-reef habitats, although the effect appears greater in Panamanian sea grass habitats, where the overall risk of dying seems higher (Table 3). The inference that male *S. radians* suffer higher rates of mortality is corroborated by direct evidence of sex-specific mortality differences in the species; in Panama, TP males suffer significantly higher rates of predation than females because of their mating activities (Clifton & Robertson 1993). Contrary to suggestions elsewhere (Muñoz & Warner 2004), the relative risk of mortality increases with size (Fig. 5), such that males larger than 11 cm (roughly the size where most TP males begin defending

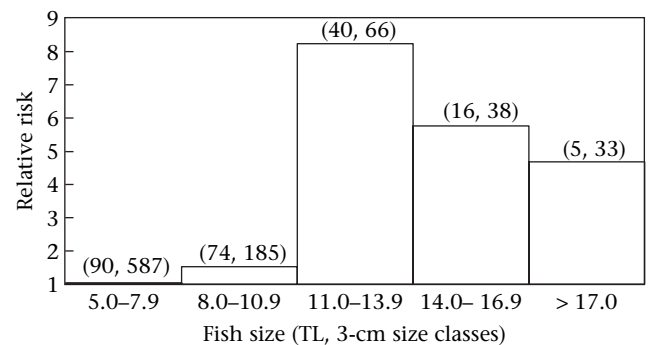


Figure 5. Relative size-specific risks of mortality for male versus female *S. radians*. Calculated from a size-specific comparison (total length = TL) of the number of terminal phase (TP) male and female *S. radians* ≥ 5.0 cm ($N = 225$) found in the stomachs of 224 yellow jacks, *Carangoides bartholomaei*, with the abundance of *S. radians* collected in sea grass trawls ($N = 1178$) from the same areas where the jacks were obtained. Numbers in parentheses above each bar indicate sample sizes for fish in gut and trawl, respectively, for each size category. Male *S. radians* that were larger than 11.0 cm were seven times more likely to die than females of the same size range.

territories in Panama; K. E. Clifton, unpublished data) are at the highest risk of dying.

In the parlance of the ERST model, the very high rates of mortality associated with being a large male, much like sperm competition, should effectively raise a female's threshold for sex change by reducing her immediate expectations of reproductive success as a male. Using more traditional size-advantage modelling, a high rate of mortality for larger males lowers expectations of future reproductive success as a male relative to females and, if sufficient, will make sex change increasingly less profitable for females beyond a certain size. With either perspective, the observed high rate of male mortality found in *S. radians* may be sufficient to predict non-sex-change by some females, with the tendency to forgo sex change increasing with size (Fig. 6). This effect may be amplified if females also grow faster than males (as suggested by Farm 1993) or if longer-lived individuals produce eggs or offspring of higher quality.

In reality, mortality rates reflect a probability of dying rather than a certainty. Expectations of lifetime reproductive success reflect these probabilities and are thus probabilistic themselves (i.e. while most individuals obtain reproductive success levels close to the population mean, others will achieve substantially more or less success depending upon when they die; e.g. Rogers 2003). Within a protogynous population, we may find that sex-change tactics across a broad range of sizes generate equal fitness, with the mean success of a particular size-at-sex-change tactic reflecting the composite of those that died early (low success) and those that survived for a long time (high success). As sex-specific costs such as mortality reduce average male reproductive success (Fig. 6a), an increasing larger proportion of females can be expected to adopt a tactic of delayed or completely forgone sex change (Fig. 6b).

Given the general premise that high risks of male mortality promote non-sex-change by a proportion of

the females within a protogynous population, we see several proximate mechanisms by which such a process might be regulated. (1) Selection resulting from a higher risk of male mortality might produce a genetically based system of sex allocation that produces both hermaphrodites and gonochores (i.e. some females will never change sex), although the variable nature of physical and social environments faced by marine fish, and their generally labile responses to such environments (e.g. Warner 1991), might argue against such a scenario. (2) A female's tendency to change sex, based on general environmental cues may be a labile function of size, such that larger females require increasingly greater stimuli from cues that may induce sex change (e.g. male interaction rates or shifts in local demography). (3) Females may respond directly to local social or demographic cues that indicate mortality risk (e.g. patterns of conspecific disappearance). There is substantial evidence that general monitoring of the social environment (a necessary component of 2 and 3) occurs in coral reef fish and that it influences sex-change (Munday et al. 2006). We note that in the 'assessment of mortality risk' scenario (3), a delay in sex change, especially by large females, is predicted following single- or multiple-male-removal experiments, as such removals mimic male mortality events. Removal experiments by Muñoz & Warner (2004) support this prediction. Further resolution of the influence of these possible mechanisms for sex change in *S. radians* awaits future investigation.

A model of non-sex-change that includes sex-specific mortality

Muñoz & Warner (2003a) described the ERST model as a first step, and suggested that future models should include elements beyond the instantaneous reproductive rate (i.e. expected future reproductive success, RV). We agree that a more complex model is probably necessary

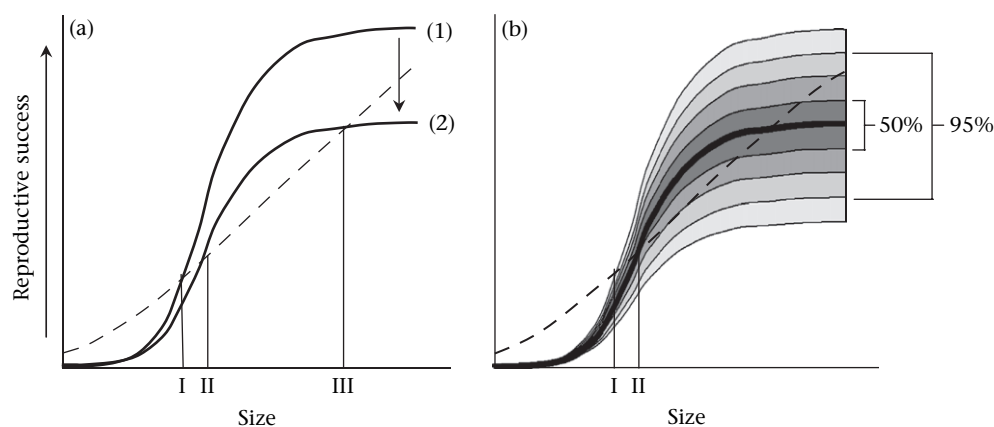


Figure 6. Reproductive success (RS) versus size for males (dark lines) and females (dashed lines). (a) Means only (i.e. no variance) for two plots of male RS. Decline (arrow) reflects increasing 'costs' of being male relative to life as a female (e.g. from sex-specific mortality, sperm competition, etc.). This alters predictions of size at sex change between populations: (1) relatively low male costs: sex change at size I; (2) male 'costs' greater than (1) with sex change at II (note: a female somehow persisting to size III (e.g. proximate cues for sex change not encountered up to that point) should never change sex). (b) Mean and variance for one plot of male RS curve (thick central line); shaded regions represent different probabilities of RS (50% and 95% probabilities noted). A 'rule of thumb' tactic based on average RS predicts sex change at size II, however, variance in the potential for reproductive success as a male should promote sex change by some females beginning at size I and a non-sex-change for other females across the entire range of sizes. Proportionally more females should adopt a tactic of non-sex-change at larger sizes. Evidence of sex change across a very broad range of sizes (e.g. Fig. 4b; transitional fish observed in most size classes) lends support to this scenario.

to fully understand *S. radians* behaviour, but note that modelling the full life history will inevitably lead to a different explanation than the one offered by ERST. Like ERST, the earliest mathematical treatments of the size-advantage model (1) assumed no sex-specific differences in growth and mortality and (2) regarded the size-specific instantaneous reproductive rate as the optimization criterion (e.g. Warner 1975; Warner et al. 1975; Leigh et al. 1976). Later treatments considered reproductive value (RV) as the fitness correlate, allowing size-specific variation in growth, mortality and reproduction across the sexes to influence the timing of sex change (e.g. Warner & Downs 1977; Warner 1984, 1988; Hoffman et al. 1985; Charnov 1986; Schultz & Warner 1989, 1991; Iwasa, 1991; Day & Aarssen 1997; St Mary 1997; Rogers & Sargent 2001). While the early treatments were extremely important and succeeded in demonstrating both the adaptive significance of sex change and of the timing of sex change, later models based on RV showed that maximizing instantaneous fitness does not maximize fitness when the other vital rates vary. Most notably, at least two models (Charnov 1986; Day & Aarssen 1997) show that sex change may be adaptive in the absence of any size-specific reproductive advantage across the sexes. In the strictest sense then, when the size-specific growth and/or mortality rates vary between males and females, sex-change models using the instantaneous reproductive rate as the optimization criterion do not necessarily maximize fitness.

We suggest, as an alternative next step, a return to traditional life-history approaches considering age/size-specific mortality and fecundity schedules to generate estimates of reproductive success at different size/ages ($\sum l_x m_x$). Such an approach seems necessary to predict sex-specific schedules of reproductive success for species like *S. radians* whose vital rates vary between the sexes, and we offer a rough guide as to how such analysis should proceed. For females, the expected reproductive success of a fish of size (TL) living to age/size-class (n) is rather easy to calculate and can be predicted by the function

$$RS_{\text{female}} = \sum_{x=1}^n l_x \times m_x = \sum_{x=1}^n (1 - \mu_{\text{female}})^x \times a(\text{TL})^b \quad (2)$$

where μ is the sex-specific mortality rate.

For males, calculations of RS are more complicated, because, in addition to the mortality rate, reproductive success will be determined by social factors such as: the size-specific probability of acquiring a territory (α_x), the average collective fecundity of females living within the territories (\bar{m}_{harem}), the amount of paternity loss arising from sperm competition within territories (a function of P and Z), the rate (Q) of extraharem mating and the associated average collective fecundity of mates outside the harem (\bar{m}_{extra}). Given this, the reproductive success of a male living to age/size-class (n) might then be described by the function

$$RS_{\text{male}} = \sum_{x=1}^n [(1 - \mu_{\text{male}})^x] \times [\alpha_x \times \{(\bar{m}_{\text{harem}} \times [(1 - P) + (P \times Z)]) + (\bar{m}_{\text{extra}} \times Q \times Z)\}] \quad (3)$$

In this equation, we imagine α_x to be a sigmoid (threshold) function of size,

$$\alpha_x = \left(\frac{\alpha_0 e^{rx}}{1 + \alpha_0 (e^{rx} - 1)} \right), \quad (4)$$

where the initial probability of acquiring a territory (α_0) is very small and, in combination with the scaling coefficient (r), describes the size/age class at which males begin to successfully compete for territories. This equation assumes that all males eventually acquire a territory beyond a certain size.

Might size-fecundity skew and sperm competition be more important elsewhere?

In its formulation, the ERST model essentially describes a harem social system of discrete female groups in which future mating opportunities for sex-changed females come from within their current social unit. Observations of *S. radians* suggest a more 'open' social organization in which males (including territory holders) regularly intrude on the spawning efforts of other males (Warner & Robertson 1978; Farm 1993; Muñoz & Warner 2003b, 2004) and outsiders move in following the disappearance of the territory owner (Farm 1993; Muñoz & Warner 2004). The nature of sea grass habitats may contribute to this less-than-harem behaviour by providing higher success for alternative male mating tactics (Robertson & Warner 1978; Robertson et al. 1982; Muñoz & Warner 2003a). These same areas, however, lacking the cover of reefs, also appear to expose males to higher risks of predation (Clifton & Robertson 1993), a feature of demography that ERST cannot accommodate. Accordingly, we suggest that advocates of the model look for species that are more closely associated with refuges from predation when seeking to address the model's utility.

Our analysis of the relationship between group size and fecundity, as modelled by ERST (Fig. 3), emphasizes that a prediction of non-sex-change arising solely from size-fecundity skew and sperm competition, if it is ever to occur, is most likely to be found in very small harems with high levels of size-fecundity skew. Strong expressions of female dominance within groups (clearly lacking in *S. radians*; Farm 1993) seem a likely means for promoting within-harem variation in female size and associated increases in the level of size-fecundity skew (beyond the obvious constraints imposed upon fecundity by body size). In this vein, examination of species that change sex within strict linear dominance hierarchies may reveal that ERST helps explain subtle aspects of the timing of sex change by larger females. We note, in conclusion, however, that observations of larger-than-male females within protogynous populations strongly suggest a situation that is unsuitable for ERST modelling, as such demography is almost certainly the result of sex-specific differences in mortality and/or, possibly, growth. Sex-specific variance in the vital rates are clearly an influential component of many aspects of an organism's behaviour, however, the effect of such variance upon an individual's life-history tactics cannot be judged using the ERST model.

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