Testing a new version of the size-advantage hypothesis for sex change: sperm competition and size-skew effects in the bucktooth parrotfish, *Sparisoma radians*

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A variety of field studies suggest that sex change in animals may be more complicated than originally depicted by the size-advantage hypothesis. A modification of the size-advantage hypothesis, the expected reproductive success threshold model, proposes that sperm competition and size-fecundity skew can strongly affect reproductive pay-offs. Size-fecundity skew occurs if a large female’s fecundity is markedly higher than the aggregate of the other members of her social group and, together with paternity dilution from sperm competition, can produce situations in which large females benefit by deferring sex change to smaller females. Deferral by large females can create sex-size distributions characterized by the presence of large females and small sex-changed males, and it is precisely these distributions that the traditional size-advantage model cannot explain. We tested the predictions of the new model with the bucktooth parrotfish, *Sparisoma radians*, on coral reefs in St. Croix, U.S. Virgin Islands. Collections and spawning observations determined that the local environmental regime of *S. radians* is characterized by pervasive sperm competition (accompanying 30% of spawns) and factors that can produce substantial size-fecundity skew in social groups. Dominant male removal experiments demonstrate that the largest females in social groups often do not change sex when provided an opportunity. Instead, smaller, lower-ranking females change sex when a harem vacancy arises. This pattern of sex change is in contrast to virtually all previous studies of social control of sex change in fishes, but provides strong support for the general predictions of the expected reproductive success threshold model. Key words: coral reefs, Labridae, protogyny, Scaridae, seagrass beds, size-fecundity skew, social control of sex change, sperm competition. [Behav Ecol 15:129–136 (2004)]

Sequential hermaphroditism (functioning as male during one life phase and as female during another) is common in marine fishes (Francis, 1992; Kuwamura and Nakashima, 1998; Shapiro, 1987; Warner, 1984), with protogyny (sex change from female to male) predominating. The size-advantage model (Ghiselin, 1969; Warner, 1975; Warner et al., 1975) has been highly successful in explaining the adaptive significance of sequential hermaphroditism. In essence, the model proposes that individuals should change sex if reproductive success increases with size or age more rapidly for one sex than for the other. Protogyny is predicted if males gain in reproductive success with size or age faster than do females (e.g., when large males monopolize matings; Warner, 1978, 1984, 1988), and protogynous life histories are frequently found in fishes with haremic social systems in which dominant males control access to females (Robertson and Warner, 1978; Ross, 1990; Warner and Robertson, 1978). In these species, sex change is often under social control (Fishelson, 1970; Fricke and Fricke, 1977; Robertson, 1972; Ross et al., 1983; Shapiro, 1980; Warner and Swearer, 1991); on removal of the dominant male, the largest remaining female changes sex and takes over the harem (Ross, 1990; Warner, 1988).

Despite the success of the size-advantage hypothesis in predicting patterns of sex allocation, a variety of field studies suggest that the process of sex change may be more complicated than originally depicted by the traditional hypothesis. For example, in some protogynous fishes, the largest females do not necessarily change sex when provided an opportunity (Cole, 1983; Cole and Shapiro, 1995; Lutnesky, 1994). In many species with clear histological evidence of the capability of sex change, males may not be the largest individuals in local populations and may not even be predominant in the largest size classes (de Girolamo et al., 1999; Robertson and Warner, 1978). This suggests that the simplest form of the size-advantage hypothesis is incomplete.

Muñoz and Warner (2003a) proposed a new version of the size-advantage hypothesis (the expected reproductive success threshold, or ERST model) in an attempt to reconcile these anomalous field data with the traditional hypothesis. The ERST model predicted the probability of an individual changing sex in local social groups by examining the effects of sperm competition and size-fecundity skew on expected reproductive success as a male or as a female. Size-fecundity skew occurs if a large female’s fecundity is markedly higher than the aggregate of the other females in her social group. Since a newly sex-changed individual mates with all remaining female harem members but no longer reproduces as a female, size-fecundity skew can create conditions for large females in which expected reproductive success as a male is actually lower than current reproductive success as a female. In addition, paternity dilution from sperm competition lowers expected male reproductive success but does not change fitness pay-offs to females. Although unconsidered in previous models of sex change, sperm competition and size-fecundity skew...
skew were found to affect reproductive expectations strongly, and the model predicted a variety of circumstances in which the largest females remaining in a social group should not change sex on disappearance of a dominant male. These same conditions were found to promote sex change in smaller females. The model suggested that deferral of sex change should be more common in species in which intense sperm competition is prevalent (such as fishes living in or adjacent to seagrass beds). This prediction was consistent with general patterns seen in nature (Muñoz and Warner, 2003a), but an experimental test has been lacking. The purpose of this study is to test the ERST model for protogynous sex change by conducting dominant male removal experiments in a system in which the model predicts that the largest female will defer sex change to a smaller female. The Caribbean bucktooth parrotfish, Sparisoma radians, is an ideal species for this test.

**Applicability of the ERST model to Sparisoma radians**

Sparisoma radians is a monandric (i.e., all males have changed sex from a prior female phase; Robertson and Warner, 1978) protogynous parrotfish. It is a common herbivorous fish in Caribbean seagrass beds and is one of the most abundant species in this habitat (Lobel and Ogden, 1981; Randall, 1968; Weinstein and Heck, 1979). Populations of S. radians form isolated aggregations in seagrass habitats (Ogden and Ziemann, 1977; Robertson and Warner, 1978), within which dominant, brightly colored males in terminal phase (TP) coloration defend contiguous territories and harems of drab colored females in initial phase (IP) coloration. These all-purpose territories are used for feeding, mating (external fertilization), and shelter. In St. Croix, S. radians also occurs on patch reefs where both large and small males maintain territories and harems; in patch reef habitats particularly, individuals can attain extraordinarily large sizes (Muñoz and Warner, 2003b). In the seagrass, nonterritorial males roam across territories as “bachelors” and can be either TP or IP males (those having retained the female coloration; Farm, 1993; Robertson and Warner, 1978). The fish spawn daily each afternoon (usually between 1500–1730 h) during a 30–90-min spawning period, and mating tends to be assortative by size (for further details of reproductive biology, see Farm, 1993). Territorial males normally spawn singly with a female (pair spawning) but will occasionally engage in sperm competition by rushing in and contributing sperm to an ongoing mating between a neighboring male and female (“streaking”; Warner and Robertson, 1978). In contrast, bachelor males nearly always face sperm competition because most of their matings involve streaking a larger male and female pair, or group spawning in which several males mate simultaneously with a female (Farm, 1993; Marconato and Shapiro, 1996; Robertson and Warner, 1978). Sparisoma radians shows a peculiar sexual pattern given its protogynous life history and harem social system, characterized by high overlap between male and female size distributions, with sexually mature individuals ranging in size from 20–300-mm standard length (SL) and high-fecundity females occupying the largest size classes in the population (Robertson and Warner, 1978; this study) (Figure 1A). Despite their sometimes larger size, females remain subordinate to the territorial male in their harem (Muñoz RC, personal observation).

Specifically, S. radians exhibits features identified by the ERST model that may critically affect the sex change process: the species resides in habitats that appear to facilitate sperm competition (i.e., large aggressive males may have difficulty preventing other smaller males from interfering with spawning because the abundant cover of seagrass allows intruders to enter or hide very close to a territory and subsequently parasitize a spawning pair; Robertson and Warner, 1978; Robertson et al., 1982), and the large size range of mature fish may allow significant size-fecundity skew in local social groups. A comparison of seven of the eight members in the genus Sparisoma (Table 1) shows that S. radians has the largest mature female size distribution, the highest proportion of spawns that are streaked, and the largest male gonadosomatic index (GSI, a measure of the proportion of the body weight devoted to reproduction and an indicator of sperm competition; see Harcourt et al., 1981; Harvey and Harcourt, 1984; Marconato and Shapiro, 1996; Möller, 1988; Warner and Robertson, 1978). Furthermore, within larger comparisons of parrotfishes and wrasses (n = 12–30 species), S. radians maintains one of the largest mature female size distributions, the highest proportion of spawns that are streaked, and the second largest GSI (Table 1).

To test the ERST model, we determined quantitative estimates of key demographic features within local social groups that we then used to direct subsequent dominant male removal experiments. Our aim was to initiate sex change in a range of social groups, including those in which the ERST model predicted sex change by females smaller than the largest remaining females.

**METHODS**

**Study site**

This study took place on patch reefs in Tague Bay (64°35’42” W, 17°45’45” N) on the northeast coast of St. Croix, U.S. Virgin Islands, from April–August 1998–2000. A bank barrier reef bounds Tague Bay to the north (Adey, 1975), and a series of patch reefs averaging about 1500 m² in area (Glädfelter and Glädfelter, 1978) are interspersed throughout a mixed seagrass community. Turtlegrass, Thalassia testudinum, is the dominant seagrass, whereas varying quantities of manatee grass, Syringodium filiforme, and shoal grass, Halodule wrightii, are locally predominant (Robblee and Ziemann, 1984). Depths within the study site range from 2–6 m.

**Quantitative estimates of female fecundity and incidence of sperm competition**

Female S. radians were collected with long-handled monofilament hand nets (1.0 × 0.5-m net aperture, 1-cm mesh size) shortly before the spawning period. Fish were measured for SL and total length (TL) and weighed to the nearest gram. We determined female fecundity by expressing their eggs into graduated tubes for measurement of wet settled volume following the methods of Schultz and Warner (1989), except that we washed the eggs with fresh water rather than with ethanol. Fish were then held in coolers of aerated seawater for a recovery period of approximately 2 h and subsequently returned to their home reefs.

To estimate male reproductive success and the incidence of sperm competition, we conducted daily spawning observations of territorial males. We determined the proportion of spawns accompanied by interfering males, the frequency of male mating, and the size and number of females in harems. We estimated harem size (number of females) from the location of female home ranges and from the number of spawnings observations made on consecutive days showed good agreement in the daily number of spawns obtained per male (Muñoz RC, unpublished data). We commenced spawning observations approximately 30 min before the first observed spawn of the focal male and concluded the observations after 30 min had passed without further sexual
activity. We recorded the number of interfering males and the time for each spawn that occurred.

**Experimental procedure**

Given the female size-fecundity relationships and incidence of sperm competition in Tague Bay, we identified local social groups for which the ERST model (Muñoz and Warner, 2003a) predicted that the largest female should defer sex change when given an opportunity for such a change via experimental removal of dominant males. We removed dominant males from 22 harems on eight patch reefs in an attempt to initiate sex change in the remaining harem members. Removals took place outside the spawning period. We confined our removals to large fish on patch reefs because the larger size of reef fish, the larger size-skew of reef harems, and the lower densities of harems on patch reefs (Muñoz and Warner, 2003b) allowed us to observe the effects of removals more easily in this habitat than in seagrass.

After removals, we conducted daily searches during the spawning period, monitoring experimental patch reefs for sex-changing individuals or roving bachelors attempting to take over the experimental harems. The rate of bachelor male arrival decreases across Tague Bay with distance from the barrier reef, and under natural conditions, roving bachelors may quickly fill harem vacancies as they arise near the barrier reef. In contrast, sex-changed males may recruit from within harems to fill vacancies that arise on more isolated patch reefs further away from the barrier reef (Muñoz and Warner, 2003b). In the removal experiments, we hoped to increase the probability that harem takeover would come from within the reef harem, but our experimental patch reefs were located at varying distances from the barrier reef. Therefore, bachelors were removed and transplanted to distant patch reefs when seen. We identified sex-changing individuals by the initiation of male behaviors and/or coloration (Muñoz and Warner, 2003b).

Once transitional individuals were identified, they were observed on a daily basis during the spawning period to determine the onset of their participation in mating. We validated our observations of external morphology and male behavior by tracking the fertilization rate of unstreaked pair spawns between transitionals and females over several consecutive days (Muñoz and Warner, 2003b). The onset of substantial fertilization rates (i.e., more than 80%, approximately the median fertilization rate of unstreaked pair spawns in nonexperimental fish; Muñoz and Warner, 2003b) was taken as an indicator of completed sex change. We determined fertilization rates and sperm concentrations by collecting gametes that were spawned, following procedures outlined in Shapiro et al. (1994).

To confirm that any sex change observed was the result of our removals (i.e., to control for spontaneous sex change), we monitored 14 harems on four additional unmanipulated patch reefs. We determined the identities of resident fish through unique natural color markings, individual sizes, and home range locations. We searched for transitional individuals and took a census of all fish every 3 days for 1 month.

**Analyses**

Before parametric analyses, data were tested for normality with the Kolmogorov-Smirnov test and for homoscedasticity with the Levene Median test, or transformed by \(1/\sqrt{x}\) when necessary.

**RESULTS**

Fifty-one female \(S.\ radians\) were sampled for fecundity. These fish ranged in size from 5.25–22.5 cm TL (mean \(\pm\) SE = 12.52 \(\pm\) 0.70 cm) and ranged in weight from 2.96–204.4 g (51.81 \(\pm\) 54.03 g). A strong positive relationship between female body size and fecundity emerged from these data, with some larger reef-based females 1.5 to two orders of magnitude more fecund than smaller females (Figure 1B).

Sperm competition is prevalent in the mating system of \(S.\ radians\), with 30% of 66 spawns observed on patch reefs accompanied by interfering streaker males (Muñoz and Warner, 2003b).

**Patterns of sex change and the ERST model**

Eight different patch reefs were chosen for experimental removals, and characteristics of their residents are shown in
Other members of the genus *Sparisoma* include the stoplight parrotfish, *Sparisoma viride*, redband, *S. aurofrenatum*, yellowtail, *S. rubripinne*, redtail, *S. chrysopterum*, greenbloat, *S. atomarium*, and Mediterranean, *S. cretense*. Data are not available for the remaining member of the genus, the strigate parrotfish, *S. striatum*. Data from de Girolamo et al. (1999), Robertson and Warner (1978), and van Rooij et al. (1996).


Table 1

<table>
<thead>
<tr>
<th>Conditions identified by the ERST model that may affect or be relevant to the expected reproductive success threshold between female fitness and fitness after sex change to a male</th>
<th>Sparisoma radians</th>
<th>Median (range) for other Sparisoma</th>
<th>Median (range) for other labroids (parrotfishes and wrasses)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mature female size range (mm)</td>
<td>160</td>
<td>116 (50–150)</td>
<td>79 (50–160)</td>
</tr>
<tr>
<td>No. of species</td>
<td>6</td>
<td>23</td>
<td></td>
</tr>
<tr>
<td>Percentage of spawns with sperm competition</td>
<td>56</td>
<td>12.0 (0–14.1)</td>
<td>3.0 (0–11.4)</td>
</tr>
<tr>
<td>No. of species</td>
<td>6</td>
<td>5</td>
<td></td>
</tr>
<tr>
<td>Male GSI (100 × [gonad wt./total body weight])</td>
<td>0.76</td>
<td>0.11 (0.06–0.2)</td>
<td>0.15 (0.09–0.85)</td>
</tr>
<tr>
<td>No. of species</td>
<td>5</td>
<td>13</td>
<td></td>
</tr>
</tbody>
</table>

- **Table 2. Harems on control patch reefs showed characteristics within the range of experimental patch reefs.** A total of seven females from five different patch reefs changed sex after removal of dominant males (behavioral details of the sex change process will be reported elsewhere). The most striking result of the removal experiments was the size of females that initiated sex change (Table 3). All but one of the sex changers were smaller than the largest females remaining in the harems, demonstrating that overall, the largest female *S. radians* in local social groups do not change sex. In addition, the females that changed sex included individuals smaller and larger than the average size of dominant males, indicating that large females are physically capable of changing sex but in certain circumstances appear to defer sex change to smaller males (Muñoz and Warner, 2003a,b). Harems in which sex change occurred tended to be larger than harems in which sex change did not occur (sex change: 5.71 ± 0.64 females, *n* = 7; no sex change: 4.27 ± 0.49 females, *n* = 15; *t* test on 1/*√x* transformed data: *t* = −1.92, *p* = .069, df = 20).

Equally striking as the pattern of sex change was the lack of sex change on three of the eight patch reefs (three of 98, two of 99, and one) and in 15 of 22 experimentally manipulated harems. In an effort to identify other correlates of sex change, we quantified the following estimates for harems with and without sex change: female size and fecundity difference between smallest and largest females, female aggregate fecundity, and fecundity skew (for this case only, we refer to skew in the statistical sense [g3], i.e., the third central moment divided by the cube of the standard deviation; Sokal and Rohlf, 1995). Harems without sex change appeared similar to harems with sex change (for all comparisons, *p* > .05) (Table 4). When examining entire reefs, there was a trend for reefs with sex change to harbor a greater number of harems than did reefs without sex change (sex change reefs: 3.60 ± 0.74 harems, *n* = 5; reefs without sex change: 1.33 ± 0.35 harems, *n* = 5; *t* test: *t* = 2.21, *p* = .069, df = 5), but it is unclear whether this is an effect of reef size per se or simply an artifact of larger numbers of harems on larger reefs. Because observations continued for 53 days after removal, well beyond the control reef observations, it is unlikely that sex change ever occurred in these harems owing to any experimental manipulation. Instead, remaining females simply continued spawning with small seagrass or reef TP males and, in most cases, were incorporated into the harems of adjacent smaller males. In a few cases, we witnessed large females making short migrations out of their home ranges to spawn with males in the seagrass and then returning to the reef (Muñoz and Warner, 2003b).

Finally, no transitionals were seen during censuses of unmanipulated control patch reefs, suggesting that our removals were responsible for the incidences of sex change observed.

**DISCUSSION**

Support for the general predictions of the ERST model

Although the protogynous life history of parrotfishes has long been known (Choat and Robertson, 1975), our removal experiments provide the first field evidence of social control of sex change in these common tropical herbivorous fishes (Muñoz and Warner, 2003b). Dominant male removal experiments in *Sparisoma radians* demonstrate that in most cases, the largest females in a harem do not change sex when provided an opportunity. Instead, smaller lower-ranking females change sex and fill harem vacancies. This pattern of protogynous sex change contrasts with virtually all previous studies of sex change in fishes (for review, see Kuwamura and Nakashima, 1998; Shapiro, 1984; Warner, 1984; but see Cole, 1983; Cole and Shapiro, 1995; Robertson and Warner, 1978).

Most of these previous studies lend support to the standard size-advantage model, which has come to be a widely accepted tenet in evolutionary ecology (Ross, 1990). This traditional theory, however, cannot adequately explain the presence of sex change in subordinate individuals.

More recent models of sex change have broadened our understanding of sex change theory by indicating that additional factors beyond size can affect reproductive expectations, including costs to sex change itself, differential growth and mortality, and the magnitude of future reproductive value relative to current reproductive value. These factors can generate conditions that favor gonochorism (separate sexes),
sex change with an extended nonreproductive period between male and female function, or a decrease in reproductive effort with size (Charnov, 1986; Iwasa, 1991; Rogers and Sargent, 2001). The ERST model for protogynous reproductive effort with size (Charnov, 1986; Iwasa, 1991; Rogers and Sargent, 2001). The ERST model for protogynous sex change (Muñoz and Warner, 2003a) generates novel predictions by indicating that sperm competition and size-fecundity skew can create conditions that inhibit sex change in large females yet promote sex change in small females; this mode of sex change can give rise to sexual patterns seen in S. radians and other fishes (de Girolamo et al., 1999; Robertson and Warner, 1978) that can be viewed as anomalous by the traditional size advantage model.

Fishes are believed to show the widest range of sperm competition for any animal group, ranging from complete mate monopolization and monogamy to the explosive breeding of communal spawners, and there is ample evidence that sperm competition affects the reproductive anatomy and behavior of fishes (see Petersen and Warner, 1998; Robertson and Warner, 1978; Stockley et al., 1997; Taborsky, 1998; Warner and Robertson, 1978). A high incidence of streaking can dramatically lower male reproductive pay-offs and, therefore, on a local level should decrease the benefits gained from protogynous sex change. The level of interference experienced by S. radians males is high relative to levels reported for the few other broadcast spawning species for which data exist. For example, sperm competition accompanies 90% and 56% of spawns on patch reefs in St. Croix (this study), and in the seagrass in Panama (Table 1), respectively. In comparison, the stoplight parrotfish, S. viride, shows the next highest reported level of sperm competition within the genus Sparisoma; yet, streaking males accompany only 14.1% of its spawns (van Rooij et al., 1996) (Table 1). Similarly, the Cortez rainbow wrasse, Thalassoma lucasanum, shows the highest level (11.4%) of sperm competition reported for the broadcast spawning wrasses (Warner, 1982); yet, the proportion of spawns streaked in this species is still markedly lower than conditions experienced by S. radians (Table 1). The sex-size distributions of a number of other species (e.g., bullethead parrotfish, Chlorurus sordidus; puddingwife wrasse, Halichoeres radiatus; redtail parrotfish, Sparisoma chrysot|mex) also show high overlap between male and female size distributions, a feature that seems to be associated with mating systems in which sperm competition is prevalent (Muñoz and Warner, 2003a). This suggests that more detailed studies of the mating systems of a number of these species may reveal comparable levels of sperm competition to S. radians, and perhaps deferral of sex change by large females.

If the mature size distribution of a species is sufficiently large, the relationship between body size and fecundity can critically affect fitness gain from sex change, because the aggregate fecundity of remaining females may not exceed the actual fecundity of a single large female. For example, fecundity in S. radians increases exponentially with female body size (note the log y-axis in Figure 1B); combined with the large size range of mature females, this can result in significant size-fecundity skew in local social groups. The ERST model predicts that in these circumstances (regardless of sperm competition), large females may not change sex. Importantly, smaller females can still realize an increase in sex-changed fitness because the aggregate fecundity gained as a male is more likely to exceed their own fecundity. The size range of mature females in S. radians is large, similar to other labroid species with anomalous sex-size distributions (Choat and Robertson, 1975; de Girolamo et al., 1999; Robertson and Warner, 1978; Warner and Robertson, 1978). However, it should be noted that the presence of large females can be both the cause and the result of deferral of sex change, so comparisons across species are more difficult here. Overall, the results of our removal experiments demonstrate strong

### Table 2

Local social group characteristics of *Sparisoma radians* on experimental removal patch reefs

<table>
<thead>
<tr>
<th>Reef</th>
<th>No. of harems</th>
<th>Harem size</th>
<th>Size difference (cm) between largest and smallest female&lt;sup&gt;a&lt;/sup&gt;</th>
<th>Fecundity difference (ml) between largest and smallest female&lt;sup&gt;b&lt;/sup&gt;</th>
</tr>
</thead>
<tbody>
<tr>
<td>15</td>
<td>5</td>
<td>4 (0.89)</td>
<td>9.88 (2.70)</td>
<td>54.91 (36.75)</td>
</tr>
<tr>
<td>13</td>
<td>5</td>
<td>4.4 (0.40)</td>
<td>5.72 (0.55)</td>
<td>5.65 (1.78)</td>
</tr>
<tr>
<td>8</td>
<td>3</td>
<td>3.6 (0.88)</td>
<td>1.67 (1.01)</td>
<td>2.91 (2.51)</td>
</tr>
<tr>
<td>2</td>
<td>5</td>
<td>5.0</td>
<td>5.2</td>
<td>7.81</td>
</tr>
<tr>
<td>2/99</td>
<td>2</td>
<td>4.5 (0.5)</td>
<td>4.9 (1.5)</td>
<td>2.12 (1.48)</td>
</tr>
<tr>
<td>3/98</td>
<td>1</td>
<td>7</td>
<td>8.12</td>
<td>5.08</td>
</tr>
<tr>
<td>1</td>
<td>1</td>
<td>4</td>
<td>2.5</td>
<td>3.93</td>
</tr>
</tbody>
</table>

Values are mean (SE).

<sup>a</sup> Female size was determined either directly by capture and measurement or indirectly by comparing the size of the focal animal against an object on the reef, which was later measured. Females measured out of water were immediately returned to their home ranges after measurement.

<sup>b</sup> Fecundity was determined directly as described in Methods or indirectly from the exponential relationship between fecundity and total length in *S. radians* (see Figure 1B).

### Table 3

Removal experiments in *Sparisoma radians* harems in which sex change occurred

<table>
<thead>
<tr>
<th>Female size (cm)</th>
<th>Harem</th>
<th>15FC</th>
<th>13B</th>
<th>13A</th>
<th>8A</th>
<th>8B</th>
<th>2</th>
<th>3C</th>
</tr>
</thead>
<tbody>
<tr>
<td>15</td>
<td>30.1</td>
<td>21.4</td>
<td>17.0</td>
<td>15.5</td>
<td>21.0</td>
<td>18.1</td>
<td><strong>13.8</strong></td>
<td></td>
</tr>
<tr>
<td>30.1</td>
<td>20.0</td>
<td><strong>16.2</strong></td>
<td>15.0</td>
<td>20.5</td>
<td>16.5</td>
<td>11.3</td>
<td></td>
<td></td>
</tr>
<tr>
<td>19.2</td>
<td>18.2</td>
<td>16.2</td>
<td><strong>14.5</strong></td>
<td>19.4</td>
<td>15.5</td>
<td>10.9</td>
<td></td>
<td></td>
</tr>
<tr>
<td>17.8</td>
<td>17.4</td>
<td>13.4</td>
<td>14.0</td>
<td>17.5</td>
<td><strong>15.3</strong></td>
<td>10.5</td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>16.2</strong></td>
<td>13.8</td>
<td>12.3</td>
<td>17.5</td>
<td>12.9</td>
<td>9.3</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>16.2</td>
<td>8.8</td>
<td></td>
<td></td>
<td></td>
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<td></td>
</tr>
<tr>
<td>15.6</td>
<td>8.0</td>
<td></td>
<td></td>
<td></td>
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<td></td>
</tr>
<tr>
<td>7.5</td>
<td>6.5</td>
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</tbody>
</table>

Females are arranged in size order, and the individual shown in bold was the one to change sex.
support for the general predictions of the ERST model for sex change.

Precision of the ERST model

Given the qualitative support for the ERST model, could the model be used to make specific predictions regarding which individual in a social group should change sex after dominant male disappearance? The answer to this question is a qualified yes, given sufficient information. Three pieces of information are necessary: (1) local population/harem size, (2) the incidence and consequences of sperm competition, and (3) size-fecundity skew of females in the harems. Given these data, it is possible to calculate expected male and female reproductive success by using formulae generated by the ERST model (see Muñoz and Warner, 2003a). Briefly, a female’s instantaneous expected reproductive success equals her fecundity, and the equivalent maximum reproductive success she could accrue after sex change equals the aggregate fecundity of all remaining females in the group. To account for the effects of sperm competition, sex-changed male reproductive success must be discounted by the proportion of spawns that experience sperm competition and the paternity retained in the presence of sperm competition. In order for sex change to be favored in the short term, an individual needs to experience a gain in reproductive success by changing sex. Because an individual’s ability to dominate others often depends on its size (Archer, 1987; Taborsky, 1998), we predicted the largest individual out of that subset of individuals that stands to gain in reproductive success from sex change (in the short term) should be the one to change sex (Muñoz and Warner, 2003a).

For *S. radians*, we lack data on the degree of paternity retained by a male when faced with sperm competition. By using an estimate of 50% paternity retained (data from the bluehead wrasse, *Thalassoma bifasciatum*; Wooninck LM and Warner RR, in preparation), the ERST model was precise in two of the seven harems that experienced sex change (no sex change occurred in 15 remaining harems, see below). One of these two cases also happened to be the only instance in which the largest female changed sex, and this female’s harem contained the greatest number of females (*n* = 8), which appears to facilitate sex change (see below; Cole and Shapiro, 1995). In the other five harems, females even smaller than predicted by the model changed sex, suggesting that male paternity expectations may be even lower than we estimated.

Using the ERST model, the observed patterns of sex change, and female body size-fecundity relationships in *S. radians*, it is possible to predict the range of paternity likely to be obtained by dominant males in the presence of sperm competition. Paternity values generated in this manner are very low or even negative (and therefore meaningless), suggesting again that male paternity is lower than the values derived from *T. bifasciatum*. Indeed, the GSIs of interfering IP male *S. radians* are larger than those of IP male *T. bifasciatum* (3.35 versus 2.71, respectively; Robertson and Warner, 1978; Warner and Robertson, 1978), suggesting that they may be more effective in securing fertilizations. Alternatively, these very low paternity estimates may indicate that other factors, such as growth rate or mortality differences (see below), may also influence the decision to change sex. Although progress has been recently made in paternity estimates for nest-building demersal spawners and internal fertilizers under conditions of sperm competition (Evans and Magurran, 2001; Fu et al., 2001; Fuller, 1999; Mjølnerød et al., 1998; Munehara and Takenaka, 2000), there are no other estimates for the distribution of paternity retained for a broadcast spawning fish faced with sperm competition, such as *S. radians*. It is noteworthy that in substrate-spawning bluegill sunfish, *Lepomis macrochirus*, dominant males fertilize an average of only 22% of eggs in the presence of sperm competition (Fu et al., 2001). If such rates are characteristic of *S. radians*, quite small females would be those predicted to change sex.

The precision of our predictions may also have been affected by the fact that the ERST model, as currently developed, examines male and female reproductive success at a single point in time, and growth and mortality rates between the sexes are assumed equal. In fact, there is evidence of sex-specific growth rates in some species of parrotfishes, with males being consistently larger than females at a given age (Choat et al., 1996). Additionally, Clifton and Robertson (1993) showed that territorial male *S. radians* in grassbeds appear to suffer higher predation from roving yellow jack (*Caranx bartholomaei*) than do seagrass females. Higher male mortality might decrease the benefits of sex change and would favor sex change in smaller females that have more to gain relative to larger females. On the other hand, risk of predation probably decreases with size (Colin and Bell, 1991), so this effect could counter the effect of higher male mortality. Finally, territorial behavior is known to increase the risk of predation (Lima and Dill, 1990, and references therein; Martel, 1996; Martel and Dill, 1995), so males engaged in territorial defense may experience higher mortality than females. A dynamic ERST model might increase its predictive capability by using reproductive value to examine the effects of differential mortality and growth on sex change (for an example of such an approach, see Rogers and Sargent, 2001).

Another factor that the ERST model did not consider is the effect of roving bachelors on the sex change process. Aldenhowen’s (1986) work with the bicolor angelfish, *Centropyge bicolor*, has shown that the frequency of bachelor males

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### Table 4

<table>
<thead>
<tr>
<th></th>
<th>Size difference (cm) between largest and smallest female</th>
<th>Fecundity difference (ml) between largest and smallest female</th>
<th>Aggregate fecundity (ml)</th>
<th>Fecundity skewa</th>
</tr>
</thead>
<tbody>
<tr>
<td>Harems with sex change</td>
<td>7 6.61 (1.83)</td>
<td>32.38 (27.64)</td>
<td>74.50 (57.17)</td>
<td>0.73 (0.28)</td>
</tr>
<tr>
<td>Harems without sex change</td>
<td>15 6.16 (1.01)</td>
<td>7.30 (3.27)</td>
<td>16.61 (5.45)</td>
<td>0.69 (0.23)</td>
</tr>
</tbody>
</table>

Values shown are means (SE). Measures of size and fecundity as in Table 2.

a Statistical skew (γ, the third central moment divided by the cube of the standard deviation) measured as in Sokal and Rohlf (1995).
is negatively correlated with the incidence of female sex change. Those study sites characterized by a greater number of bachelors had fewer females immediately change sex and take over harems after dominant male disappearance, compared with those other sites where the reverse pattern prevailed. Similar to these patterns for C. bicolor, in the present study, there was a decreasing trend across Tague Bay in the number of days after male removal before the first appearance of a transitional fish; transitions tend to appear faster in those patch reefs further away from the barrier reef, where the frequency of bachelor arrival is lower (Muñoz and Warner, 2003b). This suggests that differing arrival rates of bachelors across Tague Bay may produce local conditions that facilitate alternative contexts of sex change and harem takeover, as are known from Centropyge angelfishes (Aldenhoven, 1986; Sakai, 1997).

**Sex change was not induced on all patch reefs**

Although sex change in individuals smaller than the dominant female occurred on most experimental patch reefs, we cannot be certain why some removals completely failed to stimulate sex change. A high arrival rate of bachelors might decrease the probability of sex change in remaining females, but the three patch reefs without sex change were located far away from the barrier reef and had a low rate of bachelor arrival (Muñoz and Warner, 2003b).

Even on patch reefs where sex change did occur, it did not occur in all harems on these reefs. The difference in size between the largest and smallest females appeared similar for harems with sex change and those without sex change (Table 4). However, harems in cases with sex change tended to be larger than in those harems without sex change. These data are in concordance with a study of the protogynous bristled goby, Coryphopterus glacoufranum, by Cole and Shapiro (1995), who found that the proportion of groups in which a female changed sex increased with the number of females in the group.

Why should some harems experience sex change when others do not? Aside from larger harem size and variability in bachelor male arrival, at least two other factors may prevent sex change in these harems. First, small males present in the area have two complementary effects: they are already present and ready to mate, and they can lower a sex-changed male's reproductive expectations through sperm competition. Second, after our male removals, females interacted more strongly with females from other harems than when dominant males exerted some control over their movements (Muñoz and Warner, 2003b). Thus, the onset of sex change by the transitional female may have been communicated to the group as a whole (through direct contact or water borne-cues; Cole and Shapiro, 1995). These repression effects cannot explain the complete lack of sex change observed on other patch reefs, of course, but these small reefs tended to support a smaller number of harems than reefs where we witnessed sex change.

Rather than predicting that some species will defer sex change and others will not, the ERST conditions suggest a continuum of social and environmental situations for any sex-changing species, such that, in some cases, the largest females will defer sex change. At one end of the continuum are species such as the Spanish hogfish, Bodianus rafus, in which strict male control allows only the largest individuals in local populations to exceed their ERSTs, and then only in the absence of the dominant male. In between these two endpoints are species such as S. radians, in which protogynous life history combines with reduced male control and habitat preferences that may expose them to sperm competition. These factors can create conditions in which small females' thresholds are sometimes crossed before those of large females. In these species, females smaller than the dominant male may change sex, as occurs for S. radians in St. Croix. It remains to be seen how many additional species in a variety of geographic locations are similarly affected by sperm competition and size-ecundity skew.

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