INTRASPECIFIC VARIATION IN SEX ALLOCATION IN A SIMULTANEOUS HERMAPHRODITE: THE EFFECT OF INDIVIDUAL SIZE

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Abstract.—Within a population of simultaneous hermaphrodites, individuals may vary in both their current reproductive investment (biomass invested in gonads) and in how they allocate that investment between male and female function. In the chalk bass, Serranus tortugarum, estimates of both reproductive allocation and reproductive success as a male and a female can be made for individuals of different sizes. As individuals increase in size, their investment in gamete production increases, and there is a shift in allocation to a stronger female bias. Spawning frequency as a female in pair spawnings and as a male in both pair spawning and streaking (an alternative mating tactic) does not vary with individual size. As a result, larger individuals should release more sperm or eggs per spawn. Size-assortative pair spawning in this species leads to larger individuals having higher potential returns in total male reproductive success than smaller individuals, which should lead to increases in absolute levels of sperm production in larger individuals when individuals compete for fertilizations through sperm competition. However, smaller individuals contribute a smaller proportion of the sperm released in spawns with multiple spawners and thus are under more intense sperm competition than larger individuals, which should select for increases in male allocation in smaller individuals, all else equal. A local-mate-competition (LMC) model predicts that these factors select for increasing absolute male and female investment with individual size but a relative shift to more female-biased allocation as individual size increases. These predictions are supported by gonadal data. The predictions of average male allocation from the quantitative LMC model were 21.6% and 25.7%, whereas the collections averaged 21.3%. This close agreement of both the mean male allocation and its relative shift with individual size between model and data support the hypothesis that size-specific shifts in sex allocation in this species represent an adaptive response to patterns of mating success and sperm competition.

Key words.—Fishes, hermaphrodite, local mate competition, Serranidae, sex allocation, size-assortative mating.

Received March 6, 1994. Accepted March 8, 1995.

Sex-allocation theory for hermaphroditic organisms is divided into two distinct areas, theory for sequential hermaphrodites and theory for simultaneous hermaphrodites. For simultaneous hermaphrodites, predictions of how much energy an organism devotes to male versus female function are based on the relationship within each sex between reproductive investment and current reproductive success (Charnov 1979, 1980, 1982; Fischer 1981, 1984a; Lloyd 1984, 1988; Lloyd and Bawa 1984; Petersen 1991). These models have typically looked at the effects of selfing (Lemen 1980; Charlesworth and Charlesworth 1981; Schoen 1982; Ross and Gergiariou 1983; Charnov 1987a; McKone 1987b) or the effect of sperm competitors (Charnov 1980, 1982, 1987b; Fischer 1981, 1984a; Petersen 1991) on individual sex allocation, while assuming all individuals within a population adopt the same allocation (for an exception, see Charnov 1987b). In contrast, models of sex allocation in sequential hermaphrodites are based on differences in sex-allocation patterns among individuals within a population. Predictions of the timing of sex change are based on changes in individual reproductive success for each sex with size, age, social status, or the amount of resources devoted to reproduction (Warner 1975, 1984; Warner et al. 1975; Charnov 1982; Iwasa 1991). The purpose of this paper is to examine size-specific patterns of mating and reproductive success in an outcrossing simultaneous hermaphrodite, the chalk bass, Serranus tortugarum, and to determine whether size-specific patterns of sex allocation in these fishes can be predicted by expanding a current model of sex allocation for simultaneous hermaphrodites.

The theory of local mate competition (LMC), proposed by Hamilton (1967), has been invoked most often to explain patterns of sex allocation in which male and female offspring are not produced in a 1:1 ratio in separate-sexed species. Although originally proposed to explain sex-ratio patterns in Hymenoptera and other organisms, LMC theory applies equally well to deviations from 1:1 allocation to male and female function within outcrossing hermaphrodites (Charnov 1980, 1982, 1987a; Fischer 1981, 1984a; Lloyd 1984; Petersen 1990a, 1991; Raimondi and Martin 1991). This model predicts that the number of sperm competitors determines the optimal proportion of reproductive resources devoted to male and female function in hermaphrodites, ranging from a minimum close to 0% male allocation when there is no sperm competition to a maximum of 50% if levels of sperm competition are high. The exact relationship between the level of mate competition and the proportion allocated to male function is \( a = (m - 1)/(2m - 1) \), where \( a \) is the proportion of reproductive resources devoted to male function and \( m \) is the number of male-role individuals competing for each fertilization (Charnov 1980; 1982; Fischer 1981). Models that have attempted to use LMC to predict sex allocation in hermaphroditic species have assumed that all individuals within a population allocate the same amount of energy to reproduction and have the same mating and reproductive success (Fischer 1984a; Petersen 1991), or have divided the population into subpopulations that experience different levels of local mate competition (Raimondi and Martin 1991).

In sex-ratio theory, differences in energy devoted to re-
production and its effect on the sex ratios of broods has been incorporated into LMC theory with models that include variable female fecundity (Werren 1980; Frank 1985; Yamaguchi 1985; Stubblefield and Seger 1990). Thus, LMC theory can be applied to systems in which individuals vary in their total energy devoted to reproduction and can address sex-allocation patterns in simultaneous hermaphrodites. This is important, because simultaneous hermaphroditism often occurs in organisms with indeterminate growth or a large variation in adult size where the reproductive investment of individuals can vary tremendously.

In this paper, we quantify patterns of spawning frequency (number of spawns per day) and sperm competition (number of individuals releasing sperm in a spawn) for individuals of the chalk bass, *S. tortugarum*, with special attention to how these patterns change with individual size. Using these data and data on reproductive investment (biomass invested in gonads), sex-allocation patterns for individuals of different size classes in a population of hermaphroditic sea basses are predicted using a LMC model with multiple size classes. The predictions are then compared with levels of biomass allocation to male and female gonadal tissue. This work provides an example of how sex allocation can vary within a population of simultaneous hermaphrodites where both sex allocation and reproductive success (number of zygotes per day) for both sexes has been estimated, and the results are largely consistent with predictions from LMC theory.

**Biology of Serenus tortugarum**

**Chalk bass, S. tortugarum**, are small (maximum size observed 62 mm standard length), aggregating, planktivorous sea basses found throughout the Caribbean along reef margins over sand and rubble. Several aspects of the reproductive biology of chalk bass have been summarized previously by Fischer and his coworkers (Fischer 1984a,b, 1986; Fischer and Hardison 1987). All mature individuals are functional simultaneous hermaphrodites. Spawning occurs daily in the late afternoon. Individuals form pairs immediately before spawning begins and tend to form the same pairings on successive days. During a spawning act, one fish releases eggs while the other fertilizes them. Each mate releases eggs several times during a spawning period, and partners generally switch sex roles with each spawning. This combination of parceling of the clutch and alternation of spawning roles is called egg trading (Fischer 1980, 1984a). Larger individuals release more eggs per spawn, hydrate more eggs per day (an estimate of daily egg production) (Fischer 1986; Fischer and Hardison 1987), and egg size is independent of adult size (Fischer and Hardison 1987).

In addition to this pair-spawning behavior, many spawnings are streaked—that is, one or more fish other than the mate rush in and release sperm at the location where a pair just spawned (Fischer 1984b). Fertilization is external and eggs are planktonic; there is no parental care.

**Sex-allocation models**

Incorporation of multiple-size classes into the current LMC equations for simultaneous hermaphrodites can be easily accomplished by substituting size-specific female and male allocation for the previously used uniform male and female allocation functions (Petersen 1991) and by describing the patterns of mating among size classes. As in the single-size-class model, we follow previous authors (Lloyd 1984; Petersen 1991), and consider the fitness of an individual to be equal to the sum of the independent contributions of male and female gametes to current reproductive success, and then solve for the allocation pattern that gives the highest current reproductive success. In chalk bass, reproductive success has three behavioral components; pair spawning as a female, pair spawning as a male, and streaking as a male. The fitness for an individual in size class *i* for a fixed time interval is

\[ w_i = w_{ipf} + w_{ips} + w_{imm}, \]

where the subscripts refer to the three spawning behaviors. Although straightforward, these equations when fully expanded are cumbersome, so the complete details of the equations, and the assumptions that lead to them are relegated to an Appendix.

This model deals with current reproductive success and assumes that future reproductive success is independent of how a fixed reproductive investment has been partitioned between male and female function in the past. This assumption allows us to simultaneously solve for the sex allocation in *n* size classes that gives the highest current reproductive success for individuals in each size class in the presence of other size classes. Once solved, these allocations represent the predicted trajectory of sex-allocation changes as an individual grows, although the model is constructed as if these size classes represent different individuals. For this model, the number of size classes used was four, which allowed for good estimates of size-specific spawning behaviors while giving an idea of both the general trend and shape of the curve relating sex allocation and individual size. The parameters for the model, including the size-frequency distribution of the population, the reproductive investment of individuals of different sizes (estimated by the size of their ovotestis), and the size-specific patterns of pair spawning and streaking were all estimated from the field data and collections.

The optimal allocation for an individual is dependent on the allocation of other individuals, so the equations for the four size classes are solved simultaneously using a computer simulation. The reproductive investment of individuals in each size class was set as proportional to the average gonad size for that size class. Starting with equal relative allocation between male and female function in all size classes, the fitness of a rare individual with slightly higher and slightly lower allocation within each size class was determined. The allocation phenotype within each size class with the highest reproductive success was then made the common allocation pattern for that size class, and the process repeated until the rare individuals had lower fitness than the common individuals in that size class for all size classes. Once this potential evolutionarily stable strategy (ESS) was found, rare individuals over a wide range of sex allocations were tested against the common phenotype to determine if the allocation pattern was an ESS. In addition, several different initial sex allocations were used to verify that only one ESS existed. This model is equivalent to a phenotypic selection model and as-
sumes a constant and large population size and a heritable basis for sex allocation.

**Materials and Methods**

**Reproductive Behavior**

Data on reproductive behavior were collected in the San Blas during July to December 1983 to 1985. Individuals were captured, tagged with alcan blue to allow for individual identification, and their standard length measured before releasing them on their home reef. Data used in this analysis came from two populations, both within 2 km of San Blas point, and were part of a larger study of the reproductive biology of the chalk bass (Fischer 1986; Fischer and Hardison 1987; Fischer unpubl. data). The exact reef names and locations used in this study refer to map locations published in Robertson (1987). Observations were performed on SCUBA at a depth of 3 m to 8 m.

To collect reproductive data, individuals were followed throughout an entire spawning period. All male and female pair spawnings and streaking by the subject individual, as well as the total number of streakers, were recorded. The identity of the other individuals in the spawnings was also recorded whenever known, although we were often unable to identify individual streakers. Fifty-one individuals were followed for a variable number of reproductive periods, ranging from 1 to 13 reproductive periods per individual, during the course of the study.

For rates of pair spawning and streaking per day, values for each individual were pooled and divided by the number of days observed and represented one data point. Patterns of size-assortative pair spawning were examined using all unique pairings of tagged individuals from focal observations and tested using parametric correlation analysis after confirming there was no variation among populations using analysis of covariance (ANCOVA). Unlike most studies of size-assortative mating, these hermaphroditic individuals do not readily fall into two categories, and they were arbitrarily assigned to the x- and y-axes. The size of the focal individual was plotted on the ordinate and the size of its partner was plotted on the abscissa. Each pair was used only as a single data point in the correlation analysis, whether it was observed during only one or during several spawning periods. This was to avoid introducing bias as some individuals were followed for several (up to 13) consecutive spawning periods to determine long-term mating patterns as part of a separate study so that each focal spawning period could not be considered as an independent observation.

Patterns of size-assortative streaking, the relationship between the size of the streaker and the individual releasing eggs on a spawn, were analyzed for all records where the size of a streaker and the size of the female-role spawner were known using parametric correlation analysis. Analysis of covariance was used to test for differences in streaking behavior between populations.

**Sex Allocation**

To determine patterns of reproductive investment and sex allocation in chalk bass gonadal tissue, individuals were collected once in 1983 and once in 1988 from aggregations of comparable size at a shallow reef slope similar in character and within 1 km of the study reefs. Individuals were all captured between 11:30 A.M. and 1:30 P.M. to minimize gonadal differences due to egg hydration which begins at approximately 1500 hr (Fischer and Hardison, 1987). Individuals were either fixed in Davidson's solution and stored in 70% ethanol (1983 collection) or fixed in 10% formalin and later preserved in 50% isopropyl alcohol (1988 collection). The differences in preservation methods did not appear to differentially affect measurements of reproductive investment and sex allocation (see Results); and merely represented two methods to obtain data on sex allocation in two originally independent studies. Specimens were weighed, their standard length measured to the nearest millimeter, and their gonads removed. As with other sarrinens, the ovotestis of chalk bass consists of separate ovarian and testicular regions (Smith 1965; Bortone 1977; Fischer 1981; Hastings and Petersen 1986). The two tissue types are easily distinguished by their location, color, and texture. The reproductive system is simple, with no complex sexual organs. Male and female tissue in the ovotestis were separated, dried, and weighed using the protocol in Petersen (1990b, 1991).

A potential problem with this gonadal allocation methodology is that it assumes that testicular and ovarian biomass accurately reflect the costs of making eggs and sperm and that the cost per unit biomass are the same for these two functions. No way exists to test the assumption directly, but the available data support it. Calorimetric values for testes in fish tend to be only slightly lower than those for ovaries in the few species for which data are available. Staples (1975) found a 7% difference in the goby, *Philipnodon breviceps*, and MacKinnon (1972) found a 3% difference in the American plaice, *Hippoglossoides platessoides*. These small differences would have little effect on the validity of the measure. Although uncertainties remain, there is currently no reason to reject ovarian and testicular dry weight as a reasonable, if somewhat rough, estimate of female and male allocation.

**Results**

**Spawning Behavior**

Each individual releases eggs over an average of approximately 7.5 spawns per day, and spawning frequency as both a male and a female is independent of individual size (Table 1). Rates of streaking could be determined two ways, either

<table>
<thead>
<tr>
<th>Dependent variable</th>
<th>Mean</th>
<th>SD</th>
<th>r</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>No. pair spawnings/day</td>
<td>Male</td>
<td>7.6</td>
<td>2.2</td>
<td>0.02 NS</td>
</tr>
<tr>
<td></td>
<td>Female</td>
<td>7.4</td>
<td>2.6</td>
<td>0.19 NS</td>
</tr>
<tr>
<td></td>
<td>Combined</td>
<td>15.1</td>
<td>4.3</td>
<td>0.11 NS</td>
</tr>
<tr>
<td>No. streaks/day by focal fish</td>
<td>4.3</td>
<td>3.2</td>
<td>0.05 NS</td>
<td></td>
</tr>
<tr>
<td>Percent of spawns of focal fish that were streaked</td>
<td>43</td>
<td>10</td>
<td>0.18 NS</td>
<td></td>
</tr>
</tbody>
</table>
Table 2. Summary of individual size and patterns of mating partners among four populations of chalk bass. The sample sizes (N) are for the number of individuals measured for individual size, the number of unique pairs used in testing for size-assortative pairing, and the number of unique pairs used in the test for size-assortative streaking (tested using parametric correlation). SL = mean standard length (mm), SD = standard deviation.

<table>
<thead>
<tr>
<th>Year</th>
<th>Population</th>
<th>SL</th>
<th>(SD)</th>
<th>N</th>
<th>r</th>
<th>P</th>
<th>N</th>
<th>r</th>
<th>P</th>
<th>N</th>
</tr>
</thead>
<tbody>
<tr>
<td>1983</td>
<td>Aquadargana</td>
<td>41.1</td>
<td>(6.3)</td>
<td>164</td>
<td>0.58</td>
<td>0.13</td>
<td>8</td>
<td>0.07</td>
<td>0.65</td>
<td>40</td>
</tr>
<tr>
<td>1984</td>
<td>Aquadargana</td>
<td>43.5</td>
<td>(5.6)</td>
<td>188</td>
<td>0.90</td>
<td>&lt;0.001</td>
<td>20</td>
<td>0.31</td>
<td>0.13</td>
<td>30</td>
</tr>
<tr>
<td></td>
<td>Kwigalatupo (Site B)</td>
<td>43.3</td>
<td>(5.4)</td>
<td>218</td>
<td>0.64</td>
<td>0.003</td>
<td>19</td>
<td>-0.35</td>
<td>0.10</td>
<td>23</td>
</tr>
<tr>
<td>1985</td>
<td>Aquadargana</td>
<td>41.3</td>
<td>(6.1)</td>
<td>337</td>
<td>0.70</td>
<td>&lt;0.001</td>
<td>40</td>
<td>0.09</td>
<td>0.61</td>
<td>37</td>
</tr>
<tr>
<td></td>
<td>Combined sites</td>
<td>42.2</td>
<td>(6.0)</td>
<td>907</td>
<td>0.74</td>
<td>&lt;0.001</td>
<td>87</td>
<td>0.02</td>
<td>0.81</td>
<td>130</td>
</tr>
</tbody>
</table>

by looking at the rates the focal individuals streaked spawns or the rate that focal individuals had their spawns streaked. These two techniques gave slightly different rates, so both sets of rates were used in the computer simulation. For the focal animal, individuals streaked 4.3 times per day (Table 1), while data on streaking of focal animals gave an estimated individual streaking rate of 5.7 streaks per day. In spawns with at least one streaker, the distribution of number of streakers per spawn was the same for both estimates of streaking; the relative frequency of spawns with one to five streakers were 0.56, 0.27, 0.11, 0.04, and 0.02, respectively. However, the percentage of spawns not streaked was estimated at 57% and 65% for the high and low estimates of streaking rate given above.

Size-assortive pairing was found in three of the four populations where sample sizes were highest (Table 2), and overall there was a strong tendency for individuals to pair with similarly sized individuals (Table 2, Fig. 1). This pattern was verified using an ANCOVA with site as a category and size of the focal individual as a continuous variable; size of the focal individual had a strong effect on size of the mating partner but there was no significant effect of site or significant interaction between year and site (Table 3A).

In contrast, there was no evidence for size-dependent spawning behavior for individuals through streaking. The rate of streaking was not correlated with size (Table 1), and the size of the egg releaser in a spawn was independent of the size of the streaking individual (Table 2, Fig. 2). This pattern was mirrored in an ANCOVA that found no effect of size of the egg releaser, site, or interaction among site and size of egg releaser on the size of the streaker (Table 3B). Individuals pair spawn with individuals of similar size, whereas streakers appear to disregard the size of the pair spawners. Both pair-spawning and streaking rates are independent of size.

Gonadal Allocation Patterns

The two gonadal collections were combined in all statistical analyses after a series of ANCOVAs showed no effect of collection or an interaction of collection with individual size for any of the gonadal weight measurements (ovarian tissue weight, testicular tissue weight, total gonad weight, and sex allocation).

There is a positive correlation between body size and total gonad size ($r = 0.83$, $P < 0.001$), with both female and male gonadal tissue increasing with individual size (Figs. 3, 4). This scaling appeared to be roughly isometric with body weight; the percentage of wet body weight devoted to ovo-

Table 3. Analysis of covariance (ANCOVA) of population data on size-assortative patterns of pair spawning and streaking. A. ANCOVA of patterns of size assortivity of pair spawning partners by population. B. ANCOVA of patterns of size assortivity of streakers and individuals releasing eggs in a spawn by population.

<table>
<thead>
<tr>
<th></th>
<th>SS</th>
<th>d.f.</th>
<th>MS</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Focal individual</td>
<td>571.4</td>
<td>1</td>
<td>571.4</td>
<td>49.3</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Population</td>
<td>2.98</td>
<td>3</td>
<td>0.99</td>
<td>0.086</td>
<td>0.97</td>
</tr>
<tr>
<td>Interaction</td>
<td>3.74</td>
<td>3</td>
<td>1.25</td>
<td>0.11</td>
<td>0.95</td>
</tr>
<tr>
<td>Error</td>
<td>915.1</td>
<td>79</td>
<td>11.58</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th></th>
<th>SS</th>
<th>d.f.</th>
<th>MS</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Egg releaser</td>
<td>2.45</td>
<td>1</td>
<td>2.45</td>
<td>0.06</td>
<td>0.80</td>
</tr>
<tr>
<td>Population</td>
<td>154.34</td>
<td>3</td>
<td>51.44</td>
<td>1.28</td>
<td>0.28</td>
</tr>
<tr>
<td>Interaction</td>
<td>166.84</td>
<td>3</td>
<td>55.61</td>
<td>1.39</td>
<td>0.25</td>
</tr>
<tr>
<td>Error</td>
<td>4891</td>
<td>122</td>
<td>40.09</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Fig. 1. Size of reciprocating spawning partners in chalk bass in four populations. Data are for tagged individuals of known size. The focal individual for the mating observations was arbitrarily designated on the ordinate. Statistics for each population and the combined data are given in Tables 2 and 3.
testis did not change with individual size (ANOVA with no effect of standard length \( F = 1.02; df = 1, 63; P = 0.32 \), preservation technique \( F = 0.195; df = 1, 63; P = 0.66 \), and no significant interaction \( F = 0.86; df = 1, 63; P = 0.86 \)). Assuming the gonadal tissue mass within a sex is proportional to gamete production, and given the independence of spawning rate and individual size (Table 1), larger individuals will release more eggs or sperm in each spawn.

As individuals increase in size from 35 mm to 50mm, there is a predicted increase of 548% for egg production and 264% for sperm production. This differential increase of female tissue with size is apparent as a decreased proportion of gonad devoted to male function with increasing size \( r = -0.36, P < 0.005, N = 67 \), Fig. 5). This pattern persisted when the two small individuals with unusually high male allocation (Fig. 5) were removed \( r = -0.29, P < 0.01, N = 65 \), and when the smallest size class was removed \( r = -0.29, P < 0.05, N = 59 \), confirming that the pattern was not due to differential maturity of the two tissues or driven by a few extreme data points.

These results also predict that when multiple individuals release sperm in a spawn, the smaller individuals will release a smaller proportion of the total sperm relative to the larger male-role individuals. Thus, sperm from smaller individuals will be under more intense sperm competition from heterologous sperm (sperm from other individuals) than sperm from larger individuals.

**Predicted Reproductive Success and Sex-Allocation Patterns**

The above data provided the necessary parameters for the size-structured LMC model. Based on the summed frequency distributions of all individuals tagged in the study at least 32
Table 4. Estimated reproductive success, reproductive investment for each sex, and sex-allocation estimated from the sex-allocation model for four size classes and two different sperm-competition estimates. Reproductive investment values are standardized so that the average individual in the population has a total reproductive investment (male + female) of one.

<table>
<thead>
<tr>
<th>Size class</th>
<th>Reproductive success</th>
<th>Reproductive investment</th>
<th>Sex allocation</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Male</td>
<td>Female</td>
<td>Total</td>
</tr>
<tr>
<td>Low sperm competition estimate</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1</td>
<td>0.514</td>
<td>0.161</td>
<td>0.675</td>
</tr>
<tr>
<td>2</td>
<td>0.646</td>
<td>0.562</td>
<td>1.208</td>
</tr>
<tr>
<td>3</td>
<td>0.811</td>
<td>0.950</td>
<td>1.761</td>
</tr>
<tr>
<td>4</td>
<td>1.274</td>
<td>1.384</td>
<td>2.657</td>
</tr>
<tr>
<td>High sperm competition estimate</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1</td>
<td>0.494</td>
<td>0.136</td>
<td>0.620</td>
</tr>
<tr>
<td>2</td>
<td>0.620</td>
<td>0.534</td>
<td>1.153</td>
</tr>
<tr>
<td>3</td>
<td>0.779</td>
<td>0.916</td>
<td>1.695</td>
</tr>
<tr>
<td>4</td>
<td>1.219</td>
<td>1.339</td>
<td>2.558</td>
</tr>
</tbody>
</table>

mm standard length (the smallest size observed spawning), the continuous population size distribution was arbitrarily divided into four size classes, 32 to < 37 mm, 37 to < 42 mm, 42 to < 47 mm, and ≥ 47 mm SL with frequencies of 0.179, 0.257, 0.289, and 0.275.

Scaling the mean gonad size of an individual in the population to 1, the average gonad size of an individual in each size class, which defines current reproductive investment in the model, was 0.294, 0.712, 1.268, and 1.747.

These data plus the specific probabilities of pair spawning among size classes (listed in the Appendix) were used to predict patterns of sex allocation for the four size groupings. The mean sex allocation predicted by this model was 21.6% male and 25.7% male for the two estimated rates of streaking, slightly higher than the observed value of 21.3%. The total amount of reproductive investment to male and female function increased with individual size in the model, with the relative percentage male decreasing with increasing individual size, which is in agreement with the observed patterns (Fig. 5, Table 4).

The expected male and female fitness of individuals differing in sex allocation from a population at an ESS sex allocation is shown in Figure 6 for the four size classes. At the ESS, individuals in the smaller size classes obtained higher reproductive success through male function, and for the smallest size class the higher sperm competition estimate predicts an optimal male allocation more than 50% (Table 4, Fig. 6). For the larger size classes, the patterns are reversed, with female reproductive success higher than male reproductive success, and with a strongly biased female sex allocation (Table 4).

**Discussion**

**Changes in Sex Allocation with Individual Size**

As chalk bass grow larger, investment in sexual reproduction becomes more female biased. The LMC model, with its emphasis on mating opportunities and sperm competition, predicts several of the qualitative and quantitative changes in chalk bass sex allocation quite accurately. First, it predicts that both male and female reproductive investment will increase with individual size and increasing total reproductive investment but that female reproductive investment will increase at a faster rate. This leads to the predicted decrease in male allocation with individual size. The model also predicts that the largest changes in sex allocation should occur between the smaller size classes (Table 4), a pattern that is mirrored in the field collections (Fig. 5).

One way to understand both the empirical data and the model are to consider the two extreme cases that bracket spawning behavior in chalk bass, random mating, and size-assortative mating. At one extreme, where returns on female function are linear and spawning is completely random with respect to size, all individuals should devote equal absolute amounts to sperm production, assuming that all individuals have a total reproductive allocation equal to or greater than this amount (Petersen 1990a; Stubblefield and Seger 1990). This results in larger individuals devoting a smaller proportion of resources to male function if gonad size increases with individual size.

At the other extreme, if all spawnings, including streaking, were completely size assortative, size classes would behave as separate populations. If streaking rates are identical among size classes, then individuals in each size class should have the same proportion of their reproductive energy devoted to male function.

In chalk bass, the pattern of spawning is intermediate, with size-assortative pair spawning and nonassortative streaking. The intraspecific pattern of sex allocation is also intermediate, as predicted by the model, showing an increase in both absolute male and female investment with size, but with a decrease in relative male allocation with increasing size.

Although there are similar spawning frequencies for all size classes for both male mating behaviors, pair spawning and streaking, the model predicts differences in optimal levels of sperm release per spawn among size classes and that larger individuals will release more sperm per spawn. Because pair spawning is size assortative, and larger individuals release more eggs, larger individuals release sperm in spawns with a higher average number of eggs. This results in higher marginal returns for male function for larger individuals for any given absolute level of sperm release per spawn. The higher marginal returns for male function for larger individuals selects for a higher absolute amount of reproductive resources devoted to male function for larger individuals. For example, at the ESS the model predicts an individual in the largest size class will release 65% to 67% more sperm per spawn than an individual in the smallest size class. However, because the total investment for the largest size class is over five times the reproductive investment of the smallest size class, when viewed as the proportion of sexual resources devoted to male function, the largest size class is predicted to have a lower male allocation (53.9% for the smallest size class versus 16.5% for the largest size class given the higher sperm competition estimates). This result is consistent with the data (Figs. 4, 5).

**Alternative Hypotheses**

The decrease in relative allocation to male function with size could be caused by changes in sperm competition, as...
suggested above, or could be due to other factors not studied here. One possibility is that changes in sex allocation are phylogenetically conservative in this group. This seems unlikely given the patterns of sex allocation in closely related species. The pattern of decreasing male allocation with size in chalk bass is different from the patterns observed both in congener and in a more distantly related confamilial. In chalk bass, large individuals do not attempt to monopolize female-role mates, a tactic that has led to harem formation and increased male allocation with size in two species of territorial congener, *S. fasciatus* (Petersen 1987, 1990b,c, 1991) and *Serranus baldwini* (Petersen and Fischer 1986; Petersen 1991; unpubl. data). In the two other species of egg-trading serranines, there is an increase in male mating success with size (*Hypoplectrus nigricans*, Fischer 1980; *Serranus tabacarius*, Petersen 1995), with neither species showing a change in the percentage of gonad devoted to male function with individual size as seen in chalk bass (*H. nigricans*, $r_s = 0.19, N = 22, P > 0.2$; *S. tabacarius*, $r_s = -0.04, N = 20, P > 0.5$; unpubl. data with methods and specimens from Petersen 1991). Because the patterns of sex allocation within these species mirror intraspecific patterns of male reproductive success and LMC, and are different from the pattern of sex allocation in *S. tortugarum*, it is more likely that the pattern of sex allocation in *S. tortugarum* represents a coevolutionary response with the mating system and not a phylogenetically conservative pattern.

Levels of sperm competition are not the only factors that can affect the returns on reproductive success for a given level of male allocation and thereby affect patterns of sex allocation. In a comparative study of sex allocation in six species of simultaneously hermaphroditic sea basses, Petersen (1990a, 1991) found that interspecific differences in sex allocation due to local mate competition could be better understood by incorporating a term to represent how the amount of sperm released might affect fertilization success. In a simplified model with two size classes for *S. tortugarum*, adding one form of a fertilization success term increased predicted male allocation only slightly, by 0.4% (Petersen 1990a). Fertilization success of natural spawnings of chalk bass has not been documented but is near 100% in two congener, *S. tabacarius* and *S. tigrinus* (C. Petersen and D. Levitan, unpubl.).

Fig. 6. Estimated patterns of reproductive success from the LMC model for four size classes when the population is at the ESS sex allocation (arrows, values in Table 4). The model graphed used the high sperm competition estimates. Female, male, and total reproductive success curves for all size classes are analogous to those shown in size class 1 (the smallest size class).
SEX ALLOCATION IN HERMAPHRODITIC SEA BASSES

data). At these levels of fertilization success, the model predicts virtually no effect due to fertilization dynamics (Petersen 1990a).

Empirical data on sperm release in the bluehead wrasse (Shapiro et al. 1994) show an increase in sperm released by males in spawns with larger females. The males studied in the bluehead wrasse have much lower sperm competition levels than chalk bass, implying that factors other than sperm competition can select for higher levels of sperm release with more fecund females. If males need to release larger amounts of sperm to obtain higher fertilization success in spawns with larger females, this would be an additional factor selecting for increased sperm release per spawn for larger males even in the absence of sperm competition. However, in S. tabacarius, spawning is size assortative, yet streaking and sperm competition are virtually absent. The sperm–competition model would predict no trend of sperm release with size, whereas the concerns of size alone would predict an increase in sperm per spawn for larger male. Larger males do not appear to release more sperm per spawn based on the amount of testicular tissue and spawning rates in S. tabacarius (Petersen unpubl. data), supporting the interpretation that size-assortative spawning and sperm competition combine to increase absolute male investment as predicted by the LMC model.

Finally, in constructing causal hypotheses to explain sex allocation in these fishes, the mating system is hypothesized to affect the level of sperm competition, which in turn affects the level of individual sex allocation. An alternative hypothesis is that high levels of male allocation have led to increased levels of streaking and sperm competition, although this does not appear to be the case in S. tortugarum. Both the social and mating system and the frequency of alternative mating tactics in this species appear to be influenced by the density of individuals and their patterns of distribution in time and space (Fischer and Petersen 1987). The high-density aggregations that chalk bass often form appear to lead to an increased opportunity for streaking in this species. This and the highly variable expression of sexuality in this family of fishes make it much more likely that the causal arrow points from ecology through the mating system and then to patterns of individual sex allocation than the other way around.

Sperm Mixing

To calculate the degree of sperm competition among individuals in a spawn, sperm are assumed to completely mix. This assumption is almost certainly being violated. When sperm are released by multiple individuals in a spawn, the mixing of sperm among individuals will be incomplete, resulting in an increase in competition among sperm from the same individual. Under these conditions, the proportion of sperm released in a spawn by an individual will overestimate the degree of competition with sperm from other individuals. This incomplete mixing of sperm will reduce the level of sperm competition and select for lower male allocation than predicted by the model.

Differences in the ability of individuals to successfully obtain fertilizations by streaking could also violate the sperm-mixing assumption and cause size-related biases. Larger fish are probably stronger swimmers, and may be able to either get to a spawning site more quickly than smaller individuals, or may be more accurate in their placement of sperm release. If true, this could disproportionately increase the marginal returns on male function for larger individuals, and select for increased absolute male allocation in larger individuals. These hypotheses could be tested by videotaping streakers of known size during spawning.

Variable Sex Allocation in Simultaneous Hermaphrodites

The size-specific shifts in sex allocation in this simultaneous hermaphrodite are analogous to variable-fecundity sex-ratio models in species with separate sexes. In these models, investment in male and female offspring by females are analogous to investment in male and female gamete production in hermaphrodites. Stubblefield and Seger (1990) showed that if females with differing fecundities in a patch know each other’s fecundities, then the optimal allocation is for each of them to produce the same absolute investment in male offspring, with the number dependent on the fecundity of all of the females. This would be analogous to completely random mating in simultaneous hermaphrodites, and the solution would be for all individuals to invest the same absolute amount into sperm production (Petersen 1990a).

The change in relative sex allocation with size seen in this species has also been predicted in a model of barnacle sexuality (Charnov 1982, 1987a; but see Raimondi and Martin 1991), and Werren (1980) suggested that individuals making a relatively smaller reproductive contribution in populations with local mate competition would bias their sex ratio more towards sons. In these models and the one described in this paper, investment into female function gave a constant return, whereas investment in male function showed diminishing returns, due to increasing competition among sons or homologous sperm with increasing male investment. Changes in sex allocation with size are apparent in a wide diversity of hermaphroditic organisms and have been best documented in plants (Burd and Allen 1988; McKone and Tonkyn 1986; reviewed in Goldman and Willson 1986). These studies show both increases, decreases, and no apparent change in sex allocation with individual size. Although it is possible that some of these shifts may be caused by changes in the frequency of selfing, it is likely that patterns of reproductive success, local mate competition, and other factors such as propagule dispersal change with individual size in a variety of species (e.g., Burd and Allen 1988). This intraspecific variability in sex allocation offers a rich resource for testing hypotheses both by allowing for more specific predictions and by allowing those predictions to be made without the potentially confounding effects of phylogeny.

ACKNOWLEDGMENTS

This work was supported by a Smithsonian Tropical Research Institute Postdoctoral fellowship and National Science Foundation grants OCE-9201320 to C.P. and by BSR-8219882 to E.F. M. Buri, L. Fore, C. B. Gruper, P. Hardsion, J. Jolly, D. Parker, V. Bound, and H. Hess helped with data collection. Special thanks to R. Foster and M. Kipersztok for early help in the gonad allocation work. R. Warner, H. Hess,
D. Fairbairn, and two anonymous reviewers provided helpful comments on the manuscript. Our thanks to Recursos Marin,os, the Smithsonian Tropical Research Institute, and the people of Kuna Yala for assistance and permission to work in Panama.

LITERATURE CITED


CORRESPONDING EDITOR: D. Fairbairn

APPENDIX I

Calculating Sex and Size-Specific Reproductive Success

To calculate current reproductive success for an individual, the period of time used to sum reproductive success was arbitrarily set at 1 day.
Over that day, the female reproductive success of an individual of size class \( i \) is

\[
E_i(1 - a_i),
\]

where \( E \) is the hypothetical number of eggs produced by a hermaphrodite that devotes all of its fertility-dependent allocation to female function, and \( a_i \) is the proportion of the fertility-dependent allocation devoted to male function for an individual in size class \( i \). The model addresses only sex allocation after fixed costs of reproduction have been allocated; these fertility-independent costs appear low in hermaphroditic seabasses (Fischer 1981; Hastings and Petersen 1986). Sex allocation models predict the partitioning of only fertility-dependent allocation, after fixed costs have been removed (Charnov 1982). Equating the number of eggs produced with female reproductive success in chalk bass seems warranted because there appears to be little variation in egg size within the size class, and fertilization rates for tropical reef fishes with external fertilization are very high (C. Petersen and D. Levitan, unpubl. data), and the planktonic eggs are widely dispersed, so increasing fecundity should not result in increased sibling competition or a diminished return for investment in female function.

Male reproductive success over the same time period can be divided into two components corresponding to the two male spawning behaviors, pair spawning and streaking. To calculate male reproductive success, each possible combination of male participants and female partner in a spawn had to be determined and discounted by its frequency of occurrence. The reproductive success of an individual spawning as a male is equal to the fecundity of the female-role spawner in the spawn weighted by the estimated proportion of sperm released in the spawn by the individual. We assume that sperm production of a male for a day is directly proportional to the dry weight of the testicular portion of the ovotestis. We also assume that individual hermaphrodites release equal amounts of sperm in all of their male-role spawns but that different individuals may release differing amounts of sperm due to differences in their amount of testicular tissue or their spawning rates as males. A similar assumption is made regarding egg release in female spawning spawns.

For an individual pair, spawning as a male without streakers with an individual of size class \( j \), each has a reproductive success equal to the fecundity of the female, \( E_j(1 - a_j)r_{j,i} \), where \( r_{j,i} \) is the daily female spawning frequency for an individual of size class \( j \). When streakers are present, the reproductive success of the male-role pair spawner is reduced to the proportion of sperm he releases in the spawn. For this model, spawns with zero to four streakers were considered, with five or more streakers rare in this species (Fischer 1984b, this paper). The reproductive success for an individual of size class \( i \) pair spawning as a male for a day is

\[
M_i \sum_j \left[ P_{ij}(E_j(1 - a_j)r_{j,i}) \sum_k T_{ijk}(r_{i,k} + r_{j,k}) \right],
\]

where

\[
M_i = \text{the average number of pair spawns by an individual of size class } i \text{ in a day.}
\]

\[
P_{ij} = \text{the proportion of the male pair spawns by an individual of size class } i \text{ with a female-role individual of size class } j.
\]

\[
T_{ijk} = \text{the proportion of pair spawns of a male-role individual of size class } i \text{ and a female-role individual of size class } j \text{ that are streaked by a unique combination of individuals } k.
\]

For four size classes with zero to four streakers, there are 70 unique combinations of numbers of streakers and their size classes possible for each size-specific pair spawn.

\[
s_i = \text{the amount of sperm released by an individual of size class } i \text{ and is equal to}
\]

\[
(R_i d_i) r_{i,m},
\]

where \( R_i \) is the amount sperm an individual of size class \( i \) can produce if all fertility-dependent allocation is directed to male function, and \( r_{i,m} \) is the daily spawning frequency of individual \( i \) as a male through both streaking and pair spawning.

\[
s_{ij,k} = \text{the total amount of sperm released by the unique combination of streakers } k \text{ in a pair spawn with a male-role individual of size class } i \text{ and female-role individual of size class } j.
\]

The average daily male reproductive success of an individual in size class \( i \) through streaking is

\[
S_i = \sum_j \sum_k \left[ P_{ij}(E_j(1 - a_j)r_{j,i}) \sum_n T_{ijk}(r_{i,k} + r_{j,k}) \right],
\]

where

\[
S_i = \text{the daily streaking rate of an individual of size class } i.
\]

\[
P_{ij} = \text{the proportion of the streaks of an individual of size class } i \text{ that occur in spawns with a pair spawning male-role individual of size class } h \text{ and a female-role individual of size class } j.
\]

\[
T_{hij,k} = \text{the proportion of spawns with an individual of size class } h \text{ as a male-role pair spawner, an individual of size class } j \text{ as a female-role pair spawner, and } i \text{ as a streaker with an additional unique combination of } n \text{ streakers. There can be zero to three additional streakers, with } 35 \text{ unique combinations of numbers of individuals and their size classes.}
\]

\[
s_{hij,k} = \text{the total amount of sperm released by the unique combination of additional streakers } n \text{ in a pair spawn with a male-role individual of size class } h \text{ and female-role individual of size class } j \text{ and a streaker of size class } i.
\]

The total daily reproductive success of an individual is the sum of Equations 1–3. Using this approach, a model was written in BASIC using the specific spawning frequencies and gonad sizes given in the results section and below.

**Frequencies of Pair Spawning with Individuals of Different Size Classes**

There were 87 unique pairs of individuals that spawned during the study where the size of both individuals was known, leading to 174 unique combinations of male- and female-role pair spawns. These frequencies were used in the simulation, with the size classes numbered from smallest (1) to largest (4). The matrix of spawning partners is listed below, with the proportion of spawns for each size-class row listed in parentheses.

<table>
<thead>
<tr>
<th>Size Class</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
</tr>
</thead>
<tbody>
<tr>
<td>Size Class</td>
<td>6(0.316)</td>
<td>11(0.579)</td>
<td>2(0.105)</td>
<td>0(0)</td>
</tr>
<tr>
<td>2</td>
<td>1(0.162)</td>
<td>36(0.529)</td>
<td>20(0.294)</td>
<td>10(0.15)</td>
</tr>
<tr>
<td>3</td>
<td>2(0.033)</td>
<td>20(0.334)</td>
<td>36(0.600)</td>
<td>20(0.033)</td>
</tr>
<tr>
<td>4</td>
<td>0(0)</td>
<td>1(0.037)</td>
<td>2(0.074)</td>
<td>24(0.889)</td>
</tr>
</tbody>
</table>