SEX ALLOCATION IN HERMAPHRODITIC SEA BASSES

CHRISTOPHER W. PETERSEN*

Smithsonian Tropical Research Institute, APO Miami 34002-0011

Submitted December 5, 1989; Revised June 11, 1990; Accepted July 20, 1990

Abstract.—Local mate competition theory has emphasized the importance of sperm competition in determining individual patterns of sex allocation in outcrossing hermaphrodites. In this article I develop a more general model of local mate competition that incorporates fertilization efficiency. I use this model to predict interspecific differences in sex allocation. These predictions are tested by using dry weights of male and female gonadal tissue from six species of hermaphroditic sea basses. In all four paired comparisons, when two of the three factors presumed to determine sex allocation patterns are relatively constant, the shift in sex allocation between species is correctly predicted. Neither levels of sperm competition nor the expected effects of spawning behavior on fertilization efficiency can account for all of the differences in sex allocation, although sperm competition does correctly predict the most differences in sex allocation. Overall, the interspecific differences are predicted by either the level of sperm competition or by factors affecting fertilization efficiency. A broader view of local mate competition that includes aspects of sperm competition and the dynamics of fertilization should ultimately provide more accurate predictions of sex allocation in hermaphroditic organisms.

One goal of sex allocation theory is to predict the allocation of resources to male and female function in simultaneous hermaphrodites given 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). This theory is applicable to a wide diversity of species; it applies equally well to plant and animal mating systems and can incorporate many factors that affect the relationship between reproductive success and sex allocation. In studies of hermaphrodite sex allocation, considerable attention has been given to the predicted decrease in male allocation with increased selfing rate (Lemen 1980; Charlesworth and Charlesworth 1981; Schoen 1982; Ross and Gregorius 1983; Charnov 1987; McKone 1987). The purpose of this article is to expand a current model for sex allocation under sperm competition and to provide a comparative test of predictions by using outcrossing hermaphroditic fishes. This model reveals that a knowledge of both the intensity of sperm competition and fertilization efficiency is necessary to understand patterns of sex allocation in simultaneously hermaphroditic sea basses.

The principal model in sex allocation theory in simultaneous hermaphrodites is the local-mate-competition (LMC) model (Hamilton 1967; modified for simultaneous hermaphrodites by Charnov 1980, 1982; Fischer 1981, 1984a). This model
Fig. 1.—Fitness returns over a range of allocation patterns for rare individuals in populations at an ESS sex allocation. Populations with three different sperm competition levels are shown. A fixed total investment in reproduction is divided between male and female function; as male allocation increases, female allocation decreases. The ESS sex allocation is indicated on the overall (male + female) curve by an asterisk. This allocation occurs when the sum of maternal + paternal fitness is maximized. The initially steeper curve associated with low levels of sperm competition results in a lower ESS sex allocation than for higher levels of sperm competition. The female gain curve used for this example is linear; any saturating female curve will give similar results. Modified from Fischer (1981), Charnov (1982), and Lloyd (1984).

predicts that the number of sperm competitors determines the optimal proportion of reproductive resources allocated to male function. With larger mating groups there is an increasing probability that an individual’s sperm will displace competing sperm rather than its own. Thus, the LMC model predicts increasing male allocation from low levels, sufficient only to fertilize a mating partner’s eggs in the absence of sperm competition, to high levels, which increase to 50% male allocation under extreme sperm competition (Charnov 1982). This argument is shown graphically in figure 1. Sperm competition alters the evolutionarily stable sex allocation by altering the male fitness curve, the curve obtained by graphing male fitness against male allocation. At low levels of sperm competition the male
curve quickly saturates (shows diminishing returns), and the sex allocation that maximizes the sum of male and female fitness is strongly female biased (fig. 1). At high levels of sperm competition, the male fitness curve is more linear, and the optimal sex allocation shifts toward higher levels of male allocation.

In addition to the level of sperm competition, other factors have been hypothesized to change the male or female fitness curve and thus alter patterns of sex allocation (reviewed in Lloyd 1985). These factors include local resource competition among siblings (Lloyd 1984; Lloyd and Bawa 1984), an upper limit for female fitness as a result of restricted brooding space (Heath 1979; Charnov 1982; Strathmann et al. 1984), and selfing (Charlesworth and Charlesworth 1981; Ross and Gregorius 1983). However, few empirical studies have addressed these factors; a demonstration of decreased allocation to male function with increased levels of selfing in several plant species is the only exception (Lemen 1980; Schoen 1982; Charnov 1987; McKone 1987).

There may be additional factors that affect the male fitness curve, and thereby influence the evolutionarily stable strategy (ESS) sex allocation. If adult behavior during spawning can affect the interactions of gametes after their release, then spawning behavior can alter the fitness curves of either sex and alter the ESS sex allocation. As an example, if eggs are distributed over a smaller volume of water in an aquatic species with external fertilization, the absolute amount of sperm needed to obtain a given fertilization rate may be lower, and the shape of the male fitness function should change. The change in the ESS allocation will depend on how changes in the fertilization dynamics alter the marginal returns of the fitness functions for each sex.

In this article I develop a mathematical model that includes both sperm competition and the effect of spawning behavior on fertilization dynamics as factors that can affect the male fitness curve and thus influence sex allocation patterns. I used six species of simultaneously hermaphroditic sea basses to compare the accuracy of both sperm competition and fertilization dynamics in predicting interspecific patterns in relative allocation to male and female function.

REPRODUCTIVE BIOLOGY OF HERMAPHRODITIC SEA BASSES

The simultaneously hermaphroditic sea basses (family Serranidae, subfamily serraninae) provide an excellent system for comparative studies of sex allocation. Extensive data exist on the reproductive biology of five species from the Caribbean and one species from the Eastern Pacific, including data on the level of sperm competition, differences in spawning behavior during gamete release, and spawning frequency as a female (table 1).

In all species fertilization is external, and eggs are released in a characteristic pair spawn with each fish assuming a specific sex role associated with the release of eggs or sperm. Individuals appear to release only one type of gamete during a spawn, and selfing probably does not occur (Fischer 1981; Hastings and Petersen 1986). The eggs are planktonic and float away once released. Planktonic periods have not been established for these species, but in two other species of sea
<table>
<thead>
<tr>
<th>Mating System and Species</th>
<th>Number of Spawns Observed</th>
<th>Clutch Parceling (number of clutches day$^{-1}$)</th>
<th>Number of Complete Spawning Records</th>
<th>Sperm Competition (% streakers spawn$^{-1}$)*</th>
<th>Spawning Clasp†</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Serial monogamy:</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Hypoplectrus nigricans</em></td>
<td>806</td>
<td>Yes (4.7)</td>
<td>70</td>
<td>Absent (0)</td>
<td>Yes</td>
<td>Fischer 1980</td>
</tr>
<tr>
<td><em>Serranus tabacarius</em></td>
<td>750</td>
<td>Yes (8.5)</td>
<td>42</td>
<td>Very low (0.001)</td>
<td>No</td>
<td>C. W. Petersen, unpublished data</td>
</tr>
<tr>
<td><em>Serranus tortugarum</em></td>
<td>1,371</td>
<td>Yes (7.7)</td>
<td>168</td>
<td>High (0.58)</td>
<td>No</td>
<td>Fischer 1984b, Fischer and Hardison 1987</td>
</tr>
<tr>
<td>Permanent monogamy:</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Serranus nigritus</em></td>
<td>50</td>
<td>No (1)</td>
<td>39</td>
<td>Low (0.06)</td>
<td>No</td>
<td>Pressley 1981</td>
</tr>
<tr>
<td>Harem polygyny:</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Serranus baldwini</em></td>
<td>177</td>
<td>No (1)</td>
<td>63</td>
<td>Very low (0.01)</td>
<td>No</td>
<td>Petersen and Fischer 1986</td>
</tr>
<tr>
<td><em>Serranus fasciatus</em></td>
<td>413</td>
<td>No (1)</td>
<td>132</td>
<td>Moderate (0.12)</td>
<td>No</td>
<td>Petersen 1987, 1990a</td>
</tr>
</tbody>
</table>

* Streakers are additional male-role spawners that join the spawning pair.
† In a spawning clasp two mating partners curve their bodies to form a semiclosed space between the pair where gametes are released.
basses the larval period is 24–26 d (Brothers and Thresher 1985). Adults maintain relatively small home ranges either at or near coral and rocky reefs.

Three types of mating systems exist (table 1). Pair spawning with clutch parceling, found in Hypoplectrus nigricans, Serranus tortugarum, and Serranus tabacarius, involves pairs of individuals that take turns releasing eggs for their partner to fertilize (Fischer 1980, 1984b; C. W. Petersen, unpublished data). The egg production for 1 d is released over a variable number of spawns (table 1). Spawning partners can change both within and between days; thus this type of mating system is called “serial monogamy” (Fischer and Petersen 1987).

A second mating system, characterized by the release of a day’s egg production in a single spawn and long-term monogamy, occurs in Serranus tigrinus. Members of a monogamous pair spawn every day with each other.

The third mating system, with populations including both simultaneous hermaphrodites and pure males, occurs in S. fasciatus and S. baldwini. All individuals first mature as hermaphrodites, but larger individuals may change to pure males and defend a harem of hermaphrodites (Petersen and Fischer 1986; Petersen 1987). This mating system is referred to as harem polygyny. Hermaphrodites within the harem usually spawn as females once per day, and only occasionally spawn as males. The evolution of mating systems in the hermaphroditic sea basses is discussed elsewhere (Petersen and Fischer 1986; Fischer and Petersen 1987; Petersen 1990a).

In five of the six species, additional conspecifics have been observed to join the spawning pair. Based on behavioral observations and analogous behavior in separate-sexed species, these individuals are presumed to release sperm and are called streakers (Fischer 1984b; Petersen 1987). Streaking rates vary considerably among species (table 1). For example, in S. tortugarum as many as seven individuals may streak on a given spawn. In contrast, only one streak was observed in 750 spawns in S. tabacarius (C. W. Petersen, unpublished data), and in H. nigricans and other species of Hypoplectrus, streaking has never been observed (N > 1,000 spawns; Fischer 1980; Lobel and Neudecker 1985).

One aspect of spawning behavior also differs between Serranus and Hypoplectrus, and this behavioral difference may result in differences in fertilization rate (the proportion of eggs fertilized in a spawn) and the amount of sperm needed to attain a particular fertilization rate. In contrast to Serranus species in which spawning occurs at the apex of a rapid spawning rush, in Hypoplectrus species spawning involves a slower spawning clasp, in which pairs form a semienclosed space with their curved bodies. Once in this spawning clasp, gametes are released into the space between the fish. Thus, the gamete clouds of Hypoplectrus should be smaller than those of Serranus and may spread out more slowly because of reduced turbulence around the gamete cloud. Both spawning behavior during gamete release and the degree of clutch parceling may affect fertilization dynamics.

**DATA COLLECTION**

Collections were made of the six hermaphroditic species in table 1 to measure sex allocation in each species. All five Caribbean species were collected between
June and September 1988 in the San Blas Islands adjacent to the Smithsonian San Blas Research Station. Samples were taken during a narrow interval, between 1130 and 1330 hours, to control for possible diel changes in egg maturation (Fischer and Hardison 1987). All collections were made at the same reef where the original mating system studies were conducted or on similar nearby reefs.

The single eastern Pacific species in this study, *Serranus fasciatus*, was studied at two sites. In 1986 a Mexican population was studied that consisted of harems with one dominant individual (typically a male) and from 1 to 11 hermaphrodites. Subordinate hermaphrodites spawned with the dominant, but also occasionally spawned as males either by streaking or by pair spawning with other hermaphrodites. In 1985 the species was also studied in the Bay of Panama at Taboga Island. Hermaphrodites in this population had higher levels of male mating success through pair spawning (Petersen 1990a). Collections from the Mexico and Panama populations were compared for differences in allocation patterns.

All individuals were fixed in 10% formalin and later preserved in isopropyl alcohol. Specimens were weighed, their standard length measured, and their gonads removed. Male and female tissues in the ovotestis were separated and dried in preweighed pans at 70°C for 16–48 h before they were weighed. Preliminary weighing curves showed these times to be sufficient for complete drying. Samples weighing approximately 1 mg and heavier were weighed on an analytical balance accurate to $\pm 1 \times 10^{-4}$ g; lighter samples were weighed with a CAHN microbalance. Individuals with immature gonads and hermaphrodites in transition to pure males in the harem polygynous species were not included in the analysis. Comparisons of gonadal allocation patterns among species were made using Mann-Whitney $U$-tests. The significance level for the pairwise interspecific tests was determined by using a sequential Bonferroni test (Rice 1989) with the groupwise Type I error set at 0.05.

**THE MODEL**

To model sex allocation, I follow Lloyd (1984), who considered the fitness of an individual to be equal to the sum of the independent contributions of male and female gametes to current reproductive success. My objective is to predict the optimal sex allocation, as allocation to male and female gametes, for a particular combination of sperm competition and fertilization dynamics.

For this model I make the following assumptions. First, the rate of production of gametes is assumed to be proportional to the dry weight of tissue for either sex within the ovotestis. This assumption appears warranted given the simplicity and similarity of the gonadal structure. In at least one species, *Serranus fasciatus*, dry weight of ovarian tissue has a significant positive correlation with the number of mature eggs produced (Petersen 1990b). Furthermore, in all species both male and female tissue appears almost entirely devoted to gamete production, with very little investment to fixed or fertility-independent costs that are necessary for reproduction but do not change with increasing gamete production (Heath 1977). This is important because sex allocation models predict the partitioning of only fertility-dependent allocation, after fixed costs have been removed (Charnov 1982).
Second, the model has no age or population size structure. All hermaphroditic individuals within a species are assumed to have equal total allocation to reproduction.

Third, the reproductive success of an individual through female function is assumed equal to the number of fertilized eggs produced. This assumption seems reasonable because there appears to be little variation in egg size within species, nor are there systematic differences in spawning location among individuals that would lead to differential egg success within species (E. A. Fischer, personal communication; C. W. Petersen, personal observation); there is no parental care; 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.

Fourth, I assume the proportion of eggs fertilized to be a function of sperm concentration. This assumption is intuitively appealing and has empirical support from studies of fertilization dynamics from both fishes and marine invertebrates (Billard et al. 1974; Vogel et al. 1982). Since sperm are usually at much higher density than eggs, sperm will compete for fertilizations, while eggs ($e$) will not. This can be modeled as the exponential function:

$$\text{proportion of eggs fertilized} = 1 - e^{-s}$$  \hspace{1cm} (1)

where $s$ is the concentration of sperm in the gamete cloud. When individuals spawn once per day as males and there is no sperm competition, $s = ac$, where $a$ is the proportion of $R$, the total resources for fertility-dependent allocation, devoted to sperm production and $c$ is a constant that translates the proportion of fertility-dependent male allocation ($a$) into sperm concentration within the gamete cloud. The value $c$ reflects fertilization efficiency and is assumed constant within a species. Equation (1) is equivalent to calculating the collision frequency between a common (sperm) and a rare (egg) particle as a function of the concentration of the common particle and is similar to equations modeling fertilization used by Denny (1988; Denny and Shibata 1989). For a doubling of concentration of the common particle, the total number of particle collisions doubles, but, because a fraction of these are multiple collisions with the same rare particles (eggs), the total number of eggs collided with (fertilized) increases with increased sperm concentration at a diminishing rate. Equation (1) can be only a “best estimate” of fertilization dynamics since it assumes the sperm and egg clouds completely overlap, have consistent densities throughout their distribution, and occupy a constant volume independent of gamete number.

The exact shape of the fertilization curve depends on the constant $c$; at higher $c$, with increasing allocation to male function the fertilization rate will more quickly increase to high values and become asymptotic at complete fertilization (fig. 2). Larger gamete clouds will have lower sperm densities for the same amount of sperm released; this is expressed as a lower $c$.

Comparing figures 1 and 2 suggests that reducing $c$ has a similar effect on the male fitness curve as increasing sperm competition. Fertilization in a larger volume of water should result in a more linear male fitness curve, and this should
result in increased male allocation in species with lower $c$. This prediction is developed in the analytical model presented below.

Equation (1) can be incorporated into a model of optimal sex allocation. The reproductive success of a hermaphrodite through male function will equal the number of eggs it fertilizes. Denoted as $w_{a,M}$ for a hermaphrodite that allocates $a$ to male function, this is the product of the number of eggs its partner releases per spawn and the fertilization rate. In a population without sperm competition in which all individuals have identical allocation, this is

$$w_{a,M} = E(1 - a)(1 - e^{-ca}),$$

(2)

where $E$ is the hypothetical number of eggs released per spawn by a hermaphrodite that devotes all of its fertility-independent allocation to female function ($a = 0$).

Equation (2) can be modified to take into account the effects of sperm competition. If all individuals adopt the same strategy in a population but the average number of males in a spawn is $m$, the average ratio of male to female spawns for an individual will be $m$. Therefore, sperm allocation $a$ must be parcelled into $m$ units, each with $(a/m)$ allocation to sperm production. The general equation for male reproductive success with sperm competition must include four values: the number of eggs in a spawn, the number of spawns as a male, the proportion of sperm in the spawn released by an individual male, and the fertilization rate. This is

$$w_{a,M} = E(1 - a)(m)(1/m)(1 - e^{-cm(a/m)}).$$

(3)

Equation (3) assumes that sperm are completely mixed and that all individuals releasing sperm release the same amount of sperm independent of their spawning
role (pair spawner or streaker). It is not known whether or how hermaphrodites vary their sperm release between spawns, so a simple constant release of sperm per spawning individual within a species is assumed for this model.

The female fitness of a hermaphrodite is considered to be equal to the product of its egg production and fertilization rate, or

\[ w_{a,F} = E(1 - a)(1 - e^{-ca}). \]  

Equations (3) and (4) represent the male and female reproductive success that a hermaphrodite will accrue over the time period in which it spawns once as a female; this is also the time period in which it will, on average, spawn \( m \) times as a male. Because conditions do not change through time and lifetime male and female reproductive success (RS) are equations (3) and (4) summed over the number of female spawns in a lifetime, the allocation that gives the highest current fitness (the sum of eq. [3] and [4]) will represent the strategy that gives the highest lifetime reproductive success.

The sex allocation \( a \) will be an ESS (Maynard Smith 1982) when a rare individual allocating \( a^* \) cannot invade the population (\( w_{a^*,M+F} \leq w_{a,M+F} \)). This occurs when \( dw_{a^*,M+F}/da^* = 0 \), and when \( a^* = a \). The reproductive success through male and female function for a hermaphrodite allocating \( a^* \) in a population of individuals allocating \( a \) is

\[ w_{a^*,M} = E(1 - a)(m)/(a(m - 1) + a^*)[(1 - e^{-c(a(m - 1) + a^*)/m})], \]  

and

\[ w_{a^*,F} = E(1 - a^*)(1 - e^{-ca}). \]

Taking \( dw_{a^*,M+F}/da^* \), setting this derivative equal to zero, and substituting \( a \) for \( a^* \) yield the ESS solution:

\[ [(1 - a)/m][(m - 1/a)(1 - e^{-ca}) + ce^{-ca} - (1 + e^{-ca})] = 0. \]  

An interesting special case of this solution occurs as \( c \) increases to infinity. The solution then reduces to

\[ a = (m - 1)/2m. \]

This result is identical to that of Charnov (1980) and Fischer (1981), who assumed that fertilization rates were always 100%. When \( c \) is infinity, however, the ESS differs from equation (8) by being dependent on both \( m \) and \( c \). As an illustration, the ESS sex allocation is shown for selected values of mating-group size \( m \) and \( c \) in figure 3. There is only one ESS for each value of \( m \) and \( c \). As \( m \) increases, the optimal \( a \) increases for a given value of \( c \). At low \( c \) (low sperm concentration for a given male allocation) the optimal male allocation begins high and is always close to 50%; at high \( c \) male allocation is lower but quickly becomes asymptotic at 50% male with increasing \( m \). For a fixed level of sperm competition, increasing \( c \) decreases the ESS \( a \) (fig. 3). This verifies the prediction made earlier by comparing figures 1 and 2. Increasing \( c \) or decreasing \( m \) results in a more quickly saturating male fitness curve, and the ESS sex allocation becomes more female biased.
As \( c \) goes to infinity, the results converge with those of Charnov (1980, 1982) and Fischer (1981).

By using this model, predictions can be made concerning the effects of sperm competition and factors affecting fertilization rate on optimal male allocation. Although absolute levels of \( a \) can be estimated from the data for each species, only relative magnitudes of \( c \) can be estimated for each species. This limits the predictions of the model to directional shifts in allocation among species. I now consider three factors that may explain differences in \( a \) among sea bass species: (1) mating-group size, \( m \), which affects the level of sperm competition; (2) behavior during gamete release; and (3) spawning frequency in a female role. The two aspects of spawning behavior (factors 2 and 3) together determine fertilization efficiency, \( c \).

**TESTING THE MODEL: PREDICTIONS**

*Sperm competition.*—LMC models predict that the level of male allocation should mirror the level of sperm competition among species (Charnov 1980, 1982; Fischer 1981, 1984a). Even if all eggs are not fertilized, as long as \( c \) is identical among species male allocation should be higher in species with higher levels of sperm competition.

The level of sperm competition is dependent on both the overall level of streaking (table 1) and the distribution of streakers among spawns (Fischer 1984a). However, incorporating the distribution of streakers by using the method of Fischer (1984a; Petersen 1990c) gives the same ranking of species for the intensity of sperm competition as the mean number of streakers per spawn (table 1).
The rankings of sperm competition among species from table 1 are *Hypoplectrus nigricans* < *Serranus tabacarius* < *Serranus tigrinus* < *Serranus tortugarum* for the monogamous species and *Serranus baldwini* < *Serranus fasciatus* for the harem polygynous species. In comparison among species, the relative male allocation of the harem polygynous species cannot be compared with the purely hermaphroditic species. Hermaphrodites in the harem polygynous species are often in sperm competition with larger males, whose sperm production will depend on a different set of life-history trade-offs. Because of this sperm competition with males, hermaphrodites in harem polygynous species may respond to sperm competition differently from hermaphrodites in species without males. To avoid this problem, I compare the two harem polygynous species only with each other.

The predictions of differences in allocation due to sperm competition (table 2) were made by assuming that $c$ is equal for all species. However, male allocation within each group may not reflect levels of sperm competition if species have very different values of $c$. The most powerful tests of the importance of sperm competition in determining male allocation are comparisons between species that differ in sperm competition but have similar spawning behaviors. One such test is between *S. tortugarum* and *S. tabacarius* (tables 1, 2). Since sperm competition is higher in *S. tortugarum*, male allocation should also be higher. A further test can be made between the harem polygynous species, *S. baldwini* and *S. fasciatus*. *Serranus fasciatus* has greater sperm competition and should have greater male allocation.

*Spawning behavior: gamete release.*—The spawning clasp of *Hypoplectrus* should result in the smallest gamete cloud and thus the highest fertilization efficiency of any hermaphroditic sea bass. In contrast, the spawning rushes of the
other species should result in a lower $c$ since the quick spawning rush will result in higher levels of turbulence, which will quickly spread the gamete cloud and reduce the density of sperm. Based on the dynamics of fertilization, the lowest male allocation should therefore be found in *H. nigricans*. The most useful comparison is between *H. nigricans* and *S. tabacarius*; both are egg traders with insignificant levels of sperm competition, but only *H. nigricans* has a spawning clasp (tables 1, 2).

**Spawning behavior: spawning frequency as a female.**—The model predicts that, if mating group size ($m$) and $c$ are constant, there should be no difference in sex allocation between a species that releases all of its daily egg production in one spawn versus one that parcels its egg production into several spawns. However, parceling clutches may result in a lower $c$ even when behavior during spawning is identical to that of a nonparceler. If the cumulative volume of the egg clouds from several parcelled spawns is larger than a cloud of the same number of eggs released in one spawn, as seems likely, then the value of $c$ in species with parcelled clutches will be lower. This leads to the prediction that a parceling species should have higher male allocation than a species that does not parcel egg production (tables 1, 2). The most useful comparison can be made between *S. tabacarius*, a parceler, and *S. tigrinus*, a species in which individuals release their daily egg production in one spawn. Both species have quick spawning rushes and very low levels of sperm competition.

**TESTING THE MODEL: RESULTS**

There were significant differences among species in their sex allocation (tables 3, 4; fig. 4). Male tissue made up less than half of the ootestis dry weight, varying from an average of about 2%–19%.

**Sperm competition.**—In both pairwise predictions of species with similar fertilization dynamics, sperm competition correctly predicted differences in sex allocation (boxed comparisons in the first col. of table 2; table 4). Overall, five of seven differences in sex allocation between species pairs were predicted correctly by differences in sperm competition (table 4). In another case, the qualitative prediction was also supported, although the difference in sperm competition was slight (sperm competition observed in one spawn in *Serranus tabacarius* vs. never being observed in *Hypoplectrus nigricans*) and did not seem large enough to justify the difference in allocation (table 3; fig. 4). In the remaining case sperm competition predicted a difference in the opposite direction from the observed difference (*Serranus tigrinus* vs. *S. tabacarius*).

The intraspecific difference in sex allocation between years in *Serranus fasciatus* did not support the sperm competition hypothesis. Streaking rates and thus sperm competition levels were not different between the two years ($G = 0.29$, NS; Petersen 1990b). However, hermaphrodites in 1985 spawned more frequently as males than did hermaphrodites in 1986 (41% of the spawns vs. 27%, $G = 4.5$, $P < .05$) and had higher male allocation ($Z = 5.0$, $P < .001$; fig. 4).

**Spawning behavior: gamete release.**—The behavior during gamete release also appeared to play a role in determining sex allocation. In the pairwise comparison
TABLE 3

Sex Allocation in Six Hermaphroditic Sea Bass Species

<table>
<thead>
<tr>
<th>Species</th>
<th>Percentage Male Allocation</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Median</td>
</tr>
<tr>
<td>Hypoplectrus nigricans</td>
<td>2.19</td>
</tr>
<tr>
<td>Serranus baldwini</td>
<td>3.60</td>
</tr>
<tr>
<td>S. tigrinus</td>
<td>4.65</td>
</tr>
<tr>
<td>S. tabacarius</td>
<td>7.00</td>
</tr>
<tr>
<td>S. fasciatus</td>
<td></td>
</tr>
<tr>
<td>Both years combined</td>
<td>8.45</td>
</tr>
<tr>
<td>1985 only</td>
<td>7.30</td>
</tr>
<tr>
<td>1986 only</td>
<td>3.12</td>
</tr>
<tr>
<td>S. tortugaram</td>
<td>18.80</td>
</tr>
</tbody>
</table>

TABLE 4

Comparison of Results with Predicted Patterns of Sex Allocation in Six Species of Hermaphroditic Sea Basses

<table>
<thead>
<tr>
<th>Species</th>
<th>Observed Pattern of Male Allocation</th>
<th>Hypotheses</th>
</tr>
</thead>
<tbody>
<tr>
<td>S. tortugaram vs. H. nigricans</td>
<td>&gt;***</td>
<td>S B F</td>
</tr>
<tr>
<td>S. tortugaram vs. S. tabacarius</td>
<td>&gt;***</td>
<td>S</td>
</tr>
<tr>
<td>S. tortugaram vs. S. tigrinus</td>
<td>&gt;***</td>
<td>S F</td>
</tr>
<tr>
<td>S. tigrinus vs. H. nigricans</td>
<td>&gt;**</td>
<td>S B F</td>
</tr>
<tr>
<td>S. tabacarius vs. H. nigricans</td>
<td>&lt;=**</td>
<td>F S</td>
</tr>
<tr>
<td>S. fasciatus vs. S. baldwini</td>
<td>&gt;*</td>
<td>S</td>
</tr>
</tbody>
</table>

Note.—Inequalities are as in Table 2. The asterisks for each inequality indicate the level of significance of a Mann-Whitney U-test. The letters for each test represent the hypotheses the results support: S, sperm competition; B, behavior during gamete release; F, spawning frequency. The lowercase letter in the comparison of sperm competition between S. tabacarius and H. nigricans indicates weak support.

* P < .05.
** P < .005.
*** P < .001.

between H. nigricans and S. tabacarius, there was a highly significant difference in sex allocation between species (boxed comparison in second col. of table 2; table 4). All three predictions based on spawning behavior during gamete release were supported by the data (table 4). These tests were not independent since all involved comparisons with H. nigricans. One potential problem with these tests is that all pairwise comparisons used H. nigricans, the only species without any reported sperm competition, so the predictions based on behavior during gamete release are identical to those of the sperm competition hypothesis.

The shortcoming of behavior during gamete release in predicting sex allocation patterns was in the differences it did not address: in all four comparisons in
Fig. 4.—The frequency distributions of sex allocation as a percentage of male allocation for six species of hermaphroditic sea basses.
which spawning behavior during gamete release did not predict differences in sex allocation there were significant differences between species pairs.

*Spawning behavior: spawning frequency as a female.*—The data also suggest that the degree of clutch parceling plays a role in determining the level of male allocation in sea basses. In the pairwise comparison the difference in allocation between *S. tabacarius* and *S. tigrinus* was predicted from differences in spawning frequency alone (boxed value in third col. in table 2; table 4). Overall, three of four pairwise predictions among hermaphroditic species were supported by the data. In one case the spawning-frequency hypothesis predicted a difference in allocation the opposite of what was observed (*H. nigricans* vs. *S. tigrinus*; table 4).

**DISCUSSION**

The present study shows that when they are considered alone neither sperm competition nor spawning behavior is sufficient to predict the patterns of sex allocation among species. In all four pairwise comparisons in which either sperm competition or fertilization dynamics were predicted to be of overriding importance in determining sex allocation, the differences between species were significant and in the predicted direction. However, no single factor successfully predicted all of the interspecific differences in sex allocation. It appears that knowledge of both sperm competition and spawning behavior is necessary to predict sex allocation patterns in sea basses.

Except for the relative sex allocation of one species pair, *Serranus tabacarius* and *Serranus tigrinus*, the level of sperm competition correctly predicted relative sex allocation among the sea basses. The range of male allocation in these six species (2%–19%) is not very different from that predicted by quantitative models of sex allocation derived from LMC theory for these species (0%–24%; Fischer 1984a). Previously, only the degree of selfing has been shown to play an important role in the evolution of sex allocation in hermaphrodites (Lemen 1980; Schoen 1982; Charnov 1987; McKone 1987). The present study supports the hypothesis that sperm competition plays a role in determining sex allocation patterns in outcrossing hermaphrodites.

Although it appears that sperm competition, behavior during gamete release, and clutch parceling can all affect sex allocation, the relative weight of the three factors will be difficult to determine in this group with so few species to compare. Unfortunately, in this group of hermaphrodites the prospect of appreciably expanding the data set is not very good. There are neither quantitative spawning data nor sex allocation data for any of the other remaining shallow-water serranines, and there are only three to four species worldwide that occur in shallow enough water to make it possible to eventually add them to this type of an analysis.

The addition of fertilization dynamics to the original LMC model helps to explain the deviations from the simpler model and offers an explanation for the large difference in sex allocation in species with similar levels of sperm competition. To make this model more quantitative, a better understanding of gamete
distributions and fertilization rate in spawns with planktonic egg release is needed. No data of this type exist for natural spawns for any marine organism.

There are several additional areas requiring quantification in order to strengthen the predictive ability of this model and to test some of the assumptions required to use the model. Several assumptions have to be made to equate the measure of sex allocation used here with an absolute measure of sex allocation. First, a standing crop of dry-weight gonad may not convert equally to a common currency of sex allocation; the metabolic rate of male and female tissue or the energetic cost of producing a fixed weight of gametic tissue of each sex may be different, biasing the absolute estimate of sex allocation in favor of male or female allocation.

There are also several assumptions concerning how competing sperm may mix during spawning. All sperm released in a spawn were assumed to mix equally with each other. Violation of this assumption, with sperm from an individual in closer contact and thus in stronger competition with each other, would cause more rapidly diminishing returns for male function and lead to lower-than-predicted male allocation in species with sperm competition. The equivalence of numbers of eggs fertilized for individual streakers and pair spawners in a spawn is another assumption that has not been tested. Because of these problems, the tests presented here have been limited to directional shifts in allocation between and within species rather than quantitative predictions of absolute proportions of resources devoted to each sex.

In the absence of sperm competition LMC theory reduces to predicting that individuals should produce just enough sperm to fertilize all of a female's eggs. That idea is somewhat oversimplified. If the marginal return for male allocation drops below the marginal return for alternative allocations (growth, female function), then males should not continue to produce sperm until the fertilization rate reaches 100% (D. Shapiro and L.-A. Giraldeau, unpublished data). Although this may not be important in internally fertilizing species in which fertilization rates may reach 100% before the marginal return on male investment drops below this critical value, in externally fertilizing species this may not generally be true.

The effects of fertilization efficiency on male allocation hypothesized in this article add to, but do not change, the proposed ideas of how sexual selection operates in hermaphrodites (Charnov 1979, Fischer 1980). In these sea basses, all evidence still suggests that females (male-role hermaphrodites) are the limiting sex and that males (male-role hermaphrodites and males) compete for spawning opportunities (Fischer 1981, 1987; Fischer and Petersen 1987; Petersen 1987, 1990a).

ACKNOWLEDGMENTS

Fieldwork was funded by a postdoctoral fellowship from the Smithsonian Tropical Research Institute, and much of the writing was conducted while I was funded by a North Atlantic Treaty Organization postdoctoral fellowship. H. Hess, M. Gross, R. Warner, and two anonymous reviewers provided useful comments on drafts of the manuscript. A preliminary version of some of the ideas in this article
was first presented at the symposium "Sex Allocation: Theory and Models" organized by M. Mangel and published in *Lectures on Mathematics in the Life Sciences* (Petersen 1990c). Many of the techniques used in this study were first perfected by E. Fischer, and I thank him for his friendship and openness in sharing ideas.

**LITERATURE CITED**


HERMAPHRODITE SEX ALLOCATION 667


