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NATURAL SELECTION AND SEX CHANGE IN PANDALID SHRIMP: TEST OF A LIFE-HISTORY THEORY

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A sequential hermaphrodite reproduces as one sex early in life, then changes to the other for the rest of its life. The condition is widespread among invertebrates and fish (Giese and Pearse 1974, 1975a, 1975b, 1977; Bacci 1965, Ghiselin 1969, 1974; Reinboth 1975; Atz 1964) and is known for a few plants (Heslop-Harrison 1972).

Ghiselin (1969) suggested that natural selection should favor this form of reproduction over dioecy when an individual's reproductive success (RS) as a male or a female is closely related to age or size, and where the relationship is different for each sex. For example, if large size increases the egg output of a female but does not aid a male in competition to fertilize eggs, selection favors genes which cause an individual to operate as a male when small, then switch to a female at a later age (or larger size). The reverse order of sex change would be favored if larger size or older age was relatively more important for male RS. A series of papers employing population genetic techniques have generally supported Ghiselin's suggestion (Warner 1975; Warner et al. 1975; Leigh et al. 1976; Charnov 1979). The formal models have the added value that they allow us to make quantitative (or semiquantitative) predictions on the nature of sex change. For example, the genetical models can be used to predict the age of sex change favored by natural selection. This age corresponds to what Maynard Smith (1976) has termed an "Evolutionarily Stable Strategy" (ESS). Individuals changing at some other age are selected against if most members of the population change sex at this age. Thus selection acts to maintain the population at this value. Qualitative predictions on the age of sex change were the basis of previous tests of the theory (Warner 1975; Warner et al. 1975).

This article presents a graphical approach to the genetical theory of sex change (similar to one recently applied to the evolution of simultaneous hermaphroditism [Charnov et al. 1976]). The graphs will help clarify a set of predictions to be tested against data from Pandalid shrimp. These shrimp are protandrous hermaphrodites (reproduce first as males). The goal is to use the genetical theory to predict the age of sex change. Since these shrimp show much geographic variation in this age (Rassmussen 1953; Butler 1964; Allen 1959; Haynes and Wigley 1969; Horsted and Smidt 1956; Scrivener and Butler 1971), they provide a good opportunity to test the evolutionary model.

A GENETICAL THEORY OF SEX CHANGE

Sex change theory makes use of the following ideas. Consider a population stable in numbers, with overlapping generations and a stable age distribution. The species is a protandrous hermaphrodite with the various life-history parameters (fertility as a male or female, survival rate) assumed to be age specific. Protandry is used here simply for illustrative purposes. Let t be the age at which an individual changes sex. Define as follows (in continuous time): $b(x) =$ birth rate of an age x female relative to the birth rate of an age y female, with y an arbitrary age chosen simply to make female fertility a relative measure; $Q(x) =$ fertility of an age x male relative to the fertility of an age y male. This age y is the same as used above, so that an individual operating as a male or a female at age y has a relative fertility of one. The $Q(x)$ is the relative ability of an age x male to fertilize eggs (e.g., compete for females).

Finally, let $l(x) =$ probability an individual is alive at age x. This is the usual life table definition from demography (Keyfitz 1968). It should be noted here that these three functions could also be related to t (e.g., $b(x, t)$), with $l(x)$ both sex and age specific.

With these definitions, we may designate the genetic contribution of an individual through male function, $M(t)$, as

$$M(t) = \int_0^t l(x)Q(x)\,dx. \tag{1}$$

The genetic contribution of an individual through female function is defined in a similar way:

$$F(t) = \int_t^\infty l(x)b(x)\,dx. \tag{2}$$

Note in (1) that if $t \to \infty$, the individual is a male all of its life; thus $M(\infty)$ is the fitness or genetic contribution of a pure male. In (2), if $t \to 0$, the individual is a female for life; thus $F(0)$ is the fitness of a pure female.

Suppose now that this population consists entirely of individuals changing sex at time t. Introduce into this population a rare mutant gene which causes its bearers to change sex at some other time $(\hat{t})$. In earlier papers (Leigh et al. 1976; Charnov 1979) it is proven that this mutant is selected against, provided

$$\frac{M(\hat{t})}{M(t)} + \frac{F(\hat{t})}{F(t)} < 2 \tag{3}$$

(otherwise it is selected for), where $M(\hat{t})$ and $F(\hat{t})$ refer to equations (1) and (2) for the mutant. Equation (3) provides a rule for finding the ESS age of sex change. If we can find a t such that (3) is satisfied for all $\hat{t}$, then the t will be the ESS (which will be denoted as t^*).

Two other inequalities are important in the theory. (1) Sex change is favored over dioecy provided

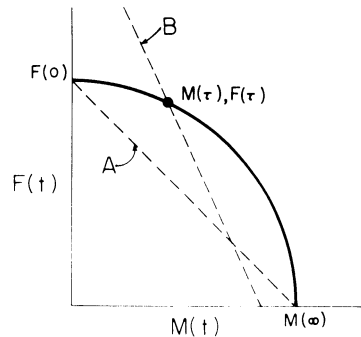$$\frac{(1 - r) \cdot F(0)}{F(t^*)} + \frac{r \cdot M(\infty)}{M(t^*)} < 2, \tag{4}$$

Fig. 1.—A fitness set for sex change. The curved surface is a plot of $F(t)$, $M(t)$ for various t. The end points are the fitnesses associated with being a pure male $M(\infty)$ or female $F(0)$. Line A connects $M(\infty)$ to $F(0)$. Line B passes through a chosen point $M(\tau)$, $F(\tau)$ with slope $-F(\tau)/M(\tau)$. These two lines are used to derive the ESS sex habit and are discussed further in the text.

where r is the fraction of males among the males and females at birth. (2) Dioecy is favored over hermaphroditism provided

$$\frac{F(t^*)}{F(0)} + \frac{M(t^*)}{M(\infty)} < 1 \tag{5}$$

(note that [5] simply inverts the ratios in [4] and sets $r = \frac{1}{2}$—which is the ESS sex ratio for the dioecious population).

These inequalities can be justified intuitively. Each is of the form

$$\frac{\text{fitness of mutant through male function}}{\text{fitness of typical individual through male function}}$$

$$+ \frac{\text{fitness of mutant through female function}}{\text{fitness of typical individual through female function}} < 2$$

Thus the equations assign equal weight to fitness gains through male and female function. Since any zygote receives half its autosomal genes from each sex, it seems reasonable that fitness measures for equilibria (or alterations) in the allocation of resources to sex function treat male and female function equally (as first pointed out by R. A. Fisher, 1958). See Charnov (1979) for a general discussion of this.

The implication of these inequalities is easier to see if they are put in graphical form. For every value of t, we find a pair of fitnesses $M(t)$, $F(t)$. If these pairs are plotted on Cartesian coordinates, a curve such as figure 1 results. Each point on the curve is associated with a t value, and the endpoints are the fitnesses for the pure males and females. This curve will be called a "fitness set" (Levins 1968), as it traces out all possible male and female fitnesses for the hermaphrodite. There are two lines in figure 1, and they correspond to boundaries of the inequalities in (3) to (5). The A connects $F(0)$ and $M(\infty)$; B is a line through any chosen point $[M(\tau), F(\tau)]$ with slope $-F(\tau)/M(\tau)$. The equation of A, which is a linear combination of pure male and female fitnesses, is

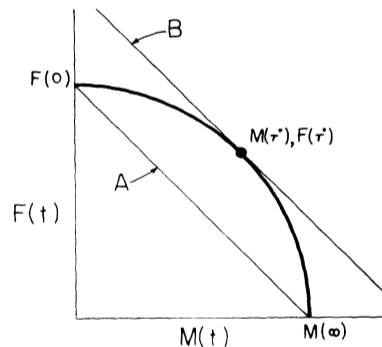$$\frac{M(t)}{M(\infty)} + \frac{F(t)}{F(0)} = 1. \tag{6}$$

FIG. 2.—A convex fitness set favors sex change. The ESS age of sex change (t^*) is where a B line is tangent to the fitness set, and where no points on the fitness set fall above (to the outside of) it. Sex change is favored since all points on the A line fall to the inside of the B line corresponding to t^*.

The equation of B is

$$\frac{M(t)}{M(\tau)} + \frac{F(t)}{F(\tau)} = 2. \tag{7}$$

Combining lines A and B with (3) to (5), I will show how the shape of the fitness set determines the sex habit. There are two cases to be considered.

Case I.—Fitness set is convex (fig. 2). Sex change is favored. The ESS age of transform (t^*) is the t which maximizes the product $M(t) \cdot F(t)$.

Dioecy is not favored, since all points on the fitness set are to the outside of line A and thus violate inequality (5). The t^* is found by constructing B lines at various points along the fitness set, until a line is found such that no points on the fitness set fall to the outside of it. This is where the line B is tangent to the curve (and ineq. [3] is satisfied). At this point the slopes of the line and fitness set are the same and $M(t) \cdot F(t)$ is maximized.

The points $(1 - r)F(0), rM(\infty)$ lie on the line connecting $F(0)$ to $M(\infty)$ and are to the inside of the B line defining $F(t^*), M(t^*)$. Sex change is thus favored over dioecy since inequality (4) is always satisfied. Intuition also leads to the idea that convexity favors sex change. With the curve convex, a sequential hermaphrodite gains more through both male and female fitness than a linear combination of males and females, which fall on the line connecting $M(\infty)$ to $F(0)$.

Case II.—Fitness set is concave (fig. 3). Dioecy is favored. All points on the fitness set lie to the inside of line A, making (5) always true. An argument similar to that given above for the B line shows that sex change cannot be favored with this fitness set. In this case the hermaphrodite never achieves the same male or female fitness as a combination of males and females.

If the fitness set is a mixture of concave and convex, the results may become rather complex. The most reasonable case is where neither (4) nor (5) is always satisfied. The ESS may then be a mixture of hermaphrodites and males or females (in stable proportions). This point is further developed elsewhere (Charnov et al. 1976).

As a final theoretical point, consider how Ghiselin's initial hypothesis necessarily
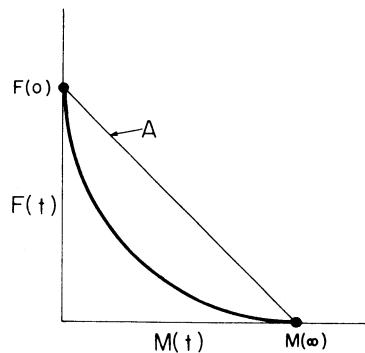
FIG. 3.—A concave fitness set favors dioecy. If all points on the fitness set fall to the inside of the *A* line, dioecy is favored over sex change. The ESS sex ratio (at conception) under dioecy is one-half males.

leads to a convex fitness set. (For alternative proof, see Leigh et al. 1976.) The fitness set is convex provided $dF(t)/dM(t)$ and $d^2F(t)/dM(t)^2$ are both < 0.

From (1) and (2), $dF(t)/dM(t) = -b(t)/Q(t)$. Thus, if $b(t)/Q(t)$ increases with t the fitness set is convex. To put it another way, if female RS, $b(t)$, increases with age relative to male RS, $Q(t)$, selection favors sex change. An individual should be a male when young, changing to a female at a later age.

These methods may be extended to cover ideas about the cost of sex change, differential mortality between the sexes, etc. So long as the relations can be represented in fitness set form, the inequalities can easily be applied.

SEX CHANGE IN PANDALID SHRIMP

Shrimp in the family Pandalidae are of major commercial importance in temperate to subarctic waters. They have been the subject of two major symposia (F.A.O. 1968–1970; Marine Biol. Assoc., India 1967), numerous life history monographs and reviews (Allen 1963; Gotshall 1972; Appolonio and Dunton 1969; Hjort and Rudd 1938; Palenichko 1941; Ivanov 1969; Mistakidis 1957; Kubo 1951; Aoto 1952) and some sophisticated population modeling (Fox 1972; Abramson and Tomlinson 1972; Geibel and Heinmann 1976). A useful bibliography also exists (Scrivener and Butler 1971).

Most commercial species are protandrous hermaphrodites. Breeding takes place in the fall. After copulation, females carry the eggs until they hatch in the spring. The larvae are planktonic, settling to the bottom in mid to late summer. Individuals breed for the first time 1.5, 2.5, or 3.5 yr after hatching. Age of first breeding is often related to the attainment of a certain size (Rasmussen 1953) and varies accordingly with growth rates. After a variable time as a male, individuals reverse sex and reproduce as females for the rest of their lives. Breeding is typically at yearly intervals, except perhaps in very cold water (Rasmussen 1953), where it may be less frequent.

Seasonal breeding means that an individual can spend only an integral number of years as a male, and that the appropriate mathematics replaces integration with
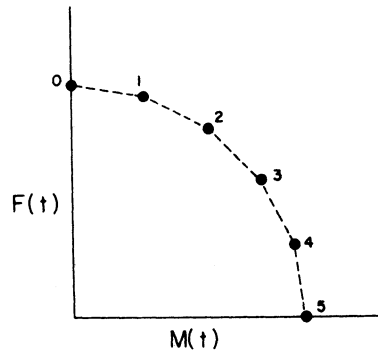
Fig. 4.—A fitness set with seasonal reproduction. The set consists of points, each referring to the fitnesses associated with spending an integral number (0–5) yr as a male. If the points are connected in succession by lines, a continuous curve results. This may be treated like the curves in fig. 1. If t^* falls on the line segment connecting two points, the population may average t^* by having a proportion of the cohort change sex at each of the two ages.

summation in (1) and (2). Likewise the fitness set will be discrete points rather than the continuous curves of figures 1–3. A hypothetical example is in figure 4. Each point (numbered 0–5) represents the fitness through male and female function for spending 0, 1, 2, 3, 4, or 5 yr as a male. The example shows a life span of 5 yr. Note, however, that the points can be connected successively with lines (as in the figure) to form a continuous curve. This curve will be convex provided $b(x)/Q(x)$ increases with x.

This curve can be treated just like the continuous fitness sets in figures 1–3. The only alteration is that if the ESS age of sex change (t^*) falls on the line segment connecting two points, it implies that the average member of a cohort spends t^* as a male (Warner 1975). For example, suppose t^* falls between ages 1 and 2. For a cohort to average t^*, one fraction of the cohort should change sex at age 1, the rest at age 2. If the fitness set is convex, t^* will either be a single age, or two successive ages with a fraction of the cohort changing at each.

The proportion (q) which should change sex at the first age is calculated as follows. It is the proportion which maximizes the product of the average fitness through male function times the average fitness through female function. Continuing the example, the product may be written as

$$[qM(1) + (1 - q)M(2)][qF(2) + (1 - q)F(3)],$$

where

$M(1)$ = male fitness for spending 1 yr as a male,
$M(2)$ = male fitness for spending 2 yr as a male,
$F(2)$ = female fitness for spending 1 yr as a male (being a female at age 2),
$F(3)$ = female fitness for spending 2 yr as a male (being a female at age 3).

This splitting of a cohort into two parts is well known for Pandalid shrimp (e.g., Rasmussen 1953). Probably the most common situation is the occurrence of "early maturing females" (EMF) (Fox 1972). These are individuals who mature or breed for the first time as females, never having reproduced as males. At the age of first

reproduction (α), the cohort splits into two parts. Some fraction of breeders are males (and typically will turn into females by age $\alpha + 1$), the rest are females. In reference to figure 4, this case would result if the product maximization fell between 0 and 1.

The absence or presence of EMF, and their frequency when present, provides a good test for sex change theory for the following reason. Theoretical presence or absence does not depend upon knowledge about the male fertility, $Q(x)$, function (which would be very difficult to measure). Since only one male age group is present (all males are predicted to change to females by age $\alpha + 1$), the potential fertility of older males is unimportant. Suppose t^* is less than 1 yr. The t^* then maximizes $F \cdot M$ where the product takes the form $[P \cdot F(\alpha) + (1 - P)F(\alpha + 1)][(1 - P)M(\alpha)] = M \cdot F$, where P is the fraction of a cohort acting as EMF.

Setting $\partial(M \cdot F)/\partial P = 0$ and letting $W = F(\alpha + 1)/F(\alpha)$ (the relative female fitness of a hermaphrodite compared to an EMF), we find that the ESS P is of the form:

$$P/(1 - P) = 1 - 2W, \qquad W < \tfrac{1}{2},$$
$$P/(1 - P) = 0, \qquad\qquad W > \tfrac{1}{2}.$$

$$(8)$$

Relationship (8) provides a rather unique hypothesis. If $W > \tfrac{1}{2}$, all individuals should spawn at least once as males (thus we predict there to be no EMF). If $W < \tfrac{1}{2}$, we expect a negative, linear relationship between W and the ratio of females to males at the age of first reproduction (with a limiting value of 1:1). Note that the relationship is the same as the predicted frequency of females in gynodioecious plant populations (Charnov et al. 1976).

Provided EMF and hermaphrodites experience the same mortality and fecundity schedules (they differ only in that EMF get one additional year as a female), W may be estimated as follows. All mortality prior to age α cancels out of the equation. We may take the cohort as beginning life at age α; so $l(\alpha) = 1$. W is then written as:

$$W = \frac{l(\alpha + 1) \cdot b(\alpha + 1) + l(\alpha + 2) \cdot b(\alpha + 2) + \cdots}{b(\alpha) + l(\alpha + 1) \cdot b(\alpha + 1) + l(\alpha + 2) \cdot b(\alpha + 2) + \cdots}.$$

$$(9)$$

To estimate W requires knowledge of (1) age of first reproduction—α, (2) age-fertility relations, in terms of egg production—$b(x)$, (3) mortality rates—$l(x)$. I will now show how these may be estimated for Pandalid shrimp.

i) Female fecundity, $b(x)$, increases with adult size. Most graphs of egg number against body length (or carapace length) are increasing and concave upward. The data usually fit a power function (no. eggs $= a \cdot \ell^b$ where ℓ = body length, a and b are constants). The coefficient b is typically near 3, which means that the egg count is proportional to body mass or carapace volume. To further test this relation, curves were fit (by least squares) to several graphs from the literature. *Pandalus borealis* (three populations—Rassmussen 1953; Allen 1959; Appolonio and Dunton 1969) gave b coefficients of 3.35, 3.29, and 3.68, respectively. *Pandalus montagui* (two populations—Allen 1963; Mistakidis 1957) gave b coefficients of 3.4 and 3.35; *P. jordani*, $b = 3.06$ (T. H. Butler, personal communication); and *P. platyceros*, $b = 3.4$ (Butler 1964). Finally, Jensen (1958) showed (for several species of marine shrimp) that egg count typically increases with the third power of body length (or a linear dimension) while Rao Vedavyasa (1968) showed the same for three Penaeid shrimp.

Given the variation present in most egg-count data, it seems unlikely that the Pandalid data would show *b* significatly different from 3. A few data sets lack a power function, or have a *b* coefficient clearly different from 3 (Haynes and Wigley 1969; Rao Vedavyasa 1968); however, given the form of most data I have seen, it appears to be a well-supported assumption.

It remains to specify how shrimp grow. As noted by several authors (Gotshall 1972; Fox 1972; Abramson and Tomlinson 1972), shrimp growth in length is well represented by the classical Bertalanffy equation (widely used to describe fish growth [Beverton and Holt 1957]):

$$\ell(x) = \ell\infty\{1 - \exp[-K(x - x_0)]\},\tag{10}$$

where

$\ell(x)$ = length at age x,
$\ell\infty$ = asymptotic or maximum length,
x_0 = hypothetical age at zero length,
K = growth coefficient (specifies how fast $\ell\infty$ is approached).

Combining (10) with the fact that the egg count increases with ℓ^3, an expression for $b(x)$ is given by:

$$b(x) \propto \{1 - \exp[-K(x - x_0)]\}^3 \qquad x \geq \alpha\tag{11}$$

ii) For $l(x)$ (survivorship), it will be assumed that after the age of first breeding (α) shrimp die at a constant exponential rate. If N is the size of a cohort, $dN/dx = -Z \cdot N$. This assumption (common in fishery work—Beverton 1963; Beverton and Holt 1959) is probably not biologically correct. Most life tables show the death rate to increase with age, and shrimp are no exception (Gotshall 1972; Geibel and Heinmann 1976). However, I will show that this assumption is robust; for the estimation of W, it makes little difference whether mortality is assumed constant or increasing with age.

Putting these factors into equation (9) provides the following formula for W,

$$W = \frac{e^{-Z}\{1 - \exp[-K(\alpha + 1 - x_0)]\}^3 + e^{-2Z}\{1 - \exp[-K(\alpha + 2 - x_0)]\}^3 + \cdots}{\{1 - \exp[-K(\alpha - x_0)]\}^3 + e^{-Z}\{1 - \exp[-K(\alpha + 1 - x_0)]\}^3 + \cdots}.$$

$$\tag{12}$$

I have used unpublished sources and published data to estimate four parameters (fraction EMF, K, α, age of last breeding) for each of 27 shrimp populations. The data are summarized in table 1. From the published literature, K was estimated using BMD asymptotic regression (unweighted) (Dixon 1970) applied to length-age curves. The program also provided an estimate of x_0. With one exception (see table 1) these values (x_0) were very small (about 15% of the corresponding α value). Notice in (12) that x_0 is always subtracted from α. Thus if $x_0 \sim -.15\alpha$, it has very little affect on W. In calculating W, I set $x_0 = -.15\alpha$, since the estimated x_0 never differed significantly at the $-.05$ level from $-.15\alpha$. Computer calculations showed that this was a robust

assumption—W varied by only a few percent to changes in x_0 in the neighborhood of $-.05\alpha--.25\alpha$.

It remains to discuss how an estimate of Z was made. There are very few mortality estimates in the shrimp literature (Gotshall 1972). However, there is an indirect way to estimate mortality sufficient for my purposes. What the literature provides are estimates of the oldest breeding age (call it T_{max}). I call this the "age of last breeding" and take it to be the age of the oldest reproducers typically identified in the population. Shrimp carry their eggs for about .5 yr, so I calculated an age of last breeding for each population by adding .5 to the typical age of last spawning (as presented in the published literature or from unpublished sources identified in table 1). There is no direct way to age shrimp, so that the values in the table reflect either the examination of length frequency diagrams or the results of following an unusually large year class as it grows older (Rasmussen 1953). There is at least one other possible source of error in this analysis. As discussed by Beverton (1963) and Beverton and Holt (1959), the oldest age observed must increase as the sample size increases. However, a large part of their analysis is devoted to showing that the oldest age observed goes up very slowly with sample size. Mortality rates for most populations increase with age and are well fit by a Gompertz function (i.e., mortality rates go up exponentially with age). Gumbel (1958) showed, using probability theory, that the average age of the oldest individual observed in a population with Gompertz mortality increases linearly with the double logarithm of the sample size. Thus, as noted by Beverton and Holt, this parameter is very insensitive to sample size in the range 10^3–10^5. All of the shrimp data are based on samples within this range and thus sample size ceases to be an important variable.

We can use the estimates of the oldest breeding age (T_{max}) to estimate an average mortality rate (for each population) using a procedure developed by Beverton and Holt and applied to fish. The procedure is simple; they showed that an estimate of average mortality (an average weighted towards the younger age classes) could be obtained by multiplying the inverse of the oldest age observed (T_{max}) by 6.4 or

$$Z = 6.4/T_{max}. \tag{13}$$

This is an empirical relation which they discovered for several fish species. They regressed Z and $1/T_{max}$ for each of several fish species (several populations within each species). The relationship between the two variables was well described by $Z = h/T_{max}$ where h fell in the narrow range 6.0–7.3. The average for all the species examined is 6.4.

I note here that the Z used in the above analysis was a weighted average, as mortality rates typically increase with age in fish (usually a Gompertz function). The empirical relation is between $1/T_{max}$ and this average Z.

TEST OF HYPOTHESIS

Using the biological relations discussed above, I will now provide two (not independent) tests for the hypothesis given by equation (8). Then I will discuss the consequences of violating some assumptions of the theory.

TABLE 1

LIFE-HISTORY PARAMETERS FOR PANDALID SHRIMP

Location, Species*	Age (Yr) of 1st Reproduction	Approx. Age of Last Breeding (Yr)	Growth Coefficient K	Source of K†	Female Proportion of 1st Breeders P	Standard Error for P	Relative Fitness W	Reference or Source
Kiluda Bay, Alaska, 1	2.5	7	.41	1	0	...	.45	Fox 1972
Ugak Bay, Alaska, 1	2.5	7	.36	1	0	...	.53	Fox 1972
Two Headed Island, Alaska, 1	2.5	7	.29	1	0	...	.64	Fox 1972
British Columbia, Canada, 1	1.5	4	.48	2	.47	...	.50	Butler 1964
Bering Sea, 1	2.5–3.5	7	.25	2	0	...	.72	Ivanov 1969
Western Gulf of Alaska, 1	2.5	7	.39	2	0	...	.49	Ivanov 1969
Gulf of Maine, 1	2.5	5	.46	2	0	...	.39	Haynes & Wigley 1969 Appolonio & Dunton 1969
Northumberland, U.K., 1	1.5	3	.71	2	.36	...	.25	Allen 1959
Duncan Canal, Alaska, 1	1.5	5	.44	3	.09‡	.01	.55	J. A. McCrary, unpublished data
British Columbia, (South) Georgia Straits, 4	1.5	3	1.18	2	.47	...	.06	Butler 1964
2	1.5	3	.87	2	.4	...	.14	Butler 1964
British Columbia, (North) Georgia Straits, 4	1.5	3	.96	3	.32¶	...	.11	T. H. Butler, unpublished data
2	1.5	3	.72	3	.26¶	...	.24	T. H. Butler, unpublished data
British Columbia, Strait of Georgia, 6	1.5	3	.55	2	0	...	.40	Butler 1964
5	2.5**	5	.27	2	0	...	.68	Butler 1964

Location								Reference
Northern California								
1964 class, 2	1.5	3	.50	1	.33‖	.04	.35	Gotshall 1972
1965 class, 2			.70	1				Abramson & Tomlinson 1972
Coos Bay, Oregon, 2	1.5	4	.59	3	.18§	.07	.35	J. Robinson, unpublished data
Duncan Canal, Alaska, 3	1.5	5	.53	3	.24‡	.05	.42	J. A. McCrary, unpublished data
4	1.5	5	.41	3	.15‡	.01	.59	J. A. McCrary, unpublished data
6	1.5	5	.36	3	0	...	.68	J. A. McCrary, unpublished data
Thomas Bay, Alaska, 1	2.5	6	.34	3	.03‡	.01	.56	J. A. McCrary, unpublished data
3	2.5	6	.47	3	.37‡	.09	.37	J. A. McCrary, unpublished data
4	2.5	6	.43	3	.07‡	.03	.42	J. A. McCrary, unpublished data
6	2.5	6	.34	3	0	...	.56	J. A. McCrary, unpublished data
Oslo Fjord, Norway (1933 class), 1	1.5	4	.70	2	.08‡	.05	.25	Rassmussen 1953
Mist Fjord, Norway, 1	2.5	6	.27	2	0	...	.68	Rassmussen 1953
Spitsbergen, 1	3.5	>7.5	.23	2	0	...	.76	Rassmussen 1953

* 1 = Pandalus borealis, 2 = Pandalus goniurus, 3 = Pandalus jordani, 4 = Pandalus hypsinotus, 5 = Pandalus platyceros, 6 = Pandalopsis dispar.

† 1, Author estimated; 2, estimated for this paper, growth data in reference; 3, author estimated, unpublished data.

‡ Author estimated.

§ Average for 3 yr classes.

‖ Average for 10 yr classes.

¶ Average for 11 yr classes.

Average for 5 yr classes.

** Actual value is 1.5 but T_0 is −.8 yr; thus, theoretically, population is closer to 2.5.
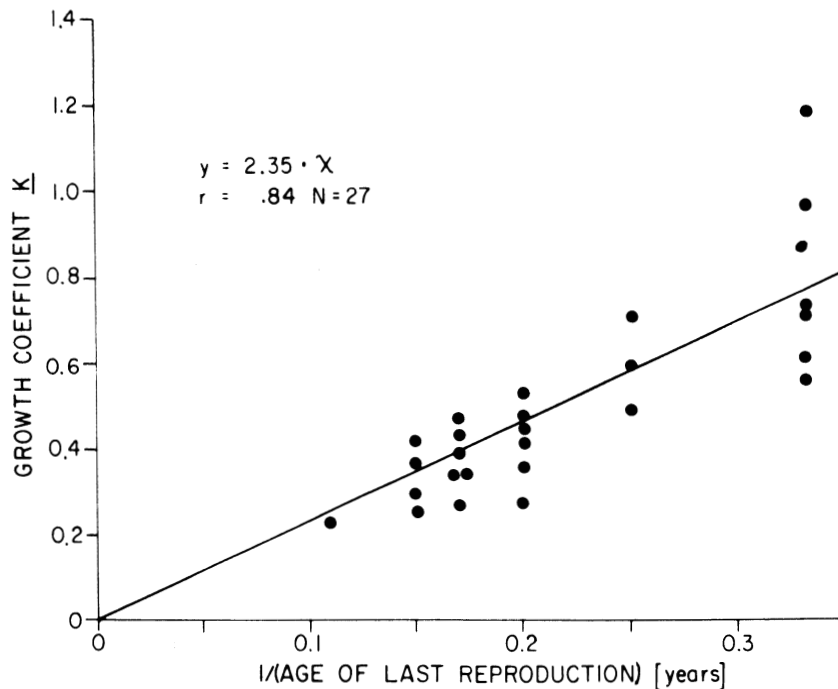
FIG. 5.—Growth and death rates are correlated. The line = least squares fit through the origin; data from table 1.

Test 1: Using K to Estimate Z.

Fox (1972) showed for several populations of Pandalid shrimp that K, the growth coefficient, was highly correlated with $1/T_{max}$. Populations with higher growth coefficients (faster approach to $\ell\infty$) had shorter life spans. Beverton and Holt had previously shown this same relation for many fish species. I have extended Fox's analysis to the shrimp populations in table 1.

Figure 5 shows a plot of K against the inverse of the age of last breeding $(1/T_{max})$. The fitted regression did not show the K intercept significantly different from zero (at the .05 level), so the line in the figure is the least-squares fit through the origin. The correlation coefficient is .84 and the hypothesis that K and $1/T_{max}$ are positively related is accepted. The resulting equation is $K = 2.35/T_{max}$. However, since we have the relation $Z = 6.4/T_{max}$,

$$Z = 2.7 \cdot K. \tag{14}$$

Thus the growth coefficient may be used to estimate an average mortality rate for the adult life span. The main advantage of using K to estimate Z is that thé individual T_{max} are rather imprecise. However, using all of the shrimp data (to estimate the relation between T_{max} and K) helps remove the effect of errors in the estimation of individual T_{max}.

For each shrimp population, W was estimated using equation (12) (with the relation $Z = 2.7 \cdot K$). These values are shown in table 1. The result of graphing the
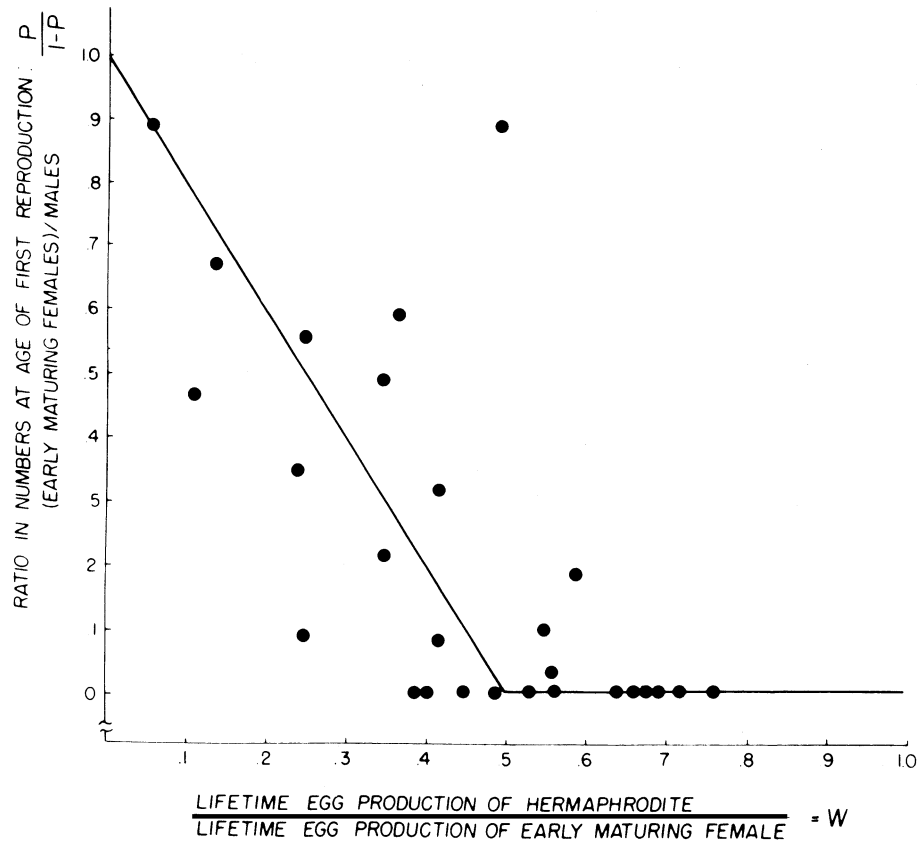
FIG. 6.—Occurrence of "early maturing females" (EMF) in Pandalid shrimp. Data are (proportion EMF):(proportion males) plotted against relative hermaphrodite fitness (W). Theoretical relationship (eq. [8]) is shown by the heavy line; data from table 1.

estimated $P/(1 - P)$ $(P =$ female proportion of first breeders or proportion EMF) against W is shown in figure 6. The heavy line is the theoretical expected relation (eq. [8]). With one exception, the points fall close to the theoretical values. Since both W and P are estimated with error, it is difficult (and of dubious value) to apply any simple statistical test. I will argue that the relation is fairly convincing in the absence of such a test. Clearly, zero values are associated with high W, positive values with low W.

Some may argue that the test (fig. 6) is not powerful since it uses the Beverton and Holt (B-H) fish relationship to estimate Z (for shrimp). To this there are three replies. (1) Figure 6 is not a regression relation; that is, I have not fitted any parameters (in either $P/(1 - P)$ or W) in relation to the theoretical curve. (2) If one does not care for the Beverton and Holt derived relationship $(Z = 2.7 \cdot K)$, there is one simple option. The weakest use of the B-H relationship is to claim that Z and K are positively related (fig. 5 supports this for shrimp). The simplest model is $Z = r \cdot K$, a one parameter model. If this is substituted into equation (12), we can then seek the r which gives the "best fit" (by some criterion, such as least squares in the vertical

plane) to the theoretical relation. I have not done this, but figure 6 shows that the parameter r would be near 2.7 (since the fit is fairly good in the figure with the exception of one point). (3) It seems likely that the B-H relationship linking Z and T_{max} follows from the adult demographic patterns rather than anything about fish per se. Thus, it seems weak to argue against using it with shrimp.

Test 2: Positive Proportion of EMF (using T_{max} to estimate Z)

Seven populations (table 1) are classified as having an age of last breeding of 3 yr. The average K (or $\bar{K}$) for these is .80. Estimating Z to be 2.1 (or 6.4/3), theory predicts that .38 of each cohort should be EMF. The average over these populations is .31. Three populations have $T_{max} = 4$ yr ($\bar{K} = .59$, $Z = 1.6$), with the theoretical P at .23. The average P is .24. Six populations have $T_{max} = 5$ yr ($\bar{K} = .41$, $Z = 1.3$). These populations are theoretically near $P \sim 0$ (regardless of the α value). The average P is .08. It would appear that P is smaller than the theoretical for the T_{max} of 3, and larger than theoretical for T_{max} of 5. However, the differences are not significant by a t test (.05 level). As suggested by the previous analysis (which did not lump the populations by T_{max}, but used the individual K to estimate Z), the shrimp come rather close to doing what theory predicts.

DISCUSSION

This section will examine the consequences of violating certain theoretical assumptions. The discussion will take the form of questions.

1. What if fecundity is not a cubic function of body length? Computer calculations show that predictions are very insensitive ($\pm \sim 10\%$) to alterations of this, provided fecundity is a power function of length with a b coefficient of 2.5–3.5. This is because the predicted values are insensitive to the age-fecundity relation itself. This is best seen in figure 7. For $\alpha = 1.5$ and $b = 3$, the computer calculated t^* (ESS age of sex change) for various K (growth coefficient) and Z (adult mortality rate). Male fertility, Q, was assumed to be constant with age. The areas marked 1 and 2 are parameter values where the population should be spending 1 and 2 yr, respectively, as males. The 1.5 line is where the cohort should split, with half spending 1 yr as a male, half 2 yr. The fractions to the right of the 1 sector are where the cohort should again split. Here the fractions give the proportion of the cohort which should operate as females at the age of first breeding (EMF). The remainder of the cohort should operate 1 yr as a male. As noted earlier by Leigh et al. (1976) and Warner (1975), higher mortality rates (high Z) and higher relative rates of increase for female fertility with age (high K) both select for less time being spent in male phase. The diagonal line is the relation $Z = 2.7 \cdot K$. Notice that the predictions are insensitive to K. For example, if $K = .47$ and $Z = 1.3$, we predict that there should be no EMF. At $K = .85$, $Z = 2.3$, we predict the proportion of EMF to be .4. This is the entire range represented by populations maturing at 1.5 yr. However, if K is held constant at .47 while Z is increased from 1.3 to 2.3, the proportion EMF goes from zero to .35. Likewise, if Z is held at 1.3, increasing K alone (from .47 to .85) changes the EMF from zero to .15. Clearly, mortality is the key parameter with age-fecundity (growth) relations of much
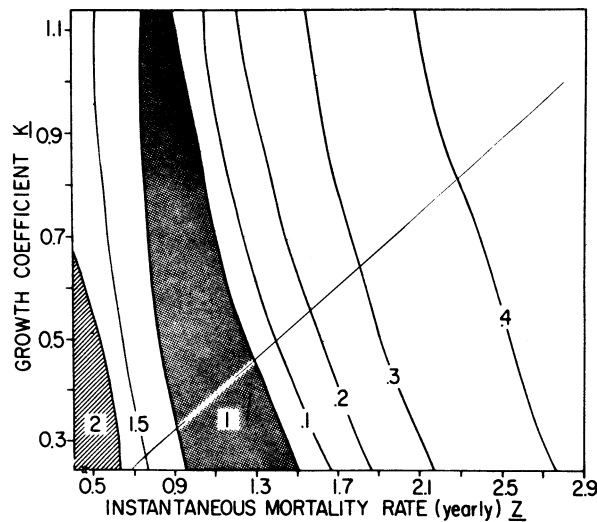
FIG. 7.—A times-of-equal-sex-change diagram. As a function of growth (K) and death (Z) rates, the graph plots the ESS time as a male, assuming an age of first breeding of 1.5 yr. Zones I and 2 refer to 1 and 2 yr in male phase. The fractions to the right of the I zone denote the fraction of a cohort which breeds as females at age 1.5 (the fraction EMF). The diagonal line is $Z = 2.7 \cdot K$.

less importance. Estimation of K is important, however, because of its use in obtaining Z.

2. What if mortality rates increase with age? Beverton and Holt noted for fish that mortality rates increase over the adult life span. If $Z(x)$ is the rate between age x and $x + 1$, the function $Z(x)$ is usually of the form $Z(x) = d\, e^{cx}$ where d and c are constants. This is termed Gompertz mortality. Their analysis fits this function to fish data. They then calculated an average Z for the adult life span using a formula equivalent to

$$\bar{Z} = \log_e \frac{\sum\limits_{x=0}^{\infty} l(x)}{\sum\limits_{x=1}^{\infty} l(x)}, \qquad \text{where age } \alpha \text{ is } x = 0. \tag{15}$$

This parameter ($\bar{Z}$) is, of course, simply a mean coefficient weighted in favor of the younger age groups.

It is this $\bar{Z}$ that Beverton and Holt correlated with T_{max} to get $\bar{Z} = 6.4/T_{max}$. In terms of my analysis, the question now becomes: Suppose mortality is of the Gompertz form; what difference does it make in W if $\bar{Z}$ is applied as a constant over the adult life span, when compared to W calculated from the original life table (the one used to calculate $\bar{Z}$)? Using a computer, I generated several thousand life tables where mortality was of the Gompertz form. From these I determined values of c and d such that the associated $\bar{Z}$ was the same. The computer then calculated W (details in caption to fig. 8) for the original life table and for $\bar{Z}$ applied as a constant over the adult life span. The results are shown in figure 8. The stippled area encloses the W
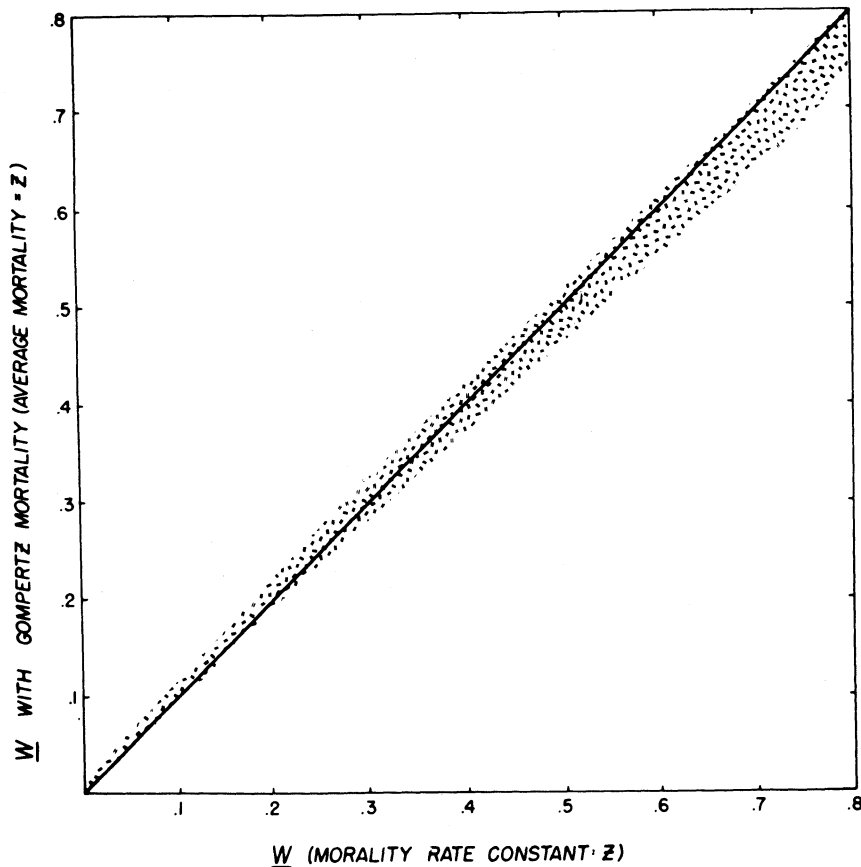
FIG. 8.—Mortality increasing with age does not alter the predicted W. The figure graphs W (assuming a Gompertz life history) against W (applying $\bar{Z}$ as a constant across the adult life span). Since-many Gompertz life histories have the same $\bar{Z}$ (eq. [15]), the W range they represent is shown by the stippled area. All the Gompertz W fall close to the 45° line. This figure assumes $\alpha = 1.5$ and $K = \bar{Z}/2.7$.

associated with all Gompertz life histories which correspond to the same W with $\bar{Z}$ used as a constant. As can be seen from the figure, the application of an average mortality rate (as a constant over the adult life span) has very little affect on the predicted W (particularly for $W < .5$). Even if mortality is not of the Gompertz form (e.g., increases linearly with age), the same robustness should be present in the calculation of W.

3. What if the population is not in stable age distribution (SAD)? This is a difficult question and I doubt that any general answer is possible (because there.are many ways to violate the SAD assumption). However, this section will discuss a special case, one which seems biologically reasonable for shrimp. Suppose that variation in age structure is caused by variation in year class strength. Sometimes many immatures survive to age α, sometimes few. Suppose further that individual growth rates and adult mortality rates are constant through time. Thus in the fall of year T, $X(T)$

age α shrimp are present; in year $T + 1$, $X(T + 1)$, etc. If the recruitment $X(T)$ is independent of population size (a common fishery assumption—Beverton and Holt 1957), it is reasonable to consider the $X(T)$, $X(T + 1)$, etc., to be independent identically distributed random variables (mean $= \mu$, variance $= \sigma^2$). Violation of the SAD assumption results because $\sigma^2 > 0$.

To even further restrict the model, consider a population such as *Pandalus jordani* off northern California (Gotshall 1972; Charnov et al. 1978). This population always has EMF and an age of last breeding of 3 yr; thus almost all the breeders are in two age groups (1.5, 2.5 yr). Earlier work (Charnov et al. 1978) developed a theory which predicted how P should change as the age distribution changes. The data supported the hypothesis that shrimp alter their age of transformation (shift P) according to the following rule. The $P(T)$ refers to proportion EMF in year T.

$$P(T) = \frac{1}{2} \left[1 - \frac{b(2.5)}{b(1.5)} \cdot \left(\frac{\text{no. of age 2.5 spawners}}{\text{no. of age 1.5 spawners}} \right) \right], \tag{16}$$

where $b(2.5) =$ egg count of female aged 2.5 yr and $b(1.5) =$ egg count of female aged 1.5 yr.

For the California shrimp $b(2.5)/b(1.5) \sim 2$. The survival rate from age 1.5 to 2.5 will be denoted s. Rewriting (16) in terms of the $X(T)$ assumption, we have

$$P(T) = \frac{1}{2} - s \, \frac{X(T - 1)}{X(T)}. \tag{17}$$

Since the shrimp adjust P each year, we need to know what the average P (over several years) will be. Call this $\bar{P}$. By use of a Taylor expansion (the "delta method"—Seber 1973), an approximate value for $\bar{P}$ is given by

$$\bar{P} \sim \frac{1}{2} - s \left(1 + \frac{\sigma^2}{\mu^2} \right). \tag{18}$$

For California $s \sim .12$ ($Z \sim 2.1$ or $T_{max} = 3$), which from (18) gives $\bar{P} = .38$ if $\sigma^2 = 0$. Note that .38 is the value predicted with the SAD assumption (and $T_{max} = 3$). If $\sigma^2 > 0$, $\bar{P}$ decreases from the SAD model prediction. The important question is: How much?

The correction factor (in [18]) is σ^2/μ^2. From table 7 in Abramson and Tomlinson (1972), I estimated the mean and variance in numbers of aged 1.5 shrimp (present in September) for 14 yr. This should give a rough idea of how large σ^2/μ^2 might be expected to be. For these years $\sigma^2/\mu^2 = .09$. This would lower $\bar{P}$ from .38 to .37. Even if σ^2/μ^2 were .3, $\bar{P}$ would only decrease to .34. When we consider that the 95% confidence interval on $\bar{P}$ for California (table 1—data from Abramson and Tomlinson [1972]) is .24–.42 (11 yr, $\bar{P} = .33$), it is highly unlikely that we will be able to detect the lowering of $\bar{P}$ due to this affect.

At least for populations with high death rates, the SAD model does fairly well at predicting the average proportion EMF. Note however that the temporal variation around this average falls outside the SAD model. To account for the temporal variation requires the non-SAD assumption (Charnov et al. 1978).

Similar results hold for other ($T_{max} > 3$) life histories. For large W ($> .6$) violation

of the SAD assumption (as developed above) does not alter the prediction of zero proportion EMF. At intermediate W (.3–.6), we predict $\bar{P}$ to be larger than predicted by the SAD model (since sometimes there will be no EMF). However, the effect is of the order $< 15\%$ of $\bar{P}$. The point I am making is that the non-SAD model makes predictions which come within $\sim 10\%$–15% of the values predicted by the SAD model. To account for the mean value ($\bar{P}$), the two models are identical in practice. Interestingly, some populations with W near .5 are predicted under the SAD model to have no EMF. Depending upon σ^2, they may or may not have a positive fraction (in some years). It is tempting to suggest that the average P of .08 for populations with $T_{max} = 5$ yr (when the predicted P is approximately zero) supports this prediction.

Many other organisms (plants and animals) which change sex also show the ability to alter the time of sex change to fit local breeding conditions (references in Bacci 1965; Reinboth 1975; Hoagland 1978; Warner et al. 1975; Charnov and Bull 1977; Ende 1976). Sometimes it pays an individual to remain a male a bit longer or to become a female right away. An analysis such as the above may well prove useful for these organisms.

4. What about predictions other than the occurrence of EMF? Figure 7 shows that slower growth (low K) and longer life (low Z) should result in more time being spent as a male. A similar result follows for populations with an age of first breeding of 2.5 yr. These predictions are qualitatively supported by Rasmussen's (1953) data for Norway, and Horsted and Smidt's (1956) data for Greenland ($P.\ borealis$). Rasmussen (1953) was the first person to point out that sex change in $P.\ borealis$ was more closely related to size than age. Shrimp populations with slower growth (and death) rates spent more time as males; these populations tended to change sex at an approximate fixed size, independent of age. My reasons for stressing the fraction EMF as the most useful hypothesis is that predictions such as the above require knowledge about the male $Q(x)$ function. If $Q(x)$ increases with age, the predictions (for age of sex change) from figure 7 (other than the EMF predictions) underestimate the length of time spent as a male. However, predictions should still be in the right direction. Warner (1975) first noted (from a table in Haynes and Wigley 1969) that the broad scale geographic patterns of time spent in male phase (for $P.\ borealis$) were consistent with sex change theory. My detailed analyses fully support his conclusion.

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