

Schmidt, V.

A REVIEW OF MODELS ON THE SELECTION OF HERMAPHRODITISM  
AND THEIR APPLICATION TO A MARINE GASTROPOD:  
HERMISSEDA CRASSICORNIS.

by  
VALERIE M. SCHMIT

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The current literature covering certain models for the selection of hermaphroditism was reviewed. The purpose of the review was to assess the models' ability to determine if there are constraints present that pressure a particular species to remain hermaphroditic. The models of Michael Ghiselin, E.L. Charnov, J.J. Bull, and J. Maynard Smith were examined in order to test their applicability to the nudibranch Hermissenda crassicornis. The ecology of H. crassicornis was reviewed in reference to the models so that their fit in relation to what is known about H. crassicornis could be evaluated.

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### DEFINITION OF HERMAPHRODITISM

The origin of the word hermaphrodite is derived from Greek mythology. The son of Hermes and Aphrodite, Hermaphroditus, became united in one body with the nymph Salmacis. "In their double form they are neither man nor woman; they seem to have no sex and yet to be of both sexes." (Larousse, 1968). Hermaphroditism, the condition of having the reproductive organs of both sexes, although not necessarily at the same time, is a normal part of the life history of many animal species (Warner, 1982).

Ghiselin (1969, 1974) has reviewed the distribution of hermaphroditism among animals and has noted several patterns which have emerged. There appears to be a correlation between hermaphroditism and the brooding of the young (Heath, 1979). Hermaphroditism also appears to be associated with sessile or benthic adult conditions (Ghiselin, 1969). There are exceptions: many groups with sessile or sedentary adults are dioecious, and hermaphroditism is widely scattered through groups typically dioecious (Charnov, 1982). The evolution of a successful reproductive tactic, one that allows for maximum fitness, will determine the survival of the group. Therefore, selection pressure for a winning sexual strategy is a strong one.

There are two types of hermaphroditism: sequential and simultaneous. Sequential hermaphrodites begin sexual

maturity as one sex. When specific characteristics are attained ,i.e., the organism reaches a certain size or the environmental constraints become optimum, the sex of the organism changes to the opposite sex. Sequential hermaphroditism would be selected for when "an individual reproduces most efficiently as a member of one sex when it is small or young, but as a member of the other sex when it gets older or larger" (Ghiselin, 1969). Within a species, sex change appears to occur irreversibly in one direction only (Warner, 1982). The most common pattern is one of females changing to males, a process called protogyny. This type of hermaphroditism is seen in many tropical wrasses (Labridae). It is theorized that the larger the male, the more effective he is in defending his territory, resulting in higher reproductive success. Protandry, changing from male to female, may be selected for in a population where female fecundity increases with age ( where a larger body means more and/or larger eggs) and where individuals choose their mates randomly (Warner, 1975).

Simultaneous hermaphroditism at sexual maturity house functioning organs for both sexes. There are some lower invertebrate species that are able to self fertilize, for example, some flatworms in the class Cestoda have been known to do so but they are not obligate (Barnes, 1980). Conversely there are non self-fertilizing hermaphrodites with very elaborate reproductive duct/organ systems that act as

mechanisms to eliminate any chance of self-fertilization. An example of this complex duct system is found within the subclass Opisthobranchia, the "snails turned slugs". (Beeman, 1977). A bifurcation of the main gonoduct prevents the individual's sperm (endogenous) from mixing with the partner's sperm (exogenous).

There have been many models proposed for the selection of hermaphroditism. This will be a review of some of the models dealing only with simultaneous hermaphroditism. There are several questions that come to mind when dealing with these models. Such as: are these models useful in determining why a particular species possesses that reproductive strategy? Is it possible to ascertain the present selective pressures that maintain the species as an hermaphrodite? Lastly, is it possible, using these models, to discover if a species is merely exhibiting a phylogenetic consequence of a strategy chosen by its ancestors? "The ghosts of pressures past"? The purpose of this review paper is to try and address these questions, using the nudibranch Hermissenda crassicornis (Cooper, 1853) as a model system.

#### HERMAPHRODITISM IN NUDIBRANCHS

##### a. Reproductive anatomy of the ancestral prosobranch.

Nudibranchs, an order of the subclass Opisthobranch, (Phylum: Mollusca; Class: Gastropoda) are functional simultaneous hermaphrodites for most of their



reproductive lives and have, as mentioned above, correspondingly complicated reproductive anatomies. Fertilization is internal and cross-fertilization is the rule (although there are exceptions) (Hadfield 1984). It is generally accepted that an ancestor first became the hermaphrodite and the order today is merely a reproductive reflection of an ancient selection. This need not be accepted as written in stone. If a species is experiencing pressures that select for gonochorism it would allow for the invasion of "pure" males and females. This condition where most of the reproductive population is hermaphroditic but males and/or females are present, is called unstable hermaphroditism and could represent a step towards the evolution of stable gonochorism (Bacci, 1965).

In order to understand the present state of hermaphroditic anatomy in nudibranchs, one can examine the components of the reproductive systems found in gonochoric prosobranch gastropods, from which the opisthobranchs are thought to be derived (Hadfield, 1984). In the model prosobranch, the female and male systems consist of a gonad and a gonoduct (Fig.1). The gonoduct is divided into two portions, the division being determined by the presumed origin of the tissue. These are the coelomic or proximal portion (mesodermal) and pallial or distal portion (ectodermal). The separation of the gonoduct into these coelomic and pallial portions is supported by embryological

FIGURE 1.

From Hadfield and Switzer-Dunlap, 1984)

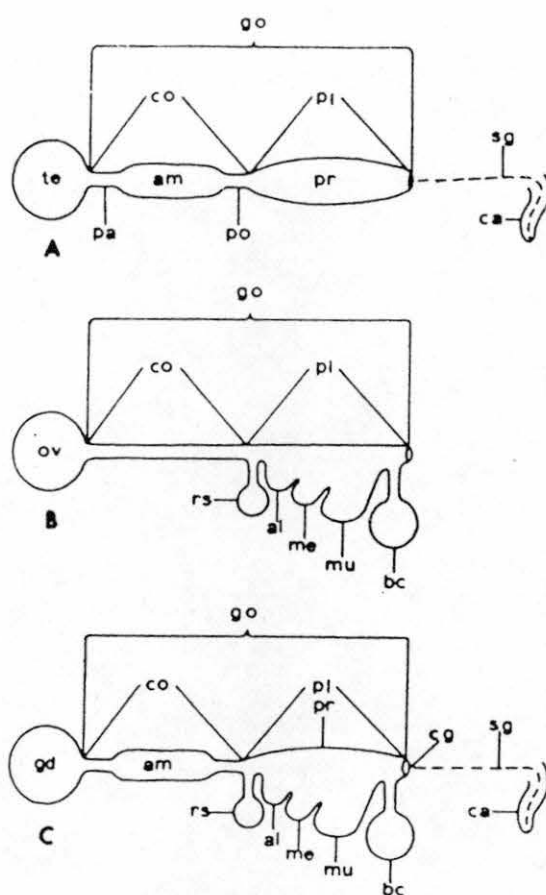


Fig. 1. Idealized diagrams of gastropod reproductive systems. (A) Gonochoric male. (B) Gonochoric female. (C) Hermaphroditic system of hypothetical opisthobranch ancestor. Abbreviations: al, "albumen" gland; am, ampulla; bc, copulatory bursa; ca, copulatory apparatus; cg, common genital aperture; co, coelomic portion of the gonoduct; gd, gonad (ovotestis); go, gonoduct; me, membrane gland; mu, mucus gland; ov, ovary; pa, preampullar portion of the coelomic gonoduct; pl, pallial gonoduct; po, postampullar portion of the coelomic gonoduct; pr, prostate; rs, seminal receptacle; sg, seminal groove; te, testis. (From Ghiselin, 1965.)

studies of nudibranchs. (Hadfield, 1984).

The gonoduct in a gonochoric male consists of two swellings: proximally, the ampulla (seminal vesicle) and distally, the glandular prostate. The ampulla is used to store endogenous sperm before copulation. The prostate gland probably serves to contribute to the seminal fluid, as the epithelium of the prostate is composed of glandular secretory cells interspersed with ciliated cells (Hadfield, 1984). A copulatory apparatus completes the male system. In the ancestral opisthobranch the copulatory apparatus probably involved a contractile penis that lacked a sheath on the right side of the head. In the female system the proximal gonoduct is merely a tube for the transport of oocytes. The distal portion contains one or more sperm storing bursa and several secretory glands that provide the vitelline layers and protective covering for the ovum.

In present day opisthobranchs the male and female systems have been combined and reduced. It originally consisted basically of a single undivided gonoduct attached to an ovotestis (Beeman 1977). The undivided gonoduct can be considered rather inefficient and the opisthobranchs have been evolving a divided duct system that is now quite complex and will be addressed below. It has been speculated (Thompson, 1976; Ghiselin, 1965) that hermaphroditism in opisthobranchs developed by the superimposition of a male reproductive system onto a female one. This would allow for

a gradual transition with the possibility of intermediates (Thompson, 1976). It seems most likely that the intermediate was a sequential protandrous h. for vestiges of protandry are present in the ontogenies of many modern opisthobranchs; sperm frequently differentiate and mature before oocytes do (Hadfield, 1984 and McCauley, 1985). It is probable that this primitive system could not carry out the female/male roles simultaneously; reciprocal copulation would have been impossible at this stage. Ghiselin (1966) treats the possible evolutionary modifications that have been thought to ease the disadvantages of the early system and thereby allowing it to succeed.

As mentioned above there is seems to be a trend towards the morphological division of the pallial gonoduct (Ghiselin, 1966). A system with a single, undivided pallial gonoduct is called monaulic; a system with a pallial gonoduct divided into two or three ducts is called diaulic or triaulic respectively (Thompson, 1978; Hadfield, 1984). The terms monaulic, diaulic and triaulic refer to the ducts only and not necessarily to the number of genital openings. (Fig.2)

This division of the gonoduct would facilitate major changes in behavior. Primarily, it would allow reciprocal copulation to occur by ensuring the endogenous gametes would not mix with incoming exogenous sperm. Indeed, reciprocal copulation is common among the Nudibranchia, considered one

FIGURE 2.

(From Thompson, 1976)

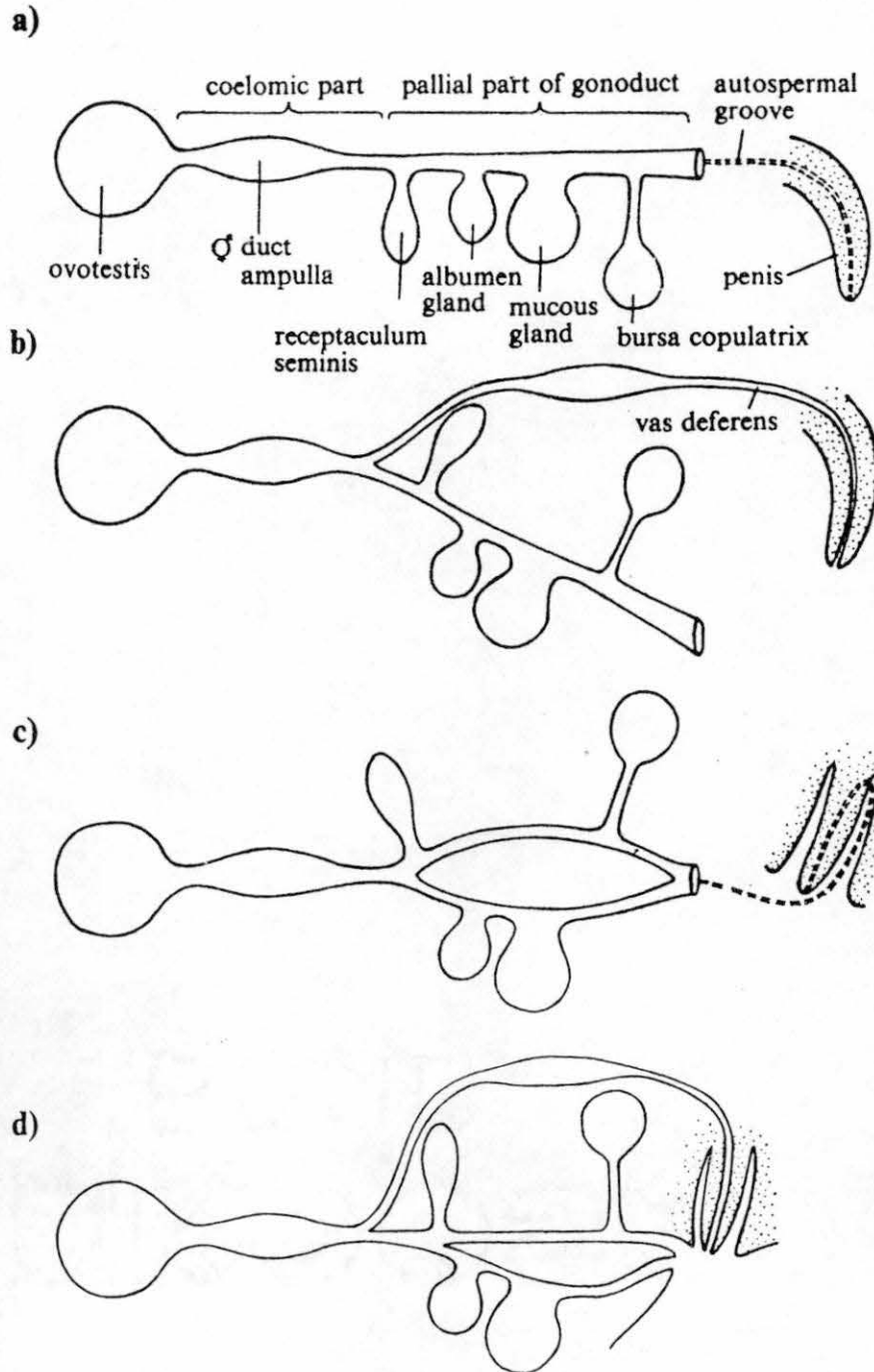


FIG. 22. Reproductive systems of opisthobranchs; diagrammatic. (a) Hypothetical ancestral hermaphrodite opisthobranch. (b) Idealized androdiaulic system, e.g. *Acteon*. (c) Idealized oodiaulic system, e.g. *Aplysia*. (d) Idealized triaulic system. (Modified after Ghiselin, 1966.)

of the more advanced orders that exhibits both the triaularic and the diaularic conditions (Beeman, 1977).

Although important, evolutionary improvements did not focus on the problem of the segregation of the gametes alone. The germ-cells of ovotestes became separated so that in some orders the ova and spermatozoa mature in discreet lobes of the gonad. Also, in some dorids and aeolids, accessory spines and glands made their appearance and these became important during precopulatory species recognition. (Thompson, 1976).

#### HERMISSENDA CRASSICORNIS

##### a. Ecology.

The aeolid nudibranch, Hermissenda crassicornis is a fine example of a successful hermaphroditic species. It ranges from Sitka, Alaska to Baja California and the habitats it enjoys vary from rocky tidepools as well as floats to mud and sand flats to eelgrass beds to bare rock (Rudy, 1983). It is considered one of the most common aeolids in the northeastern Pacific, but regional populations can fluctuate wildly at any one time (Rudy, 1983). The average lifespan of a lab animal is approximately 165 days, 35 days for the veliger stage and 128 days for the adult; it is considered a subannual species (Harrigan 1978). It varies in size, from 30 mm to 80 mm long (Rudy, 1983). H. crassicornis is a generalist, carnivore as well as

scavenger. From lab observation it was noted that it enjoyed a wide variety in its diet (no preference studies were done). It eats the blue mussel (Mytilus edulus), the tadpole larvae of colonial ascidians, the chondrophoran Velella velella, hydroids, bryozoans, medusae (Polyorchis and Aguoria), carrion as well as sea pens (subtidally in the Puget Sound) (Birkland, 1974).

In contrast to other species of nudibranchs when H. crassicornis is found it tends to be abundant. In Monterey Bay it was found to be the most common nudibranch of the 22 species collected throughout the year (Costello, 1936). Jaeckle (1984) listed H. crassicornis as "the dominant littoral opisthobranch in Humboldt County" in terms of geographic distribution and abundance. As mentioned before, the actual number of individuals in different populations fluctuates. It has been proposed that this is a seasonal variation caused by a change in salinity. More work needs to be done in this area but from observations in the field the changes in population that do occur seem unpredictable and related to more than just one perturbation in the environment. In the field it was observed that the animals' distribution was patchy but dense within those patches. The animals in the patches spanned in size from those just settled to large adults. This would discount the theory of a group of same-age recruits settling together.

#### b. Mating behavior

The mating behavior observed in this species is initiated with caution. The two animals flagellate wildly with their oral tentacles and recoil when contact is made (Zack, 1974 and Longley, 1982). After they gingerly move into the proper position, "sidling" as it has been termed, simultaneous copulation occurs in seconds (Rutowski, 1983). The animals pull apart and begin to evacuate the area in a hurry with one animal lunging, jaws agape at the retreating partner. In personal observations there were several instances where it seemed as if only one animal of a pair was able to successfully copulate with its partner. Rutowski (1983) did in fact note that sperm transfer was not reciprocal in almost 50% of the observed couplings where both animals everted their penis. The other animal's penis either deflected off the side of its partner and sperm was released to the water or the unsuccessful animal was unable to intromit in time. The animals always immediately separated after successful intromission by either animal (or both if that occurred) (personal observation).

#### c. Social behavior.

Personal observations in both the lab and in the field of social interactions between H. crassicornis individuals were limited primarily to mating behavior. When meeting a feeding conspecific the smaller of the two individuals would avoid confrontation and leave the prey item, regardless of



who was there first. When two individuals of approximately the same size met over a prey item there would be a confrontation with an unpredictable outcome. The display was usually composed of lifting the head and forebody off of the substratum, opening the jaws and lunging at the other animal. There were instances where successful bites were taken. H. crassicornis is not the only nudibranch to display agonistic behavior towards its conspecifics but it is one of the most documented. (Zack, 1974, Rutowski, 1983)

Being hermaphroditic has been successful for this species; one can not help but wonder why. In order to more fully address the question one must look at the different models proposed for being an hermaphrodite. In this review, some theories proposed by Michael Ghiselin, Eric Charnov, J.J. Bull and J. Maynard Smith will be considered with reference to Hermissenda crassicornis.

#### MODELS FOR THE SELECTION OF HERMAPHRODITISM

##### a. M.T. Ghiselin

Michael Ghiselin, (1969) proposed three possible reasons an organism might "choose" hermaphroditism. One, the Size Advantage model deals only with sequential hermaphroditism. and will not be addressed here. The next is the Low Density model. This actually was the classical explanation of hermaphroditism in terms of selection theory dating back to the last century. (It has been treated

mathematically by Thomlinson (1966)). It stands as relevant today. It states that in an organism that possesses a characteristic that reduces opportunity for mating, such as low motility or a low population density, the probability will be high that the conspecifics it encounters will not be of the opposite sex. Sluggish simultaneous hermaphrodites would have twice the probability of survival over single sex individuals in an unstable environment that may be frequently depopulated.

The last is the Gene Dispersal model. It is based on the idea that limited dispersal of offspring could affect the structure of the entire population. In this situation low motility is a main factor. When the availability of mates is hampered by lack of mobility, hermaphroditism may help to alleviate the problems associated with a small genetic pool. Ghiselin (1969) recognizes two versions of this hypothesis: the inbreeding version and the sampling-error version. The inbreeding version, again, deals with sequential hermaphroditism. In short, protandry and protogyny help to prevent inbreeding by self-fertilization as well as reduce the possibility of inbreeding taking place among siblings.

The sampling-error version takes into account genetic drift within small isolated populations. Often, in small populations there will be an unbalanced ratio of males to females (or females to males). This leads to a decreased

variety of crosses and lowers the effective population size. Hermaphroditism essentially insures a 1:1 sex ratio, effectively maximizing the population size.

The basic difference between the Low Density and the Gene Dispersal models is that in the Low Density model the "functional influence is the dispersal of individuals relative to each other" (Ghiselin, 1969). In the Gene Dispersal model the limited gene flow in and between populations is the important factor.

b. E. Charnov

Eric Charnov and his colleagues have proposed several reasons for selection favoring simultaneous hermaphroditism (SH) over dioecy. In this particular theory Charnov (1979) postulates that "Bateman's principle" can account for the selection of SH in animals. "Bateman's principle" asserts that fertilized egg production by an individual is limited not by the ability to get sperm, but by resources allocated to eggs. In order for Charnov to illustrate this proposal he uses a mathematical model where the assumptions are made that the mortality rates for males, females or hermaphrodites do not differ and that each has R resources to allocate to reproduction. There are two kinds of costs for reproduction. The first he terms "fixed" or fertility-independent cost. It consists of the structures that need to be built to reproduce. The second cost involves the resources left over after the fixed cost has been paid. If these resources can

be allotted to reproduction it will increase an animal's reproductive success. Pure males and pure females pay only one fixed cost whereas hermaphrodites have to pay both male and female fixed costs. Charnov is able to show graphically and mathematically that a dioecious condition is favored by high fixed costs for male and female function. Under Bateman's principle, simultaneous hermaphroditism will be selected for when a combination of low fixed costs and limited opportunities for an individual to reproduce through male function occur.

There are at least three factors, according to Charnov, that may limit male reproductive success in animals. The first is adult immobility and copulation, which may combine to limit the number of partners per breeding period. (Groups that are relatively immobile and practice external fertilization tend towards dioecy.) Male reproductive success in external fertilizers would be nearly proportional to the amount of sperm shed into the environment. Also as an external fertilizer, hermaphrodites would have difficulty keeping its sperm from fertilizing its own eggs. Small group size is the second factor, for example, some parasitic molluscs. The small group size serves to limit the availability of eggs to be fertilized. Thirdly, the male reproductive success is directly affected by how a sperm recipient uses its partner's gametes. There are many hermaphroditic animals that have structures for the

digestion of sperm and other products of cross-copulation, so that an animal is not certain if its gametes are going to be used for fertilization or food.

c. E. Charnov, J. Maynard Smith and J.J. Bull.

In the last theory proposed in this review, E. Charnov, J. Maynard Smith and J.J. Bull developed a model and its biological interpretation to determine from a genetic point of view the determination of hermaphroditism in animals (and plants).

In this model the assumptions that (1) genes in a zygote can act as switches, directing development into males, females or hermaphrodites, or, in hermaphrodites, can alter the allocation of reproductive resources to male or female functions. (2) The total production of male plus female gametes by an individual is constrained to a "fitness set" which cannot be altered by genetic change.

(Fig.3) Using "fitness" to mean the number of offspring produced by the individual, and supposing the population produces R offspring the model asserts that

fitness of a male =  $R/(m + ah)$ ,

fitness of a female =  $R/(f + Bh)$ ,

fitness of a hermaphrodite =  $R[a/(m+ah) + B/(f+Bh)]$ .

where m, f, and h are the number of male, female and hermaphroditic individuals respectively in a population; and assuming survival rate to adulthood is identical.

If this situation is to be evolutionarily stable, the

FIGURE 3.

(From Charnov, Smith and Bull, 1976)

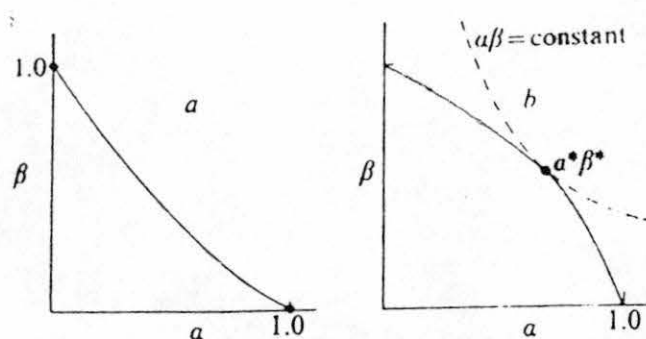


Fig. 1 *a*, A "fitness set" for the allocation of sex function.  $a$  is the pollen produced by an hermaphrodite, as a fraction of the total produced by a male individual.  $\beta$  is the corresponding parameter for a female. All possible values are assumed to be to the interior of the curve. With a concave curve, the hermaphrodite population is not an ESS, but a dioecious population is. *b*, Optimal resource allocation for an hermaphrodite. With a convex tradeoff curve, the hermaphrodite is an ESS. The ESS resource allocation ( $a^*\beta^*$ ) is the point on the curve which maximises the product  $a\beta$ .

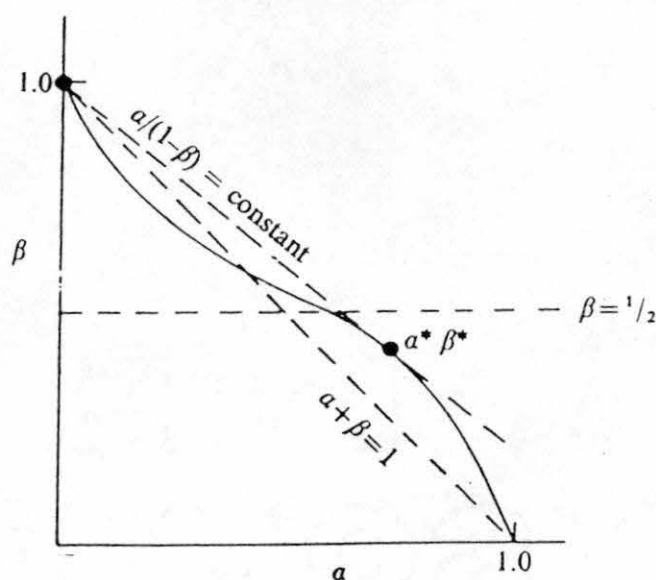


Fig. 2 An ESS which is a mixture of sexual types. If the curve is convex-concave, it may be possible for a pure sex (in this case a female) to invade. The resulting mixture is stable if (i)  $a^* + \beta^* > 1$ , (ii)  $\beta^* < 0.5$ , (iii)  $a^*\beta^*$  is the point which maximises  $a/(1-\beta)$ . This curve illustrates gynodioecy.

workers insist that two conditions be met. The first being the fitness of any types actually present in the population must be equal. This simply means that if the population is primarily hermaphroditic, but has pure males and females present, the number of individuals produced by each type needs to be equal for the components of the population not to evolve towards a different strategy (if constraints favor it). Secondly, the values of  $a$  and  $B$  in hermaphrodites must be an "evolutionary stable strategy" (ESS). This means that the hermaphroditic phenotype ( $a*B^*$ ) must be as fit (or more fit) as any invading mutant phenotype ( $aB$ ) lying in the fitness set.

To summarize their conclusions, one would expect to find hermaphroditism when the fitness set is convex, dioecy if the fitness set is concave. These workers offer three general theories as to why a fitness set would be convex, but only two deal with animals so the third will not be addressed.

First, low mobility (this differs from Ghiselin's low density model) will tend to be connected with a convex fitness set because in such species there would be little or no sexual dimorphism (no special locomotory or aggressive structures to seek out, defend, or hold females). So any individual can effectively serve both functions. Also, (paralleling Charnov's previous theory) low motility will limit male reproductive success; the number of eggs

that an individual can fertilize should rise linearly with the allotment of resources to the male function. Even if all the eggs in a population are fertilized, a convex fitness set still indicates hermaphroditism.

The second possibility is low resource overlap. In a process where, because of time lapsed, male and female expenditures depend on different resources, a hermaphrodite might be expected to do better than a linear combination of male and female.

#### DISCUSSION

Does H. crassicornis fit any of these models using what is generally known about it? With Ghiselin's low density model the statement is made that any group that has reduced opportunity for mating will evolve towards hermaphroditism. He offers three suggestions why a species would have a reduced opportunity for mating. The first, low mobility does not apply to H. crassicornis because relative to other marine invertebrate creatures it gets around quite well. In a chemoreception experiment, starved animals had been clocked, moving on food stimuli, going as fast as .63 cm/sec. (personal observation). The second model, low population density, probably does not apply to H. crassicornis. On the basis of abundance and frequency of occurrence, H. crassicornis is considered one of the dominant species in its range (Jaekle, 1984; Nybakken, 1978; Costello, 1936). One might think that the documentation of



the seasonal variation of the population could account for a low population density situation. As it stands the documentation has been contradictory so that one cannot assume that the population fluctuation is a timed reoccurrence. Costello (1936) found H. crassicornis to be rare in his July and August collections, while Manley (1987) found the population to be most abundant in July and August. Nybakken (1978) in his 40 month study located H. crassicornis 100% of time. The location of these study sites differ, but if these were indeed seasonal fluctuations, one would not expect such wild variations. So H. crassicornis does experience low population density on occasion, but it is not a constant compelling factor.

The third suggestion, unstable environment, ties in directly to the population fluctuation and may indeed account for H. crassicornis's continued hermaphroditic state. If a group is unsure of how long optimum conditions may last it would behoove them to maximize the benefits. Even though the habitats it occupies can vary they are littoral in nature and are subject to the various perturbations that can include. There are winds (translated to surge underwater), changes in salinity, temperature and tide fluctuations. This variable environment coupled with a low male reproductive success (Charnov, 1979) could be the modern day constraints that assure hermaphroditism in H. crassicornis.

Ghiselin's gene dispersal model is not applicable to H. crassicornis either in the inbreeding version or the sampling error version. H. crassicornis has dispersive, pelagic, planktotrophic veliger larvae which insure that barriers to gene flow are limited (Todd, 1983).

Charnov's theory using Bateman's principle is the most persuasive argument for the continued selection of hermaphroditism in H. crassicornis. In order for hermaphroditism to be selected, the fixed costs for the reproductive structures must be low in comparison to the fixed costs for pure male and pure female reproductive structures. In H. crassicornis sperm and ova are produced in a single organ, the ovotestis, (Beeman, 1977 and McCauley, 1985) and the affiliated reproductive structures are small in comparison to the ovotestis. By reducing the superimposed female/male reproductive system H. crassicornis is able to minimize its fertility-independent costs. This allows the organism to devote more resources to its limiting factor, the production of eggs, thereby boosting its reproductive success by female function.

The second criteria in the favoring of hermaphroditism over dioecy, low male reproductive success is also evident in H. crassicornis. This success is not related to adult immobility or small group size but rather access to eggs. If successful intromission and sperm deposition occurs only 50% of the time (Rutowski, 1983) this would greatly decrease

male reproductive success by limiting the amount of eggs each individual is able to fertilize in its lifetime. The cause of this low success rate of intromission is unknown but could be due to the rapidity of copulation (Rutowski, 1983)

In the last model Charnov, Smith and Bull presuppose a great amount of lability in the determination of the sex of the organism. Although such organisms are plentiful in the marine environment (for example, the larvae of the echiurid worm Bonellia viridis are sexually undifferentiated; the sex of the individual is determined by the substrate settled on.) it has been concluded that fertilization is the decisive event for the determination of sex in diploid organisms (Bacci 1965). The shifting of reproductive resources in H. crassicornis from the female function to the male function would be an abortive effort because the male function success rate is so low. Since H. crassicornis is unable to meet with the primary assumptions it is not eligible for inclusion in this model.

#### CONCLUSIONS

It would be impossible to determine the adaptive significance for the selection of hermaphroditism in the entire class of opisthobranchs using these models because the strategy was most likely chosen much farther back on its evolutionary time scale. However, on an individual species basis one could look to see if there were modern day

constraints favoring hermaphroditism. One would expect there to be a benefit for each individual species to continue being a hermaphrodite or the strategy would change.

The model that fits H. crassicornis the best is the one proposed by Charnov (1979) utilizing Bateman's principle. Basing the conclusions on the information available about H. crassicornis it seems as if there are in fact, pressures present that favor hermaphroditism. Organ sharing and reduction in the reproductive system has allowed the organism to lower its fertility-independent costs. Thereby allowing the allotment of resources to female function to increase. Also, perhaps because of its aggressive nature and very brief copulation time, the male reproductive success of the individual is hampered. Both of these situations coupled with the relatively unstable environment that H. crassicornis lives in, serve to insure hermaphroditism over dioecy as a reproductive strategy.

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