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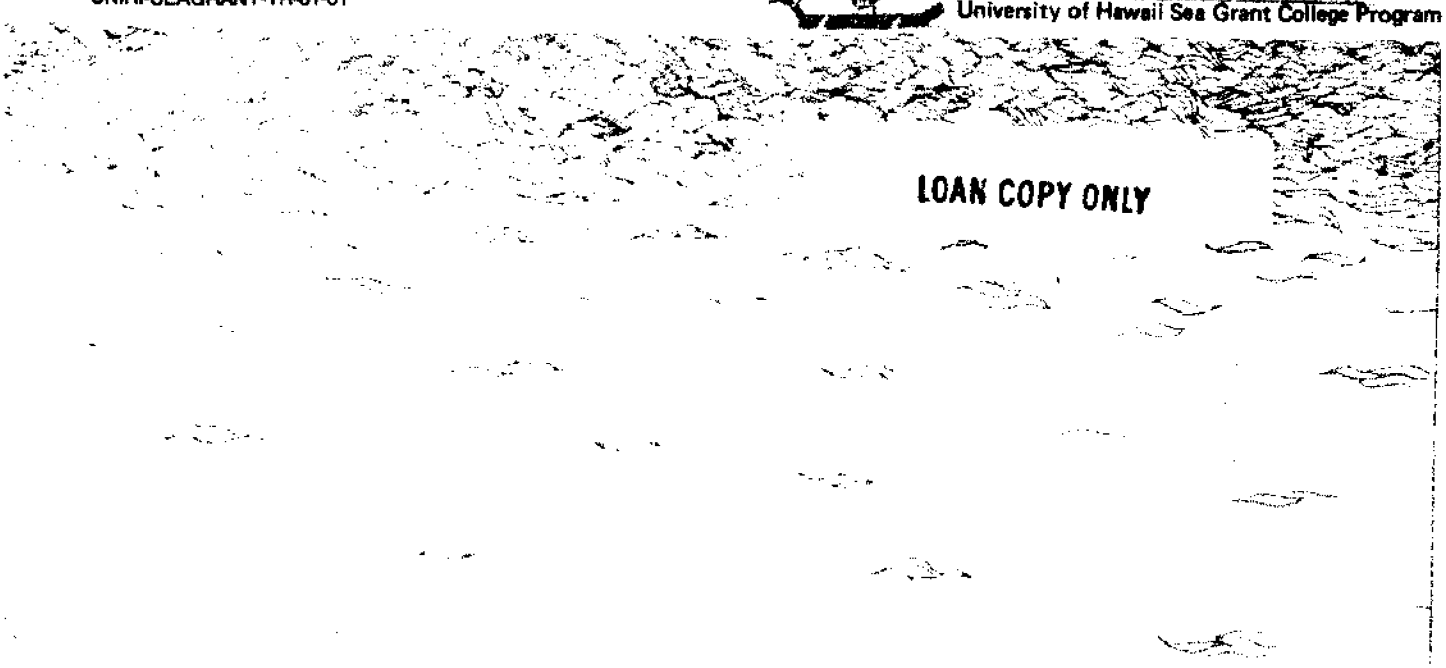
University of Hawaii Sea Grant College Program



Multi-Stage Rotational Stocking and Harvesting System for Year-Round Culture of the Freshwater Prawn, *Macrobrachium rosenbergii*

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September 1981

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Report on the Sea Grant project, Hawaiian Prawn Aquaculture Experimental Research Project (A/R-8); Edward A. Laws and Spencer R. Malecha, Principal Investigators; Sea Grant Years 11 to present.

Sea Grant Technical Report
UNIHI-SEAGRANT-TR-81-01

September 1981

This work is the result of research sponsored in part by the University of Hawaii Sea Grant College Program under Institutional Grant Nos. 04-8-MO1-178 and NA79AA-D-00085 from NOAA Office of Sea Grant, Department of Commerce, and the Aquaculture Development Program, State of Hawaii. Publication funds were provided in part by the Office of the Marine Affairs Coordinator, State of Hawaii.

ABSTRACT

This report calls attention to the drawbacks of the continuous stocking and harvesting (by seining) management system that is practiced in rarely drained commercial prawn ponds and presents theoretical considerations and a description of an alternative system which can be used to overcome many of the drawbacks. The alternative management system is predicated on variable density culture during growout stages, stock division, manipulation, and size-grading. Results of laboratory-level experimentation suggest that the degree of animal to animal competition that develops within populations is underestimated under the current management system; large animals suppress the growth of smaller ones which have a high compensatory growth potential once they are consistently and periodically removed into their own size-classes. Moreover, the prawn sexual dimorphic growth pattern is ineffectively managed so theoretical arguments are presented for the possiblity of practicing unisex culture or culture involving skewed sex ratios and also the harvesting of males and females at different times. Implementing the alternative system will depend on the development of appropriate hardware for accurate sampling, sorting by size, high density culture during juvenile stages, and unisex culture and considerably improves the accountability of stock not possible under current management practices. It is hoped that culturists and researchers will begin to closely examine aspects of both the theoretical and physical components of the alternative system and test them in currest research efforts and production practices.

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INTRODUCTION

The freshwater prawn, *Macrobrachium rosenbergii*, is a large decapod crustacean whose natural geographical range encompasses areas of Southeast Asia, India, and Australia, as well as areas around the South China Sea. Commercial prawn farming is a fledgling industry in Hawaii (Lee, 1979) and Thailand (IFS, 1980) and has high potential for establishment in other areas (Smith et al., in press; Brody et al., 1980). Two large U.S.-based companies, Weyerhaeuser Corporation and General Mills, have prawn farming operations in Brazil and Honduras, respectively.

In Hawaii and other tropical areas, current prawn farming management practices and husbandry systems are based upon stocking of small juvenile postlarvae (PLs), which are produced at local hatcheries, directly into earthen ponds. Stocking is made on an annual or biannual basis whereby PLs are put into ponds that contain a mixed population of various-sized prawns from previous stockings. Following the growth period, market-sized adults are seine harvested at regular intervals. This system, referred to as the Continuous Stocking and Harvesting System (Figure 1), is supposed to take advantage of the fact that small animals

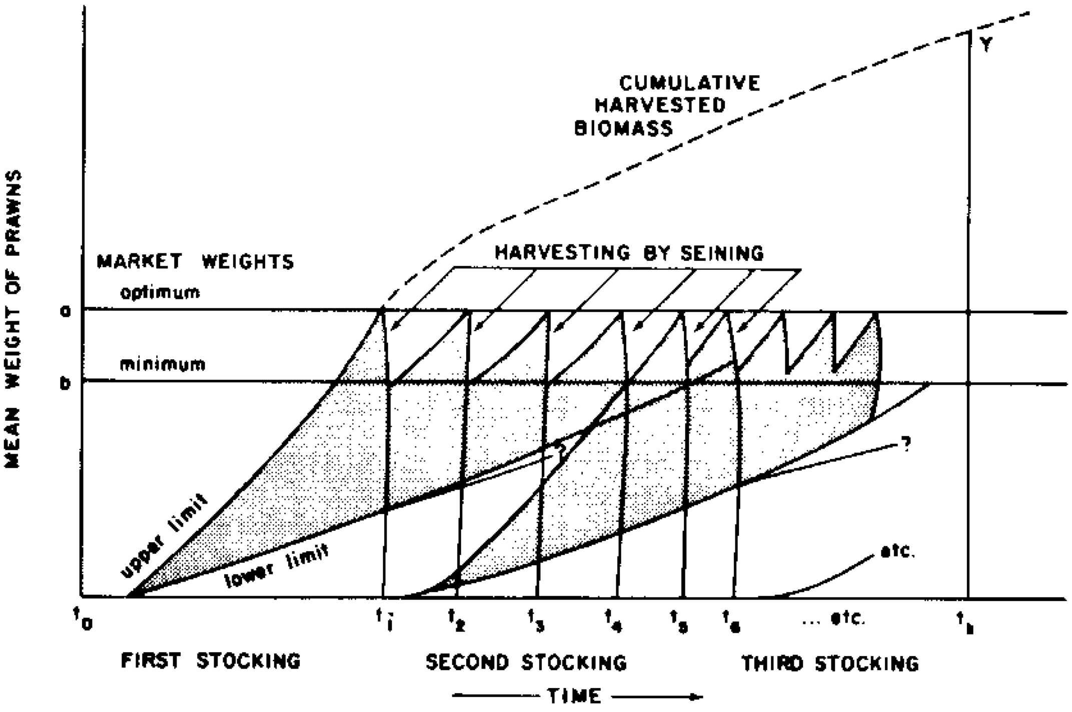


Figure 1. Hypothetical yield and mean weight of prawns in a pond under a Continuous Stocking-Harvesting System (after Moav et al., 1977). At time t_1, following a first stocking, the population biomass reaches a level where mean weight is optimum, *a*. Following the harvest the mean weight drops to level *b*. At time t_2, the mean weight has again reached level *a* and hence the pond is harvested again, and so on from time t_2 to t_k. The dotted line represents cumulative harvested biomass which eventually reaches overall yield Y at time t_k. The shaded portion represents the upper and lower limits to prawn growth, i.e., first harvest can be anywhere from t_1 to t_6. The question mark indicates that the lower limit to prawn growth is not known and may in fact be lower than shown. Notice that harvesting of animals from the first and second stockings overlap in periods t_4, t_5, and t_6.

"grow into" the size classes vacated by harvested, larger ones and is supposed to produce high yields uniformly distributed throughout the year if stocking and harvesting schedules and rates are properly chosen (Fujimura and Okamoto, 1972; Gibson and Wang, 1979).

In practice there are serious drawbacks with this system even though it proved to be economically sound during the industry's formative years (Shang and Fujimura, 1977). The major problem with current prawn management technology is that it does not manage, but rather accommodates, the prawn's biological habits; it precludes the direct manipulation of various life cycle components and growth pattern (sexual dimorphic and heterogeneous individual growth) and the accurate accounting of the biomass and numerical census. Much of the production industry suffers from this problem yet management based on accurate stock assessment and manipulation of life cycle components is a *sine qua non* for economical production of other agricultural crops. Because of this there is great need for innovative management technologies in prawn aquaculture.

In this report an alternative system called the "Multi-Stage Rotational Stocking and Harvesting System" is introduced. This system appears to remove the major drawbacks of the Continuous S-H System by allowing the direct management of various components of the prawn's life history and husbandry. An attempt is made to introduce the rotational stocking and harvesting system in as much detail as possible in hopes that culturists and researchers will begin to test the various aspects or the entire system. Finally, details regarding alternative management systems of both sexual dimorphic and heterogeneous individual growth are presented. To accomplish stock rotation size-grading and water management, hardware will be needed for the prawn industry.

STOCKING AND HARVESTING MANAGEMENT SYSTEMS

Continuous Stocking and Harvesting System

The advantages of this system are:

1. It may be practiced within a single pond.
2. It is relatively simple to practice.
3. It allows continuous marketing (necessary for maintenance of consistent market outlets) for a small farm.
4. It is operable when postlarvae are available for stocking only once a year.
5. There is no need to drain the ponds.

However, the Continuous Stocking and Harvesting System has the following major drawbacks:

1. Harvesting is labor-intensive. It accounts for about 48 percent of the labor requirements in Hawaiian prawn aquaculture, ranging from 42 percent of the total annual operating expenses for a 0.4-hectare (1-acre) farm to 23 percent for a 40-hectare (100-acre) farm (Shang and Fujimura, 1977).
2. Harvesting efficiency (catch/unit labor) is low. Terrestrial agricultural harvests are optimally efficient only when all "new" growth is harvested at the same

time. In the case of prawns, only 25 to 65 percent of the market-sized animals may be captured during any one harvest. Consequently, extra labor is expended in attempting to capture the same animals in subsequent harvests. Moreover, market-sized animals not caught during the harvest most likely cause growth suppression of the smaller remaining or newly stocked animals.

3. Management of heterogeneous growth pattern is inefficient. The large variance and skewness of the prawns' size-frequency distribution (Smith et al., 1978) indicate that the degree of growth suppression of small animals by larger ones could be as substantial as it is for fish with similar distributions (Gunnes, 1977; Magnuson, 1962; Nakamura and Kasahara, 1955; Wohlfarth and Moav, 1972). These intraspecific competitive effects may be overcome with periodic (pre-harvest) size-grading of the stock.

4. Mortality may be high among PLs stocked in ponds containing larger prawns. Unpublished data collected by the Anuenue Fisheries Research Center of the Hawaii Department of Land and Natural Resources involving eight commercial ponds show that an average of 60 percent of the PLs in the first stocking of a "new pond" were eventually harvested at market size. This figure dropped to 35 percent for subsequent stockings when PLs were placed in ponds containing larger prawns from previous stockings, indicating that mortality may be high possibly as a result of predation or other factors related to the presence of larger animals.

5. Mortality among stocked cohorts is difficult to detect. Unexpected mortality (as mentioned above) goes undetected and cannot be corrected in a short time because it is impossible to obtain good estimates of the numbers of prawns in a pond that is never drained. Since small mesh seines are only able to capture animals above a certain size, sampling efforts only give estimates of the population size distribution, and not population biomass and numerical census.

6. Management of the standing crop and yield is inefficient. The lack of accountability (as mentioned above) makes it impossible to insure that an "optimal standing crop" is being maintained. However, even if an optimal standing crop could be maintained through a stable size-class structure, it will not achieve maximum yields since maximum weight gains are different for different sizes.

7. Management of "resident time" is inefficient. In ponds which are never drained, the time limit for removal of small (below market weight) prawns cannot be determined. In one study, a 0.23-hectare (0.5-acre) commercial pond was first harvested 7 months after stocking and harvesting continued for 16 more months before all the animals in the stocked cohort were removed (Fujimura, 1974). Thus, some animals were in the pond for only 7 months whereas others remained for as long as 23 months. The longer resident time represents inefficient use of production resources.

8. Genetically superior broodstock is impossible to obtain with certainty. The wide variety of prawn sizes and ages that develop in undrained ponds could represent a mixture of genetically and developmentally superior and inferior individuals. Broodstock chosen from such ponds for subsequent stockings contribute little to genetic progress (Malecha et al., 1980).

9. Management of sex-specific performance characteristics is awkward. Strategies for managing sexual dimorphic growth differences (i.e., use of different stocking densities and market weights for each sex under unisex culture) are difficult to practice in the Continuous S-H System because it cannot accommodate different harvest times for males and females.

10. Management of fish and prawn polyculture is cumbersome. Frequent harvesting of prawns by seining is difficult and cumbersome when fish larger than the harvest net mesh size are present in the pond. Polyculture holds promise for improving the economics of prawn production by the addition of fish production, improving natural productivity of the pond environment, and contributing to pond ecosystem (especially phytoplankton) stability (Malecha et al., 1981).

General Description of the Multi-Stage Rotational Stocking and Harvesting System

This system will be illustrated through three examples. The first, presented in Figure 2, involves two ponds which may not be of identical size. At time zero PLs are stocked into pond 1 at, say, double a hypothetical optimal final harvesting density (2X) plus a surplus to accommodate for expected mortality. This initiates stage I which, in the hypothetical example in Figure 2, lasts for three months during period A after which time the animals in pond 1 are "thinned out" either with a suitable small mesh net or by pumping following draindown. The thinned out animals (50 percent of the total) are then transferred to pond 2. This thinning out is not selective and marks the beginning of period B in which stage II animals are grown out at a lower density (1X).

The growout period for stage II covers periods B and C and is terminated by the draining and harvesting of the two ponds. At this time a large proportion of the animals would probably still be below optimal (or even minimal) market weight because of the great variance in prawn size. Consequently, these small animals are transferred to pond 2 for an extra growth period (stage $\underline{III}$, period D).

In the following examples which involve more than two ponds, the cycles of the additional ponds are initiated at the beginning of period C. The stages prior to cull size-grading are called primary stages and later ones secondary stages. In the example given in Figure 2 the underscored numerals indicate smaller animals not removed during the harvest which are allowed additional time for growth during period D. Simultaneously, pond 1 is again stocked with PLs to start a new stage I in period D, and so the cycle continues. Note that periods (A, B, etc.) refer to a calendar time dimension whereas stages (I, II, etc.) refer to a class or group of animals at a particular growout stage, irrespective of the duration. Under the hypothetical system presented in Figure 2, a relatively large (double) harvest occurs every 10 months and a smaller harvest in between for the stage $\underline{III}$ culls. Since the system represents efficient use of the ponds at the cost of losing harvesting continuity, one or two seine harvests can be conducted at any time prior to the primary or secondary drain harvests.

Figure 3 presents an application of the rotational system to a set of four ponds (again, not necessarily of equal size). Here, there are two primary stages plus a secondary one. Since stage I (in periods A, C, E, and G) is stocked at three times the standard density (3X) stage II reaches the standard density (1X), at the harvest.

The stage lengths in the example were arbitrarily chosen. Specific scheduling procedures are not recommended at this time. Construction of a definite commercial scheduling procedure would depend upon specific markets and management practices.

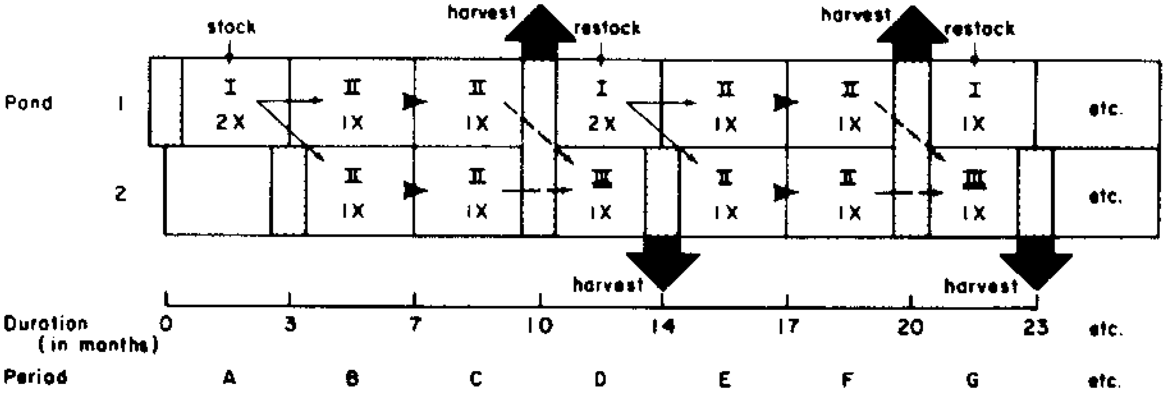


Figure 2. Two-Pond, Two-Stage Rotational Stocking and Harvesting System (some size-grading). Ponds can vary in size. Each horizontal row of "boxes" represents growout periods A through G for each pond. The Roman numerals represent growout stages and imply an age as well as a size-class characterization of the population, e.g., stage I refers to animals ranging from newly stocked PLs to three-month-old juveniles. Stage II animals are largely derived from a divided stage I population. In stage III size-graded animals culled from below the mode of the population are represented. The line under (e.g., II) or over (e.g., II) certain Roman numerals refer to a stage in which animals have been size-graded. The number of X's refers to a stocking density where "X" is some standard density. The common vertical line between boxes refers to events involving the movement of animals and marks the transition between growout periods or stages. Hatched lines refer to either a pond draindown accompanied by a harvest—indicated by broad arrows—or to a pond "cleared" for the beginning of a growout cycle. The unbroken, thin arrows connecting stages refer to the movement of thinned out cohorts between periods. The unbroken, thick arrows refer to a transition from one stage to another without the movement of animals. The broken, thin arrows refer to the movement of size-graded animals.

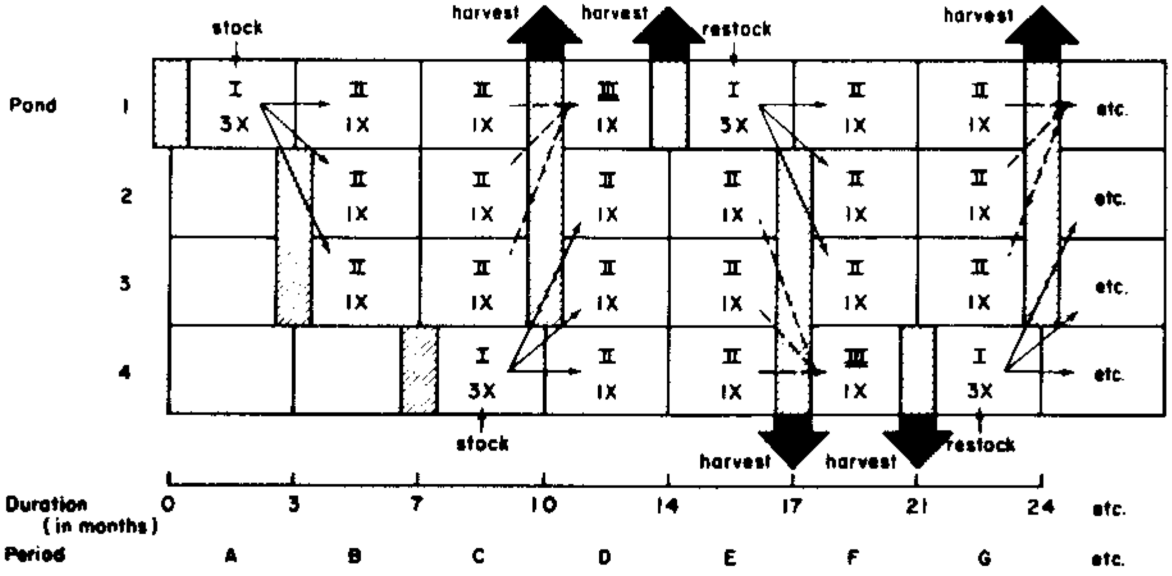


Figure 3. Four-Pond, Three-Stage Rotational Stocking and Harvesting System (some size-grading). Symbols are as given in Figure 2. Secondary stage III represents small animals allowed to grow out for additional periods (D in pond 1 and F in pond 4).

Comparative Aspects of the Continuous and Rotational S-H Systems

Heterogeneous individual growth pattern management

The size-frequency distribution of freshwater prawns "depensates" as it does in fishes; the variance increases as the mean increases (Ricker, 1975; Magnuson, 1962) due to the fact that weight gain is allometric, i.e., it is a power function of initial weight (Brody, 1945; von Bertalanffy, 1938). This can be expressed as $dw/dt = \alpha w^{\beta}$, where dw/dt is an increase in weight per interval of time, α and β are constants, and w is initial individual weight at the beginning of the interval. In general, β is determined partially by the genetics of the animal and other factors, including temperature and food availability and quality. The authors believe that in *M. rosenbergii*, β is greatly affected by behavior interactions.

In most populations of animals, growth can be expressed as the power function $d\bar{w}/dt = \alpha\bar{w}^{\beta}$, where $\bar{w}$ is mean population weight. When expressed in this manner it is assumed that the effect of heterogeneous individual growth is minimal, i.e., the variance of individual weight is small. However, the prawn's depensation pattern cannot be described in this manner because it is greater than expected based only on allometric growth. The net result is considerable variation in growth between individuals and highly skewed size-frequency distributions (Figure 4).

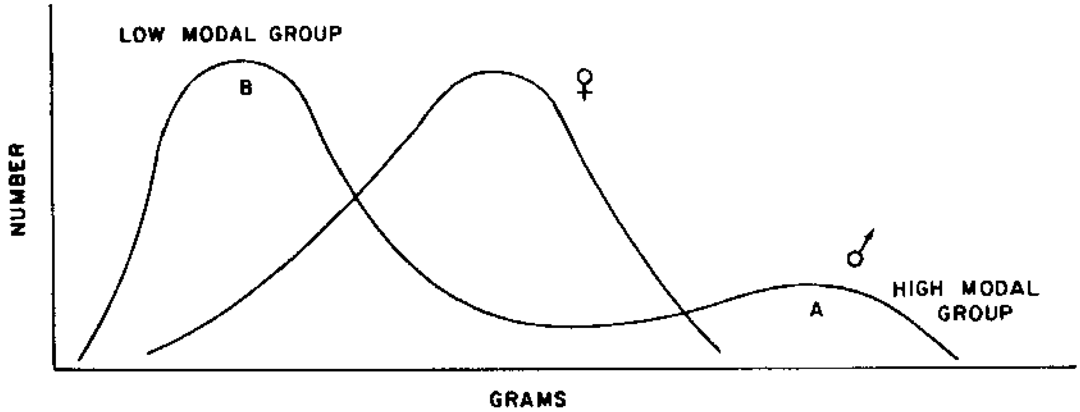


Figure 4. Schematic of a hypothetical size-frequency distribution for an unculled bisexual population of *M. rosenbergii* at critical standing crop

A full sib population of identically aged individuals can have size ranges spanning from four to six standard deviations and coefficients of variation of up to 70 percent compared with below 20 percent for other terrestrial agricultural animals (or their products). The prawn depensation growth pattern would not be of any special economic significance were it not for the fact that prices ($\$kg^{-1}$) paid for crustaceans are a function of their size (no. kg^{-1}) to a greater degree than for other aquatic groups. Because the prawn size-frequency distribution directly affects its product value distribution (Table 1), it therefore constitutes one of the most economically important biological characteristics of the animal. Current prawn farm harvesting practices have been designed around this characteristic. For example, in order to consistently meet market consignments, market-sized (large) animals are cull-harvested from the population to "make room" for under-sized animals to grow. Basically, this practice is an aquacultural analogue to harvesting "new growth" such as done with perennial fruits. In practice, the system is inefficient, but more importantly it may be predicated on an underestimation of the intra-populational competitive effects. The large animals

TABLE 1. TAIL WEIGHT AND VALUE DISTRIBUTIONS FOR PRAWNS REARED IN A SOUTH CAROLINA POND IN 1978 (after Smith et al., 1980)

Tail Count (No./kg)	Price ($/kg)	Male* Value ($)	Female† Value ($)	Total Value ($)
24-33	13.75	39.60	--	39.60
34-44	12.65	487.15	--	487.15
45-55	11.44	787.30	--	787.30
56-66	10.56	452.50	74.34	526.84
67-77	9.68	334.64	308.02	642.66
78-88	7.92	211.78	542.05	753.83
89-99	7.26	116.89	570.70	687.59
100-110	6.82	56.33	405.11	461.44
111-121	5.94	34.87	128.30	163.17
122-132	5.28	26.82	59.35	86.17
133-154	4.40	39.03	30.18	69.21
155-176	3.74	22.93	2.09	25.02
176+	2.42	67.69	3.94	71.63
Total		2,677.53	2,124.08	4,801.61

*293 kg ha^{-1}
†287 kg ha^{-1}

in the high modal group not only magnify (through time) slight initial size differences into large ones but may also actively suppress the growth potential of the smaller ones. Consequently, the present system, even if it were 100 percent efficient, inefficiently manages the prawn's growth pattern.

Laboratory-level studies have clearly demonstrated the compensatory growth capacity of the freshwater prawn. Malecha (1977) showed that some juvenile prawns with a large size variance graded into size classes and grown out separately attained approximately the same final size in the same time period despite varying initial sizes.

Recent work (Malecha, 1981) shows that animal interaction in populations is responsible for the development of the depensation pattern which can be reduced considerably by rearing individuals in separate units. In addition, small or runted animals (present in the low modal group in Figure 4) can undergo considerable compensatory growth when removed from a space-restricted container.

A field study by Willis and Berrigan (1978) showed that selectively removing large animals (whose total biomass was small) greatly enhanced the growth capacity of those remaining in ponds. Their study strongly suggests the growth repression capacity of larger animals on small ones under commercial field conditions.

These experiments clearly show that a prawn's age and size are not indications of its growth capacity and suggest that the latter may be depressed in smaller animals by the presence of large animals. Consequently, it may be possible to manage this phenomenon by size-grading. Gunnes (1976) showed that Atlantic salmon size-graded at six months showed better growth than controls after five subsequent months of growth. The reasons why size-grading "works" are obscure, but most likely amelioration of some growth-reducing competitive interactions plays a large role. In one way or another, "competition" has been considered to be the cause of skewed length-frequency distributions in most studies. Symons

(1971) found that even when food was abundant, the growth rate of subordinate salmon was 66 percent that of dominant individuals Magnuson (1962) demonstrated that in the medaka fish, food dispersion availability and quantity have a significant effect on individual growth variance. The development of a social structure containing large dominant or territorial prawns may cause a skewed length-frequency distribution. Nakamura and Kasahara (1955, 1956, 1957, 1961) showed that skewed length-frequency distributions for the cultured carp are the result of competition; large animals ("shoot carp") out-compete smaller ones for food. When the large ones are removed, the growth rate of the smaller ones accelerate, and they in turn become shoot carp.

Work needs to be performed that tests the concept that the inherent behavioral characters of a prawn population are more economically managed by periodic stock division and size-grading. This should ameliorate the growth repressive effects of large animals by continually removing them from the ponds where smaller ones can then undergo compensatory growth. Experimental field trials will entail detailed experimental observations and animal manipulation. Work should be directed at assessing the effects on yield of size-grading as compared with traditional practices. The theoretical considerations described below serve as predicators of the expected outcome of stock manipulation and are presented to encourage culturists and researchers to test stock rotational/size-grading systems. A close fit between the predicted and observed outcomes will enhance knowledge of the basic biological properties of the freshwater prawn, *vis a vis* its potential to respond to commercial-scale manipulation.

Figure 5 provides a hypothetical scheme which emphasizes how a size-graded population may possibly out-yield ungraded populations. Frame A refers to a non-size-graded population. This population should be left intact so that maximum agonistic interactions among animals will develop as the population grows. For purposes of discussion, groups of animals are shown as a_1', a_2', and a_3', which are comparable with graded classes a_1, a_2, and a_3 in frames B, C, and D derived from "parental" populations. These groups are assumed to competitively interact such that the relative influence on each other's growth is described as: I > II > III. When animals from groups I, II, and III are size-graded, they are regrouped into classes a_1, a_2, and a_3, respectively. Since there are three parental populations and three graded classes, the populations can be standardized for density (but not biomass) so that production measured as biomass per unit of area per unit of time can be compared with that of the ungraded population shown in frame A.

The ungraded population will grow at a mean rate described by the power function:

$$\frac{d\bar{w}}{dt} = \alpha\bar{w}^{\beta}$$

as shown by the top equation in frame A. However, for the purposes of comparison the growth rates of the ungraded size classes, a_1', a_2', and a_3', can be described by the power functions shown by the remaining equations in frame A. All equations can have different constants, α and β, because they describe the growth of groups in a depensating population; subscripts are added to the weight variables, $\bar{w}$, and β values to identify a specific graded group.

Frames B, C, and D are shown with power functions describing the growth rate of the graded size classes, a_1, a_2, and a_3, respectively. If the effect of size-grading is the removal of the growth repressive effect of large animals on smaller ones, then the smallest size-graded

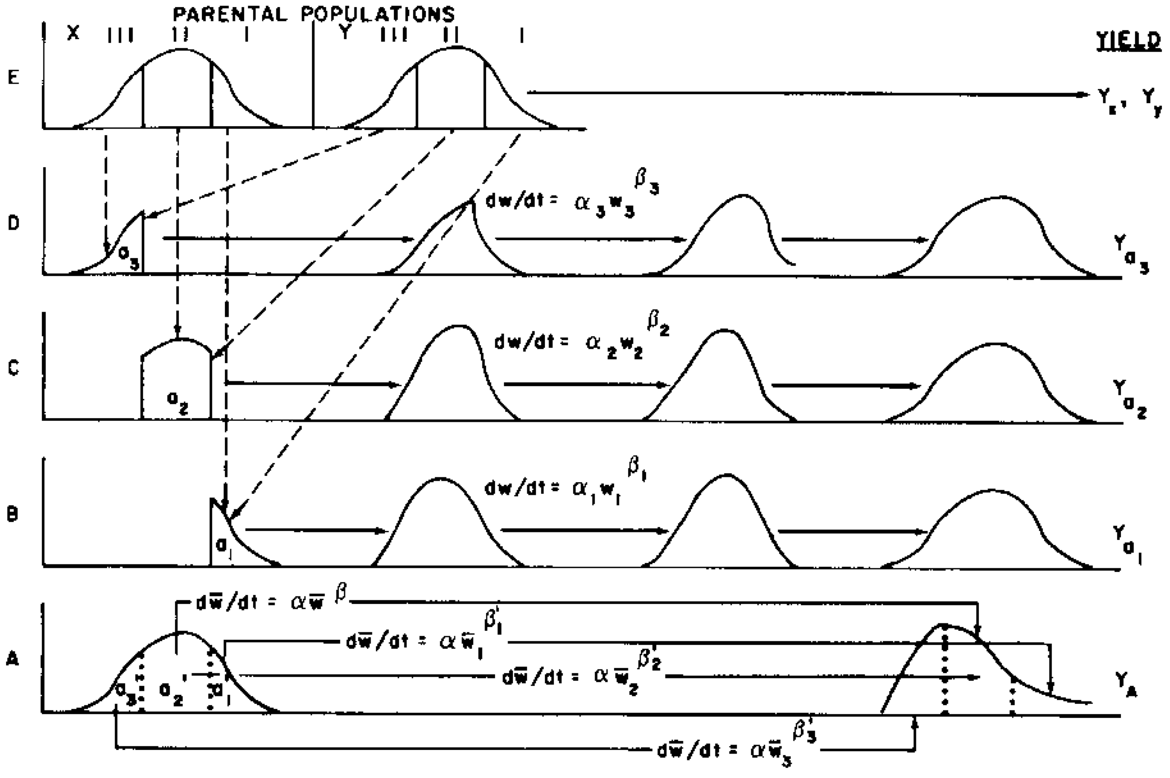


Figure 5. Schematic representation of the effect of size-grading. Diagram shows prawn control and experimental populations which will undergo evaluation in phase I. Population A represents the current traditional management practice.

group will grow at a rate which would allow it to achieve a larger size than it would have had it stayed in an ungraded population. This case can be described by the inequalities:

$$\beta_3 > \beta_3' \therefore \frac{dw_3}{dt} > \frac{d\bar{w}_3}{dt} \tag{1}$$

Analogous inequalities for the middle size-graded group can also be written:

$$\beta_2 > \beta_2' \therefore \frac{dw_2}{dt} > \frac{d\bar{w}_2}{dt} \tag{2}$$

These will describe the relative growth rates of the graded and ungraded groups, a_2 and a_2', depending upon how much of an influence the large animals, a_1', have on a_2'. The reason for this uncertainty is that the a_2 group (frame C in Figure 5) may possibly be put under more restrictive growth conditions by being graded out of the population; the large animals have been removed but so have the smaller ones, only to be "replaced," so to speak, by "larger" a_2 animals. The magnitude of inequality relationships given in inequalities (2) will be determined by the degree to which replacing a_3 animals by those in the a_2 group (in creating the a_2 group) is offset by removing the influences of a_1 individuals.

If conditions are altered to promote greater growth in a_1 as compared with a_1', then the inequalities

$$\beta_1 > \beta_1' \therefore \frac{dw_1}{dt} > \frac{d\bar{w}_1}{dt} \qquad (3)$$

will apply. The reasons why this may not be true are easier to see here than in the previous case. Size-grading animals into an a_1 group under the same density conditions as present in the parental populations may restrict their growth because all small animals (i.e., a_2, a_3) are removed from a_1 only to be replaced by larger ones. This may cause greater competition among individuals in a_1 so that they will have reduced growth compared with those animals in a_1'. It is suspected that to achieve the effect described below, perhaps a_1 and a_2 populations should be assembled at density and standing crop levels lower than the parental populations, X and Y. Optimum levels would have to be determined operationally, first in preliminary work and later on a commercial scale.

If carried out properly to account for the constraints discussed above, the net effect would be that the average yields in populations a_1, a_2, and a_3 be greater than those in population A, a "control" population:

$$(Ya_1 + Ya_2 + Ya_3)/3 > Y_A. \qquad (4)$$

Considered in another perhaps more important way, the probable yields of populations X and Y left ungraded would be less than the total graded ones, a_1, a_2, and a_3, or:

$$(Y_X + Y_Y) < (Ya_1 + Ya_2 + Ya_3) \qquad (5)$$

In the example, inequality (5) cannot be proven directly unless the X and Y parental populations are left intact. For experimental purposes, this should be done to test the theory. Size-graded groups then should be subsamples of parental populations. To do this, the optimum time for size-grading, cutoff points, proper densities, and biomass levels will have to be determined. However, the experimental design must accommodate the possible restrictive effects of environmental conditions on the growth rates of graded groups.

Field manipulations

Figure 6 gives a multi-stage rotational scheme which can be tested under field conditions. Tests in control ponds should also be run with the same monoculture husbandry regime comparable with current industry practice; harvesting can be carried out by seining.

Many of the specific logistic details will have to be worked out as field tests progress. For the sake of illustration, Figure 6 shows the 4X density level chosen as the nursery density. Consequently, the subsequent stock divisions are shown as 4X → 2X → 1X. The survival and growth depensation pattern behavioral interactions should be monitored in the nursery phase.

The mean growth rate and population depensation should be evaluated to make a decision as to when to begin period B; theoretically it should be when the critical standing crop is reached. It may be necessary to split the nursery populations and start the period sooner because the population may be depensating at a fast rate. If the nursery density is 4X (where X = 100) with a 50 percent nursing mortality, which is common, then at the end of period A these will be roughly (100 x 4)/2 = 200 ind m^{-2}. If the average weight is

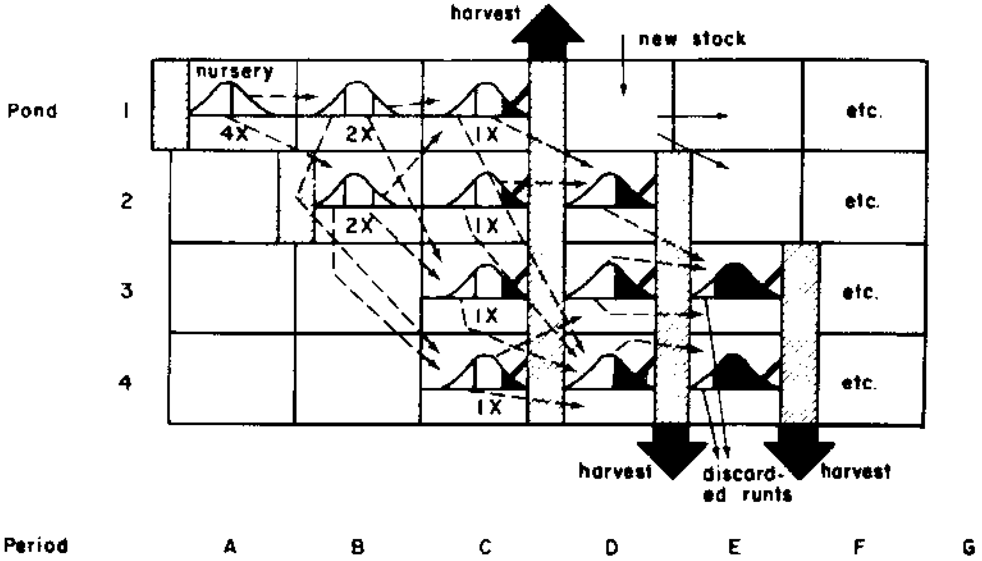


Figure 6. A four-pond multi-stage rotational scheme with size-grading. Dotted arrows represent stock division and rotation to homogeneous size class. Shaded areas in distribution represent harvested class. Hatched bars between periods represent harvest. Periods can be of different lengths. Ponds may be completely drained between periods during which time stock is rotated and size graded. X represents a certain density which may vary at each stage depending upon empirically derived growth rates.

.5 g, then they will be 100 g m^{-2}, about 50 percent of the critical standing crop calculated for an adult population (Polovina and Brown, 1978).

To calculate the probable mean growth rate during a PL to juvenile phase similar to the period A nursery phase, the data of Smith and Sandifer (1979a) were used. Based on their data, mean growth should be at least 2 g in 90 days. They achieved a mean size of 2 g in 70 days for animals stocked at 300 m^{-2}. Therefore, one has the option of stocking at much higher densities during period A and/or extending this period until a greater biomass is reached. For various practical reasons, it may be different to achieve stock division at the beginning of period B. In experimental systems depensation as measured by the coefficient of variation [CV = (variance/mean) x 100 percent] reaches 40 percent in about 70 days. This represents a range of animal sizes over at least three standard deviations on either side of the mean. Consequently, it is felt that stock division should be done when the population depensates to at least a CV level of 40 percent.

The population from period A should be split and size-graded into populations for grow out during period B, which, like period A, can have variable lengths. Again, close monitoring of mean growth and depensation pattern should be carried out using seine sample methods. In period B, ponds 1 and 2 will receive animals of different sizes because of size-grading, but the ponds will be stocked at the same density. The populations will be stocked well below the critical standing crop level in both ponds so that the disparity between them will not matter. However, if there is differential growth between the two ponds during the initial trials, then some animals could be culled.

After period B the two populations should have depensated again to a CV = 40 percent level and be amenable to size-grading into three size-classes, equivalent to populations a_1, a_2, and a_3 shown in Figure 5. Ponds 2 and 3 will receive animals from the same size-class derived from the "middle" of the distribution. Since this area of the curve contains the most animals it may be necessary to utilize two ponds in this manner. In theory only one pond per size-class is needed. After period C, which should be from six to nine months from the beginning of the experiment, all ponds will be harvested for the larger animals. Two size-classes will be "left over."

The operation shown in period B of Figure 3 should be conducted so as to leave the parental populations in ponds 1 and 2 "intact" to serve as a control [described above, in Figure 5, and inequalities (5)]. In this regard the size-graded groups will be subsamples of the two parental populations.

The large median group should again be divided between two ponds (2 and 3). The smaller and less dense group should be put into pond 4 during period D which is followed by a harvest. A new cycle will also begin in period D in pond 1 which should be left vacant due to size-grading, harvesting, and stock rotation. During period D three populations will grow out, again under close monitoring of mean growth and depensation pattern, followed by a harvest and size-grading. Period E will complete the first cycle and by this time most of the animals in ponds 3 and 4 should be of harvest size. Those that are not should be discarded.

Either density or biomass can be standardized (but not both) in experimental and control populations. Wohlfarth and Moav (1972) showed that weight gain and yield in carp are related to initial starting weights. Gunnes (1976) had to apply a correction factor for starting weights in order to show the significant effect of size-grading. However, tests should focus on the operational aspects of size-grading and strive to define sets of conditions that will allow one to conclude that manipulations are causing changes in the growth equation power functions that would not otherwise occur. Consequently, the standardization of these groups is not highly important. However, certain obvious effects of environmental growth conditions should be accommodated. For example, one must take into account the possibility that the critical standing crops of graded groups are being exceeded. If a plateau effect on growth is observed, an attempt to decrease the density by random culling should be made. Continual sampling for growth rate calculations should also be done.

There is no doubt that many unknown problems lie ahead in attempting to field test a multi-stage rotational scheme such as shown in Figure 6. It is anticipated that many experimental decisions will have to be made along the way which may involve departures from what are shown in the figure. For example, it is not certain when ponds should be divided and when the stocks should be rotated and size-graded.

Control ponds can be selectively harvested beginning at the time of the first harvest in the experimental system. Attempts will be made to simulate as nearly as possible current commercial harvesting practices.

Analysis can be straightforward—simple comparisons of the growth, survival, and overall production of the four rotational ponds with the four control seine-harvested ponds. Currently, it is not known what the "turn-over time" of a seine-harvested pond is. Yet this information is needed to make a valid comparison between the seine harvest and rotational system. It may be that the production of the two systems, including residual biomass, will have to be compared at some defined point in time.

Labor economy

A major drawback of the Continuous S-H System is the excessive amount of labor required for frequent harvesting by seining. An index of labor requirements for seining plus harvesting was computed (Table 2) for the examples in Figures 2, 3, and 6. Two assumptions were made in computing data for Table 2: (1) under the Continuous S-H System each pond is seined once a month; and (2) seining for thinning-out during the transition from one stage to the next in the Multi-Stage Rotational S-H System has about the same labor requirements as seining the same pond.

TABLE 2. COMPARISON OF THE LABOR REQUIREMENTS FOR SEINING AND DRAINING THE VARIOUS SYSTEMS

S-H System	No. of Ponds in a Minimal Set	Duration of a Complete Cycle (months)	No. of Seinings and Drainings Per Cycle	No. of Seinings or Drainings Per Pond Per Month*
Two-stage rotational without size-grading	2	10	4	0.2
Three-stage rotational without size-grading	4	7	5	0.18
Four-stage rotational without size-grading	3	10	8	0.27
Continuous	Variable	Continuous	--	1.0

*For harvesting of the various systems with alternative continuous S-H system

Comparing the number of seinings or drainings per pond per month under the Multi-Stage Rotational S-H System (the last column of Table 2) with one seining per pond per month of a typical Continuous S-H System shows that, at least under the above assumptions, the former system requires less than 30 percent of the harvesting labor necessary for an equivalent of the latter system.

Water economy

Theoretically, a Continuous S-H System is the one with the best water economy since the ponds never need to be drained. A farm design that takes full advantage of land grades plus proper water management, primarily through water recycling, ameliorates this apparent advantage of the Continuous S-H System. Figure 7 illustrates this point using the four-pond example of the Multi-Stage Rotational S-H System in Figure 6. In Figure 7, the four ponds were rearranged from highest (pond 4) to lowest (pond 3) elevation. At each primary harvest, pond 3 is emptied first, and the water is discharged into and conserved in a reservoir. Pond 2 can then be emptied into pond 3. Subsequently, pond 1 can be emptied into pond 2 and then refilled with freshwater or with the pumped water of pond 3 after temporary storage in other ponds or a reservoir. The water from draining ponds 4 and 1 for the secondary harvest can be distributed (by gravitation) into the lower ponds. Thus, this system may operate without any loss of drained water and very little pumping.

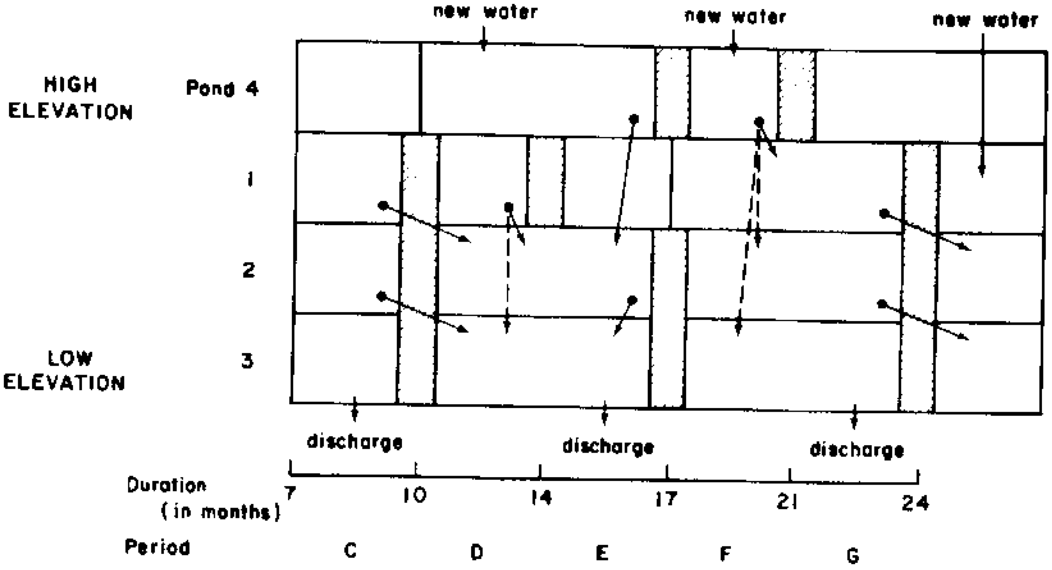


Figure 7. Four-Pond system showing water movement between ponds for a Rotational Stocking and Harvesting System comparable with that shown in Figure 3. Symbols are as given in Figure 2. Periods A and B are not shown; ponds are arranged by elevation. Thin and broken arrowed lines represent water movement by gravity from adjacent and non-adjacent ponds, respectively. Lower arrows represent discharge to a reservoir or outflow.

Marketing

A major advantage of the Continuous S-H System is the continuity of the market supply it provides. This is especially advantageous for small farms. However, larger farms can also provide continuity by synchronous scheduling of several "batch" harvests. With the rotational S-H system there is no reason why intermittent harvesting by seining cannot be accomplished between scheduled drainings if marketing considerations justify the extra cost. Moreover, the rotational S-H system allows a farmer to exploit markets for small (i.e., bait) and large (i.e., lobster) size-classes if economic consideration permits this. Large size-classes can be efficiently exploited by size-grading large animals into their own pond. It is possible to harvest and market small size-classes at any time.

Polyculture

Polyculture, the rearing together of more than one species of animals within a single pond, is a proven way of producing high yields from a single unit of physical resources, i.e., land, water, food (Bardach et al., 1972; Moav et al., 1977; Tang, 1970; Tapiador et al., 1977). Improved prawn production *per se* may result from increased availability of natural food, better phytoplankton management, and better water quality due to the presence of fish.

Polyculture of prawns and fishes has been successfully demonstrated (Brick and Stickney, 1979; Malecha et al., 1981; Ryther et al., 1977), it can be easily and effectively incorporated into the rotational S-H system. In a two-stage system (such as shown in Figure 2) fish may be stocked immediately following the seinings that mark the transition from stage I to stage II. In a three-stage system the fish fry may be stocked in stage II, provided they are small enough to pass through the net during the seinings that mark the transition from stage II to stage III. Figure 8 shows how fish may be incorporated into the two-stage

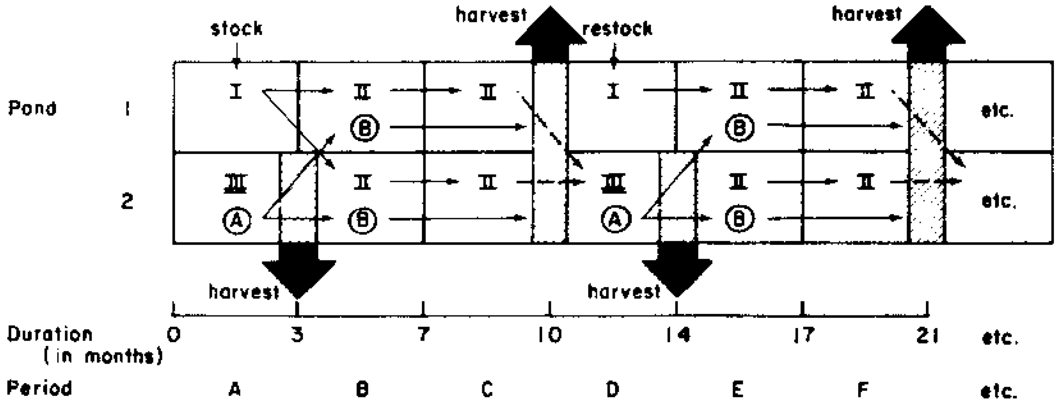


Figure 8. Two-Pond, Two-Stage Rotational Stocking and Harvesting System using polyculture with fish. Symbols regarding prawn population are as given in Figure 2. Ⓐ and Ⓑ refer to primary and secondary stages of fish growth, respectively. Notice that analogous prawn and fish stages are assumed to be asynchronous. Consequently, a primary fish stage, Ⓐ, is stocked with a secondary prawn stage, III. This allows either splitting or harvesting of fish stock to coincide with prawn splitting or harvesting.

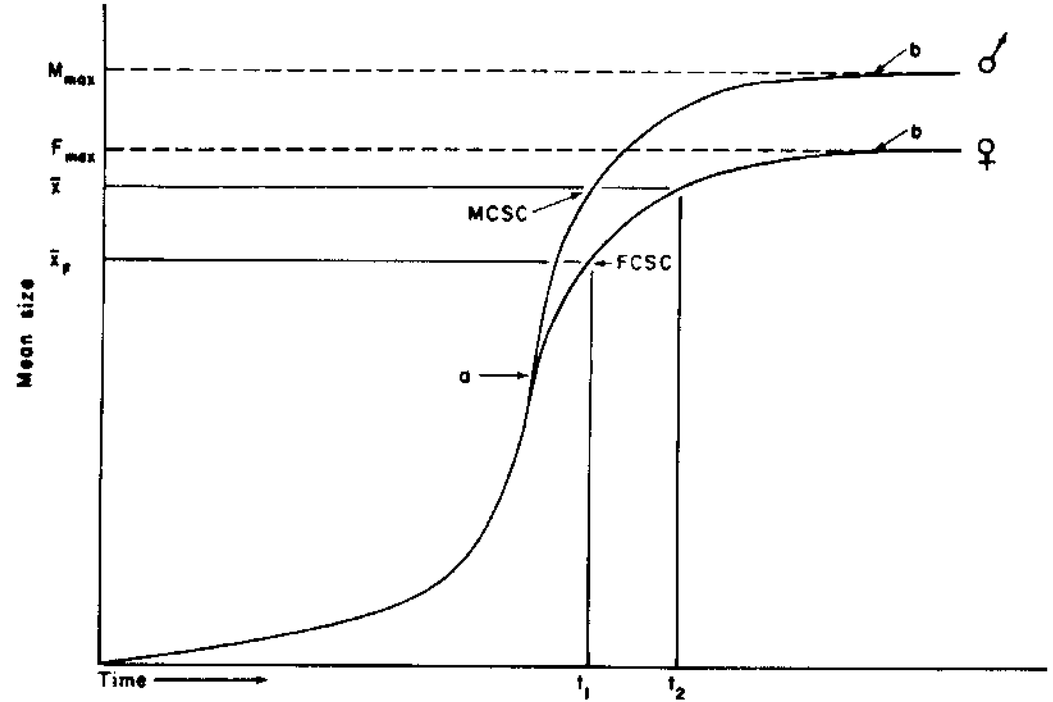
rotational system shown in Figure 2. It is assumed that fish can have distinct growth phases but do not need to be size-graded and should be distributed to ponds from stage to stage only during a pond draindown so as not to present a problem during prawn size-grading operations. Thus, in Figure 8 the fish in primary growth stage Ⓐ can be stocked at a relatively high density with a prawn secondary stage (III) and then divided between the two ponds for secondary stage Ⓑ following a draindown harvest.

Alternatively, fish could be managed so that it does not interfere with size-culling. One method would be to herd stage Ⓑ fish to one section of the pond with a large-eyed net through which even large prawns could easily pass, and then pull a smaller-eyed seine net through the pond to accomplish the cull size-grading of the prawns.

Management of growth differences between sexes

Sexual dimorphic growth following the onset of sexual maturity is a common phenomenon in animal production, and it is usually managed directly. For example, in swine, sexual dimorphic carcass quality is managed by castration so that farrows (castrated males) and gilts (unmated females) are both marketed as finished hogs of similar size. When sexual dimorphic growth cannot be "equalized" through castration, it is managed by means of different harvest times in order to maximize the use of space and food resources. In poultry, sexual dimorphic growth begins at two weeks of age so broiler hens are slaughtered earlier than cocks (Soller and Moav, 1973). Analogously, the opposite happens in *M. rosenbergii*. Consider frame A of Figure 9 which shows a hypothetical mean size vs. time growth for male and female prawns. Under the Continuous S-H System males are harvested before females at time t_1 since they have a "faster" mean growth rate. This sexual dimorphism in mean growth rate is due largely to the accelerated growth of the large "bull" males (Figure 4, modal group A). Females are left to grow until they reach the mean harvest size, $\bar{x}$, at time t_2. This represents the worst possible management of the sexual dimorphic growth rate since females are not being harvested at their most efficient (not maximum) growth. This point corresponds to the female critical standing crop (FCSC) and is shown to occur at the same time, t_1, as the male critical standing crop (MCSC) in Figure 9 (frame A); it actually

Ⓐ Hypothetical mean size vs. time growth for male and female prawns



Ⓑ Hypothetic curve for male and female growth using log transformation $\ln G = \ln\alpha + \beta \ln w_i$

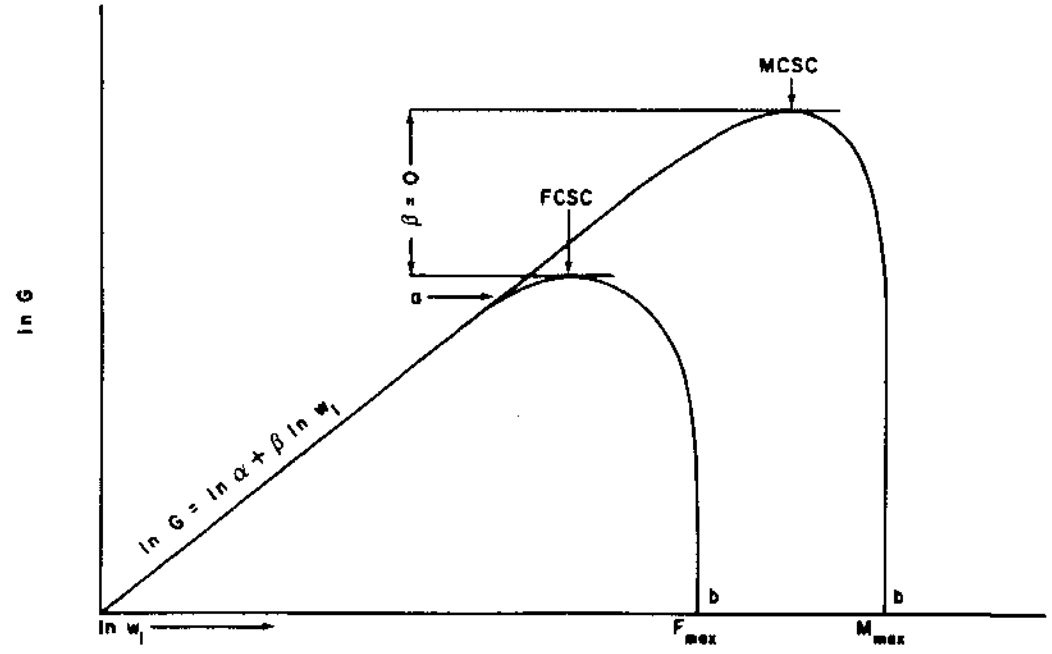


Figure 9. Profiles of prawn sexual dimorphism growth

may occur at slightly different times in females and males. The absolute values of the parameters described here and in Figure 9 (frame A) depend on the particular husbandry system used. The relative values due at sexual dimorphic disparities are less subject to this influence.

It is these differences which mandate separate management of males and females. The time between the ideal harvest time, t_1, and the actual harvest time, t_2, represents an inefficient use of resources by the females which should be harvested at a lower mean weight, $\bar{x}_F$, representing the female critical standing crop.

Critical standing crops cannot be readily seen in mean size vs. time growth plots such as shown in Figure 9 (frame A). This is because the CSC is a certain population biomass (density x number) above which the amount of food (and other "essential" resources) becomes less than that required to maintain full growth. CSC occurs at some point between *a* (shown also as the point of divergence between male and female growth in Figure 9, frame A) and *b*, the size at which growth ceases (M_{max} for males, F_{max} for females). Critical standing crop can be early "seen" and defined in terms of the change in the power function, β, of the allometric growth equation: $G = dw/dt = \alpha w_i^{\beta}$. This equation describes growth, G, as an exponential function of weight, w_i, at the beginning of the growth interval. Changes in the power function, β, can best be seen when the growth equation is transformed into logarithms, i.e., $\ln G = \ln \alpha + \beta \ln w_i$. β is the slope of the line defined by this equation. Figure 9 (frame B) is a hypothetical curve for males and females using this log transformation. Hepher (1978) presented a thorough discussion of the use of the allometric growth equation, pointing out that food limitations will cause a change in β which leads to a deflection in the straight line of the log equation (Figure 9, frame B). The point at which $\beta = 0$ is the critical standing crop. However, because of the sexual dimorphic growth pattern, CSC will differ in males (MCSC) and females (FCSC) as shown in Figure 9 (frame B). Beyond the CSC, growth is not optimal because animals are not gaining weight at the optimal rate in a given time and intake is devoted disproportionately to non-growth metabolic requirements. Growth occurs, but not at the most efficient rate. It can be shown that populations should be harvested at or near their CSC for maximum economic yield (Hepher, 1978). Since CSC is clearly sexually dimorphic in *M. rosenbergii*, the current system of harvesting males and females of the same size is, by definition, not optimal.

Better management of sexual dimorphic growth is clearly needed. This could come about by growing males and females separately or at certain ratios once the technology is available to "create" unisex broods. The Continuous S-H System is so cumbersome in this regard that direct management of sexual dimorphic growth differences has been completely ignored even though it is an important production-related attribute.

What is the "reason" for sexual dimorphic growth in *M. rosenbergii*? It must not be assumed that the lower mean female size is due to greater gonadal growth unless there is a big difference in gonadal weight vs. somatic weight for a given volume; this is unlikely. Furthermore, the "tails only" product value distribution of females (Table 1) seems to be symmetrical with the size-frequency distribution (Figure 4). The disparity between male and female growth is expressed on a population mean weight basis and is due to the large-sized males (modal group A, Figure 4) which not only undergo increased allometric growth but suppress the allometric growth of the smaller males (modal group B, Figure 4).

Large males (Figure 4, modal group A) are characterized by large, well-developed chelae and body size not essential for feeding and maintenance. Characteristics such as these usually develop in a species as the result of sexual selection (Darwin, 1874; Ghiselin, 1974; Trivers, 1972). There are many forms of sexual selection but all involve in one way or another the access of mates to one another. In *Macrobrachium rosenbergii* large size in males is most likely used to compete for female mates and to control the access of other males to these females and/or may be used to "protect" ovigerous females. Single pair bonds are formed in prawns after a female prenuptial molt and the male (usually a large animal with well-developed chelae) protects the female from cannibalism during this time. It has been shown that most intra-population cannibalism is directed at newly molted animals (Peebles, 1977).

The authors maintain that the increased body weight of the bull males is a sex-limited secondary sexual characteristic due to sexual selection and is analogous to other male-specific (i.e., sex-limited) characteristics found throughout the animal kingdom that are used in sexual selection (e.g., antlers and plummages). Because these characteristics have high genetic fitness values, they would be expected to have very little genetic variance of the kind which would respond to selection. Indeed Malecha et al. (1981) have shown evidence to this effect. If this is confirmed there is little hope of changing sexual dimorphic growth through genetic selection; therefore, the only viable alternative is to manage it better.

Broodstock selection

Under the Continuous S-H System, broodstock for commercial ponds is made up exclusively of gravid females collected from commercial harvests; consequently, both genetically inferior and superior animals may be selected.

Since ponds are never drained, it is impossible to determine whether genetically inferior (i.e., small) males that avoid the harvest net in the Continuous S-H System are able to reproduce more often than the culled "genetically" superior males. Those that avoid the net will have longer residence time which would maximize their chances of mating with broodstock females. The latter is obtained from commercial harvests and could be anywhere from seven months to several years old and could represent the full spectrum of genetically controlled growth rates.

Figure 10 portrays three possibilities that could occur in selecting female broodstock under a system of continual harvesting. In this figure a full spectrum of genetically controlled growth rates is represented. In some circumstances the worse case scenario could prevail, i.e., the largest animals could represent the older but slowest growers. Depending upon how much of the variance in growth rate is genetically controlled, this practice could be directly counterproductive to progressive domestication of *Macrobrachium rosenbergii*. Malecha et al. (1980) found that there appears to be little divergence of performance between the ubiquitously cultured Anuenue stock in Hawaii and an experimental one recently derived from the former's wild relative. This means that very little genetic progress has been made in the years that *M. rosenbergii* has been cultured.

Changes will have to occur in the current practice in order to improve stock rather than just propagating it. Since the management system for most farms involves seine harvests and multiple stocking, there is no way to establish the age of any prawn collected from the pond and no way to control the mating of the broodstock female. Because of this there is no control over the breeding value of the parents. Breeding value is broadly defined as the genetic worth for a specific trait of an animal's genotype. No other modern agricultural system relies on such "natural service" in this manner.

The Multi-Stage Rotational S-H System could easily accommodate a proper assessment of the breeding value of individuals because fast-growing animals could be continually identified during the size-grading operations.

Accountability and nursing

There is a wide variation in post-stocking mortality which cannot be detected by early pond sampling (Sarver et al., 1980); consequently, early corrective measures are not possible. With the Rotational S-H System an accurate assessment of population size is possible at

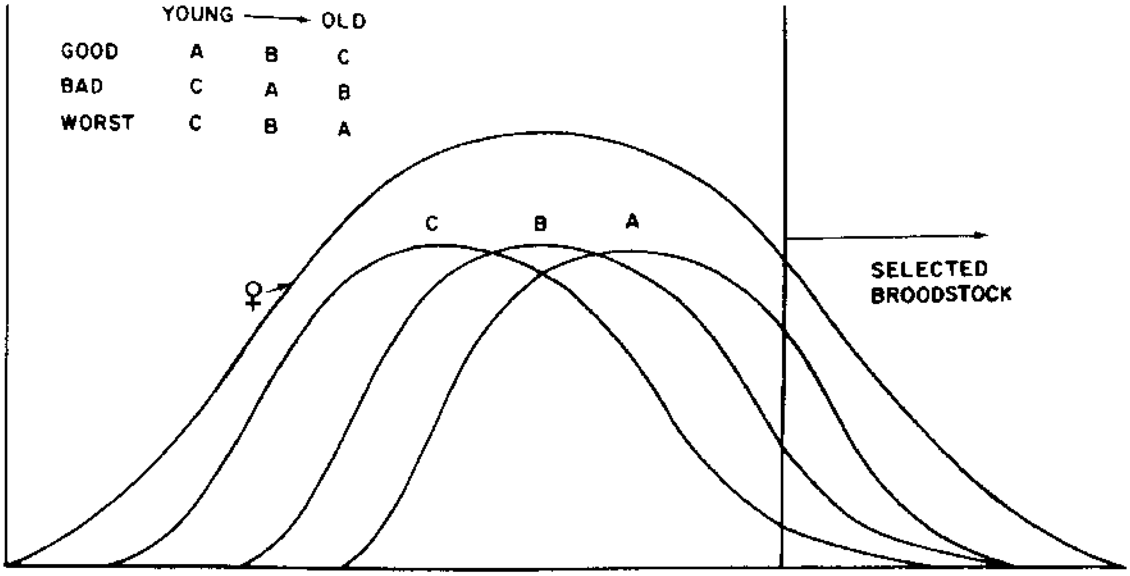


Figure 10. Three possible interpretations of a pond size-frequency distribution of females cultured in ponds with continual harvesting by seining, some of which are removed for broodstock. Underlying distributions A, B, and C represent different age classes. Genetically inferior broodstock could be selected if culled females represent older, slower growing individuals (from Malecha et al., 1980).

the end of each stage. Moreover, early mortality may be much lower in this system because stage I "water" can be predator-free and "fresh" and can easily accommodate a nursery phase. A number of laboratory-level studies on the behavior and production capacities of juvenile prawns reared in high densities immediately following larval to juvenile metamorphosis have been completed (Eble et al., 1977; Foster and Beard, 1974; Kneale and Wang, 1979; Mancebo, 1978; Sandifer and Smith, 1975, 1977; Segal and Roe, 1975; Smith and Sandifer, 1975, 1979a; Willis et al., 1976). These studies clearly show the potential for incorporating a high density nursery phase into prawn farming which would considerably improve the accountability of stock. The nursery operation can be incorporated as the first stage of the multi-stage rotational system. Specialized nursery installations using habitats and shelters could be used to provide better protection and improved growth conditions for the fry. In areas characterized by year-round warm climate, such as in Hawaii, the cost of a nursery will have to be justified by the increased survivability of small juveniles.

Theoretical Aspects for Unisex Culture for Increased Product Value

This section includes a discussion of theoretical arguments for the implementation of unisex culture for the culture of males and females in skewed sex ratios. Unisex culture *per se* is of itself an alternative management system and may be practiced with or without the Multi-Stage Rotational S-H System but can easily be handled in the latter. Moreover, if heterogeneous individual growth develops within unisex populations, then the Multi-Stage Rotational S-H System *vis a vis* size grading would be the system of choice.

Besides the obvious sexual dimorphic mean growth rate differences (Figure 9), there may be an even more compelling motivation for managing sexes separately; sexual dimorphic growth has a large effect on the size-class product value distribution due to the highly depensated male size-frequency distribution. This was shown by Smith et al. (1980) who analyzed the effect of sexual dimorphism on processing yields and the product value size-frequency distribution. Table 1 is modified from Smith et al. (1980) and is presented to illustrate the fact that the major product value characteristics of the sexual dimorphic size-frequency distribution should be considered in any effort to study the development and management of sexual dimorphic growth. Table 1 shows that the high price paid for large tails (i.e., low count kg^{-1}) accounts for the fact that male product value exceeds female product value in a mixed-sex population. Males account for about 56 percent of the total product value based on tails (kg^{-1}). As seen in the table, the price for each tail count category drops non-linearly over the range of tail count values for the prawn population sampled. The highest product value for males is contributed by a relatively few very large animals (e.g., see 24 to 55 tail count groups) that represent a clear modal group (group "A" in Figure 4) in a bimodal size-frequency distribution. One can see that the percentage of contribution to the product value is highest in the high modal group. The top three tail count groups account for 47.6 percent of the total male product value.

There are several things to note about the differences between the size-frequency distribution of male and female *M. rosenbergii* and their product values. First, even though the mean size of males exceeds that of females, the female median is greater. This means that most females, on an individual basis, are larger than males. Second, the product value of the females, despite their overall smaller mean size, is still quite high ($2,124 vs. $2,678 for males). This suggests that if total female production could be increased over that of males, then total female product value may be greater despite smaller individual mean size. This could be accomplished if it were possible (e.g., with monosex stocking) to increase the standing crop of females without a resultant decrease in mean size. The working hypothesis is that either unisex female or unisex male populations can increase the standing crop by increased densities, but that in a male population these increases are not uniform for all size-classes. The opposite is true of females; each size class will uniformly increase. The net effect will be that female-dominated populations will have an increased product value over unisex male or female ones and over bisexual populations.

The following is offered as a possible scenario. Looking at Table 1, an assumption will be made that the density of an all-female population can be increased by 100 percent. If the above is correct then each female size-class will increase by 100 percent and there will be a similar net increase in their product value (from $2,124 to $4,248). What will happen in an all-male population if the density is increased by 100 percent? According to the hypothesis, only the smaller size-classes will increase by this amount; the larger modal class containing the bull males will increase at a lower percentage. If it is assumed that only the smaller (67 to 176) male tail size-classes will increase by 100 percent, the increase in product value will only be from $911 to $1,822. It can easily be shown that the product value of an all-male population stocked at twice the density of the males in a mixed-sexed population will be below a similar all-female population unless the high modal group increases its biomass by 37 percent. Therefore, the top size-classes would have to increase their product value from $1,767 to $2,426 in order for the male product value to equal that of the female. Can this be done? If the high modal group is behaviorally as well as food resource (biomass) limited, then this may not occur and the product value of an all-male population will not exceed that of an all-female or female-dominated one.

Is the product value of a dense population of all females maintained at a higher CSC (after Hepher, 1978) greater than the product value of a mixed-sex population at that same CSC? Data from Table 1 indicate that the answer may be "yes," but the final answer will depend on the price structure for the different weight classes and also on the relationship of the price structure to biomass. The price structure given in Smith et al. (1980) and Table 1 is for a specific U.S. mainland locale in 1978 and will change from time to time. It is clear however that the biological and economic feasibility of increasing the product value of an all-female population beyond that of a bisexual population should be investigated.

High density all-female population

Another possibility is that the CSC for an all-female population exceeds that for a bisexual population. Such would be the case if there were male-specific resource limitations. The concept of CSC is usually related to food as the resource which limits growth beyond a certain biomass and density (Hepher, 1978). However, the results of Malecha et al. (1981) suggest that growth rate can be reduced despite *ad libitum* food and space. It may be that the bisexual CSC value (assumed to be around 200 g m^{-2}) is influenced by male behavioral mechanisms that, once removed, would allow an all-female CSC to reach new levels. Even a modest percentage increase in an all-female population CSC may increase its product value enough to exceed that of a bisexual population.

All-male populations

It is tacitly assumed that if the technology is developed for easily creating unisex broods (either male or female) that commercial culture would favor all-male populations. Consider what would have to happen for this to be true. As with the above discussion first assume that there is a species-specific (i.e., prawn) CSC regardless of sex. Consequently, the biomass difference between a bisexual and a "females-removed" population would have to be made up from an increased density of males. The key question is, how will these individuals distribute themselves in a bimodal male size-frequency distribution?

In dealing with the "worst" case scenario, suppose these were two different CSCs for the male modal groups and that the higher modal group is more resilient to change. Consequently, a disproportionate number of the male individuals stocked to take up the slack from the "missing" females will be shunted in the lower male modal group. One can readily see from Table 1 that the product value of that group is much lower than that of the female group. Hence, there may be no economic advantage to unisex stocking of males despite the overall greater mean size and biomass of males over females in a mixed population.

There are two main arguments which suggest that this scenario will occur.

The energetics argument. The CSC may be dimorphic in an all-male population: one level for the high modal group and another for the low modal group. Hepher (1978) showed how the CSC varies for different weight classes: large animals devote a greater percentage of their nutritive intake to maintain metabolism and the energetic cost of digestion rather than growth *per se*; the opposite is true for smaller animals. The overall effect is that the CSC of larger animals is reached at a lower density (for a given growth rate) than for small individuals. Furthermore, the intrinsic growth rate of males in the higher modal group is much greater than those in the lower modal group; hence, their CSC will be reached faster due to this fact alone. On the other hand, the lower modal group will reach its CSC not because of an increased relative growth, but because of the increased biomass due to the greater numbers of males occupying the "missing female" niche. It is hypothesized that the net effect will be greater numbers of males in the lower modal group so that an all-male population will have a lower product value than a bisexual population because the product value of females is greater than the low modal male group.

It should be noted that the discussion of critical standing crop in Hepher (1978) is in terms of different size groups representing different populations and not modal groups from the same population.

The behavioral argument. Let us assume that food and the space to eat it in are not limiting within the density range represented by the higher modal group. The limitation could have a behavioral etiology and consequently the CSC of the higher modal group may be even more resilient to change than it would be if it were limited by food only. For example, the males in higher modal groups may be "dominant" ones which require a larger territory than smaller ones. If this territorial behavior is evolutionarily fixed regardless of the amount of resources, then the CSC of the higher modal group is likewise "fixed." It is assumed that the territorial boundaries are between dominant high modal group animals and that lower modal group males (and females) can move about freely among territorial spaces. The economic implication of this is that the product value of the higher modal group cannot be increased in an all-male population beyond what it is for a bisexual one.

It is likely that some combinations of the two scenarios apply to pond populations of *M. rosenbergii* in sort of a feedback loop—behavioral interactions restrict territorial movement and contribute to the development and maintenance of a high modal group which is restricted in its CSC value by intrinsic behavioral factors and the energetic cost of metabolism and nutrition.

Finally, an all-male population will be either bimodal or skewed to the right regardless of the presence of females. If it is assumed that the large size of dominant males is largely due to sexual selection, evidence from other species (Darwin, 1874) and observation on the development of secondary sexual characteristics in isolated male prawns suggest that the presence of females is not required for the characteristics to develop.

Female-dominated populations

Another possibility is to stock heavily with females and a smaller number of males. If assumptions are correct regarding behavioral limitation of male CSC and female tolerance to higher densities, then using this strategy it may be possible to recover the "high" product value of high modal group males and the product value of females which is greater than lower modal group males. This presupposes that light stocking of males will result in a unimodal distribution which is equivalent to or near the product value of the high modal group. This needs to be verified experimentally.

All in all the sexual dimorphic size-frequency distribution that develops in prawn populations is so prominent and economically significant that techniques and technologies must be developed to manage it better. It is suggested that researchers and culturists begin testing the feasibility of creating and rearing monosex broods.

CONCLUSIONS

The Continuous Stocking and Harvesting System introduced by the Anuenue Fisheries Research Center (Fujimura, 1974; Malecha, 1977) has contributed substantially to the successful establishment of the fledgling prawn industry because continuous marketing and simplicity of all aspects of production were initially of overwhelming importance. However, the time has come to critically examine *a priori*, and then empirically, more efficient alternatives.

The use of the Multi-Stage Rotational S-H System will improve survival, accountability, total production, and labor economy, and perhaps will provide extra income from polyculture, differential marketing of males and females, and size-grading. For an existing farm the transition from the Continuous S-H System to the Multi-Stage Rotational S-H System can be gradual and does not need to involve substantial risks because it does not require any strong commitment to a given formula to densities, stage durations, etc.; such variables can be easily changed as knowledge resulting from research efforts improves. In addition, sorting and grading equipment and methods, including a new pond design, must be devised for transferring and size-grading of prawns; ponds must have a pump to facilitate harvesting by draindown and a pump which does not cause damage to the prawns will be needed for transferring animals between ponds. Finally, alternative technologies for more efficient managing sexual dimorphic growth must be explored since there are sufficient *a priori* reasons why monosex culture may be more profitable than culturing the sexes together.

ACKNOWLEDGMENTS

We thank Amy Dicksion, Jacqueline Glipa, and Deb Ciampa for clerical and editorial aid in preparation of this manuscript.

LITERATURE CITED

Bardach, J.E., J.H. Ryther, and W.O. McLarney. 1972. *Aquaculture: The Farming and Husbandry of Freshwater and Marine Organisms*. New York: Wiley-Interscience.

Brick, R.W., and R.R. Stickney. 1979. Polyculture of *Tilapia aurea* and *Macrobrachium rosenbergii* in Texas. *Proc. World Maric. Soc.* 10:222-228.

Brody, S. 1945. *Bioenergetics and Growth*. New York: Reinholt Publishing Company.

Brody, T., D. Cohen, A. Barnes, and A. Spector. 1980. Yield characteristics of the prawn, *Macrobrachium rosenbergii*, in temperate zone aquaculture. *Aquaculture* 21:375-385.

Darwin, C. 1874. *The Descent of Man, and Selection in Relation to Sex*. 2nd ed. New York: Hurst.

Eble, A.F., M.C. Wans, N. Delais, and N.E. Stolpe. 1977. Maintenance of broodstock, larval rearing and nursery techniques used to grow *Macrobrachium rosenbergii* in waste-heat discharge waters of an electric generating station in New Jersey (U.S.A.). Third meeting I.C.E.S. Working Group on Mariculture, Brest, France, May 10-13, 1977. *Actes de Colloques du C.N.E.X.O.* 4:233-245.

Foster, J.R.M., and T.W. Beard. 1974. Experiments to assess the suitability of nine species of prawns for intensive culture. *Aquaculture* 3:355-368.

Fujimura, T. 1974. *Development of a prawn culture industry in Hawaii*. National Marine Fisheries Service, N.O.A.A., Dept. of Commerce.

Fujimura, T., and H. Okamoto. 1972. Notes on progress made in developing a mass culturing technique for *Macrobrachium rosenbergii* in Hawaii. In *Coastal Aquaculture in the Indo-Pacific Region*, ed. T.V.R. Pillay. London: Fishing News (Books) Ltd.

Ghiselin, M.T. 1974. *The Economy of Nature and the Evolution of Sex*. Berkeley: University of California Press.

Gibson, R.T., and J.K. Wang. 1979. A prawn population management model. *Trans. Amer. Soc. Agric. Engin.* 22(1):207-214.

Gunnes, K. 1976. Effect of size grading young Atlantic Salmon (*Salmo salac*) on subsequent growth. *Aquaculture* 9:381-386.

Hepher, B. 1978. Ecological aspects of warm-water fishpond management. In *Ecology of Freshwater Fish Production*, ed. S.D. Gerlsing. New York: John-Wiley & Sons.

IFS (International Foundation for Science). 1980. Provisional Report No. 9, Proceedings of the Giant Prawn Conference, Bangkok, Thailand, June 15-21, 1980. Sibgllegatan 47, S-114 42, Stockholm, Sweden. ISBN:91-857, 98-08-8.

Kneale, D., and J.K. Wang. 1979. A laboratory investigation of *Macrobrachium rosenbergii* nursery production. *Proc. World Maric. Soc.* 10:359-368.

Lee, S.R. 1979. *The Hawaiian prawn industry: a profile*. Aquaculture Development Program, Department of Planning and Economic Development, State of Hawaii, Honolulu.

Magnuson, J.J. 1962. An analysis of aggressive behavior growth and competition for food and space in Medaka (*Oryzius latipes* Pisces, Cyprinodontidae). *Can. Journ. Zoo.* 40:313-363.

Malecha, S.R. 1977. Genetics and selective breeding. Chap. XIV. In *Shrimp and Prawn Farming in the Western Hemisphere*, ed. J.A. Hanson and H.L. Goodwin. Stroudsburg, (Pennsylvania): Dowden, Hutchinson and Ross, Inc.

Malecha, S.R. Genetic and environmental sources of growth pattern variation in the cultured freshwater prawn, *Macrobrachium rosenbergii. Proc. World Maric. Soc.*, in press.

Malecha, S.R., D. Sarver, and D. Onizuka. 1980. Approaches to the study of domestication in the freshwater prawn, *Macrobrachium rosenbergii*, with special emphasis on the Anuenue and Malaysian stocks. *Proc. World Maric. Soc.* 11:500-528.

Malecha, S.R., D.H. Buck, R.J. Baur, and D. Onizuka. 1981. Polyculture of the freshwater prawn *Macrobrachium rosenbergii*, Chinese and common carps in ponds enriched with swine manure. I. Initial trials. *Aquaculture* 25:101-116.

Mancebo, U. 1978. Growth in tank reared populations of the Malaysian prawn, *Macrobrachium rosenbergii* (de Man). *Proc. World Maric. Soc.* 9:83-90.

Moav, R., and G. Wohlfarth. 1973. Carp breeding in Israel. In *Agricultural Genetics: Selected Topics*, ed. R. Moav. New York: John Wiley & Sons.

Moav, R., and G. Wohlfarth. 1974. Magnifications through competition of genetic differences in yield capacity in carp. *Heredity* 33:181-202.

Moav, R., G. Wohlfarth, G.L. Schroeder, B. Hulata, and H. Barash. 1977. Intensive polyculture of fish in freshwater ponds. I. Substitution of expensive feeds by liquid cow manure. *Aquaculture* 10:25-43.

Nakamura, N., and S. Kasahara. 1955. A study on the phenomenon of the Tobi koi or shoot carp. I. On the earliest stage at which the shoot carp appears. *Bull. Jpn. Soc. Sci. Fish.* 21:73-76. Translated in G.W. Wohlfarth (1977) *Bamidgeh* 29(2):41-44.

Nakamura, N., and S. Kasahara. 1956. A study on the phenomenon of the Tobi koi or shoot carp. II. On the effect of particle size and quantity of the food. (In Japn.). *Bull. Jpn. Soc. Sci. Fish.* 21(9). Translated in G.W. Wohlfarth (1977) *Bamidgeh* 29(2):44-47.

Nakamura, N., and S. Kasahara. 1957. A study on the phenomenon of the Tobi koi or shoot carp. III. On the result of culturing the modal group and the growth of carp fry reared individually. (In Japn.). *Bull. Jpn. Soc. Sci. Fish.* 22(1). Translated in G.W. Wohlfarth (1977) *Bamidgeh* 29(2):48-52.

Nakamura, N., and S. Kasahara. 1961. A study on the phenomenon of the tobi-koi or shoot carp. IV. Effects of adding a small number of larger individuals to the experimental batches of carp fry and of culture density upon the occurence of shoot carp. *Bull. Jpn. Soc. Sci. Fish.* 27(11). Translated in G.W. Wohlfarth (1977) *Bamidgeh* 29(2): 53-56.

Peebles, J.B. 1977. Behavioral factors influencing movement, dispersion of mortality in *Macrobrachium rosenbergii*. Ph.D. dissertation, Department of Zoology, University of Hawaii, Honolulu, pp. 1-27.

Polovina, J.J., and H. Brown. 1978. A population dynamics model for prawn aquaculture. *Proc. World Maric. Soc.* 9:393-404.

Ricker, W.E. 1975. Computation and interpretation of biological statistics for fish populations. *Bull. Fish. Res. Can.* 191:232-233.

Ryther, J.H., L.D. Williams, and D.C. Kneale. 1977. A freshwater waste recycling aquaculture system. *Florida Sci.* 40(2):130-136.

Sandifer, P.A., and T.I.J. Smith. 1975. Effects of population density on growth and survival of *Macrobrachium rosenbergii* reared in recirculating water management systems. *Proc. World Maric. Soc.* 6:45-54.

Sandifer, P.A., and T.I.J. Smith. 1977. Intensive rearing of post larval Malaysian prawns, *Macrobrachium rosenbergii*, in a closed cycle nursery system. *Proc. World Maric. Soc.* 8:225-235.

Sarver, D., S. Malecha, and D. Onizuka. 1980. Possible sources of variability in stocking mortality in post larval *Macrobrachium rosenbergii*. Paper presented at Giant Prawn Conference, June 15-21, 1980, at Bangkok, Thailand.

Segal, E., and A. Roe. 1975. Growth and behavior of post juvenile *Macrobrachium rosenbergii* (de Man) in close confinement. *Proc. World Maric. Soc.* 5:67-88.

Shang, Y.C., and T. Fujimura. 1977. The production economics of freshwater prawn (*Macrobrachium rosenbergii*) farming in Hawaii. *Aquaculture* 11:99-110.

Singholka, S., M.B. New, and P. Vorasayan. 1980. The status of *Macrobrachium* farming in Thailand. *Proc. World Maric. Soc.* 11:60-72.

Smith, T.I.J., and P.A. Sandifer. 1975. Increased production of tank-reared *Macrobrachium rosenbergii* through use of artificial substrates. *Proc. World Maric. Soc.* 6:55-61.

Smith, T.I.J., and P.A. Sandifer. 1979a. Development and potential of nursery systems in the farming of Malaysian prawns, *Macrobrachium rosenbergii*, (de Man). *Proc. World Maric. Soc.* 10:369-384.

Smith, T.I.J., and P.A. Sandifer, 1979b. Observation on the behavior of the Malaysian prawn, *Macrobrachium rosenbergii*, (de Man), to artificial habitats. *Mar. Behav. Physiol.* 6:131-146.

Smith, T.I.J., P.A. Sandifer, and M.H. Smith. 1978. Population structure of Malaysian prawns, *Macrobrachium rosenbergii* (de Man), reared in earthen ponds in South Carolina 1974-1976. *Proc. World Maric. Soc.* 9:21-38.

Smith, T.I.J., P.A. Sandifer, W.E. Jenkins, and A.D. Stokes. Effect of population structure at stocking and density on production and economic potential of prawn (*Macrobrachium rosenbergii*) farming in temperate climates. *Proc. World Maric. Soc.*, in press.

Smith, T.I.J., W. Waltz, and P.A. Sandifer. 1980. Processing yields for Malaysian prawns and the implications. *Proc. World Maric. Soc.* 11:557-569.

Soller, M., and R. Moav. 1973. Broiler breeding: practice and perspectives. In *Agriculture Genetics: Selected Topics*, ed. R. Moav. New York: John Wiley & Sons.

Symons, P.E.K. 1971. Behavioral adjustment of population density to available food by juvenile Atlantic salmon. *J. Anim. Ecol.* 40:569-587.

Tang, Y.A. 1970. Evaluation of balance between fishes and available fish foods in multispecies fish culture ponds in Taiwan. *Trans. Amer. Fish. Soc.* 99:708-718.

Tapiador, D.D., H.F. Henderson, M.N. Delmendo, and H. Tsutsui. 1977. *Freshwater fisheries and aquaculture in China.* FAO Fish. Tech. Paper No. 168.

Trivers, R.L. 1972. Parental investment and sexual selection. In *Sexual Selection and the Descent of Man*, ed. B. Campbell. Chicago: Aldine.

von Bertalanffy, L. 1938. A quantitative theory of organic growth. *Hum. Biol.* 10(2):181-213.

Willis, S.A., and M.E. Berrigan. 1978. Effects of fertilization and selective harvest on pond culture of *Macrobrachium rosenbergii* in Central Florida. Completion report, U.S. Dept. of Commerce, N.O.A.A., N.M.F.S., PL 88-309, No. 2-298-R-I, Job 3B. Florida Dept. of Natural Resources, Marine Research Laboratory, 100 Eight Ave., S.E., St. Petersburg, Florida, 33701.

Willis, S.A., R.W. Hagood, and G.T. Eliason. 1976. Effects of four stocking densities and three diets on growth and survival of postlarval *Macrobrachium rosenbergii* and *M. acanthurus*. *Proc. World Maric. Soc.* 7:655-665.

Wohlfarth, G., and R. Moav. 1972. The regression of weight gain on initial weight in carp. I. Methods and Results. *Aquaculture* 1:7-28.