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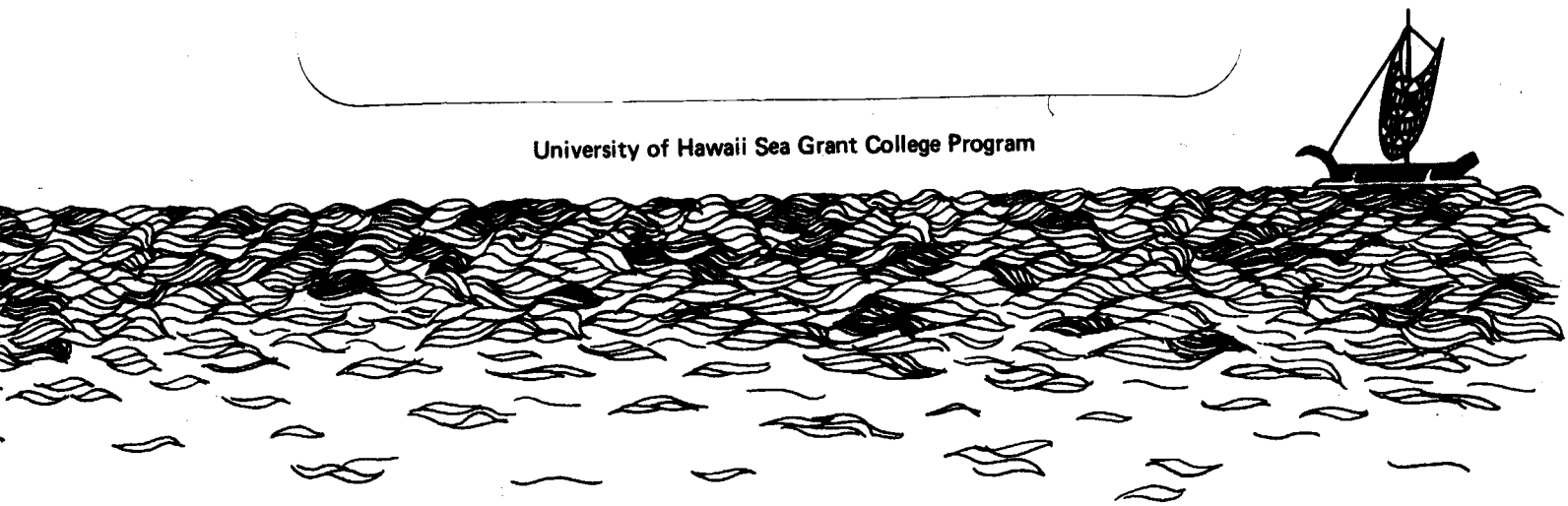

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PROSPECTS FOR DOMESTICATION AND BREEDING OF MARINE SHRIMP

Spencer R. Malecha and Dennis Hedgecock

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About the Authors

Spencer R. Malecha is president and CEO of the Hawaii Aquaculture Company, Inc., Kaimuki Technology Center, Honolulu, Hawaii, and a professor in the Aquaculture Research Program, University of Hawaii, Honolulu, Hawaii.

Dennis Hedgecock is an associate geneticist with the Aquaculture and Fisheries Program, Department of Animal Sciences, University of California, Davis, Bodega Marine Laboratory, Bodega Bay, California, and vice president of Research and Development of the Hawaii Aquaculture Company, Inc.

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INTRODUCTION

Economic Importance of the U.S. Marine Shrimp Industry

Demand in the United States for marine shrimp, together with declines in yields from traditional fisheries, has created a large trade deficit in this commodity. The U.S. shrimp fishery landings in 1986 were 182,000 metric tons of shell-on headless shrimp compared to 223,000 metric tons of imported product (U.S. Department of Commerce 1988). Of the countries importing shrimp to the United States, Ecuador leads the way followed closely by Mexico. A majority of the shrimp from Ecuador is now aquacultured in ponds seeded with postlarvae, either captured from the wild or reared in hatcheries from the spawns of wild-caught gravid females. In almost all cases shrimp aquaculture is a very extensive, low-input, pond operation. A higher input pond culture of marine shrimp in the southern continental United States (Chamberlain, Haby, and Miget 1986), Hawaii, and the U.S.-affiliated Pacific islands holds potential for increasing U.S. shrimp production using improved husbandry methods.

Advances in U.S. Culture Industry: Closed Populations

Advances in the ability to promote sexual maturation of penaeid shrimp have led in the 1980s to the development of a handful of closed or nearly closed populations in the commercial shrimp culture industry (Sandifer and Lynn 1980). Closure of cultured breeding populations to the immigration of animals from the wild is a significant milestone on the road to domestication. This advance mandates the development of breeding programs that can avoid the pitfalls of closed populations and at the same time can fully and rapidly exploit opportunities for genetic improvement. However, breeding programs for marine shrimp require long-term commitments to the housing and maintenance of experimental breeding populations as well as to facilities dedicated to the development of the technology and testing of genetic groups. The expense of such commitments has thus far stymied the emergence, in the United States or elsewhere, of private or public research programs specifically addressing domestication and breeding.

The La Jolla Workshop

Both the U.S. Department of Agriculture and the U.S. Department of Commerce National Sea Grant College Program, identify marine shrimp as a prime target for commercial development in the United States and recognize genetic improvement as an integral part of this national effort (National Aquaculture Development Plan 1983). Thus, under the sponsorship of the Sea Grant College Programs of Hawaii, Texas, and California, a workshop was convened at the Scripps Institution of Oceanography, La Jolla, California, January 24–25, 1986, for the purposes of: (1) documenting the need for a marine shrimp domestication and breeding program; (2) outlining the scope, components, and costs of such a program; (3) exploring the opportunities for the development of a coordinated public and private

program; and (4) suggesting how such a program might be established. The workshop was well attended by representatives of public agencies, research scientists, and representatives from private industry.

The workshop format consisted mainly of a roundtable discussion of agenda topics. Free and, at times, spirited exchange of information among participants characterized the first day's morning and afternoon plenary sessions. In the evening session, participants were divided into three panel groups — academic, industry, and public agency. During the concluding morning session of the second day, reports of panel discussions were given and participants forged a consensus concerning the future of marine shrimp breeding (see "Conclusions").

Format of Report

A general overview of the aquacultural genetics of marine shrimp culture — the diversity of species cultivated and of husbandry systems that exist, consideration of which systems warrant commitment of resources to genetic improvement, and a discussion of the dangers and opportunities posed by the reproductive isolation of cultured populations — is presented in the next section. Actions required for the development of commercial breeding programs are then listed and discussed in the first part of the third section. Listing the desiderata of a shrimp breeding program exposes gaps in knowledge or technology that constrain the development of commercial domestication and breeding. The second part of the third section then addresses research and experimental methods needed to remove the key constraints on marine shrimp breeding. Finally, in the last section, "bricks-and-mortar" requirements for research facilities are stated and justified, and the roles of public agencies and industry in enabling the development of a coordinated program are discussed. Throughout the second and third sections, we emphasize how the cultivation and breeding of marine shrimp differ from the husbandry and breeding of traditional farm animals (Harris, Stewart, and Arboleda 1984; Shultz 1986a).

Though departing from the order of topics in the workshop agenda, the authors hope to have captured the spirit of the discussions as well as the substance of the consensus reached by workshop participants.

THE AQUACULTURAL GENETICS OF MARINE SHRIMP

Diversity of Species and Culture Systems

Many species of marine shrimp are cultured in diverse ways throughout the tropical and subtropical regions of the world. The more important cultured species are: *Penaeus monodon*, *P. japonicus*, *P. penicillatus*, *P. semisulcatus*, and *Metapenaeus ensis* from the western Pacific Ocean and Indian Ocean, Red Sea, and Mediterranean Sea; and *P. stylirostris*, *P. vannamei*, *P. braziliensis*, *P. setiferus*, and *P. schmitti* from the eastern Pacific Ocean, western Atlantic Ocean, and Caribbean Sea. A major difference between the farming of these

shrimp and the farming of livestock is that the vast majority of penaeid shrimp produced worldwide are the offspring of adults collected from the wild. The U.S. culture industry is less reliant upon wild-caught brood stock, having developed nearly closed populations of *P. vannamei* and *P. stylirostris*, which were chosen on the basis of their superior pond survivals, growth rates, and reproductive performances in preliminary comparisons of species.

The most common husbandry system, pond farming, may be subdivided into extensive and semiextensive types depending upon the degree of water quality management, whether an indigenous or exotic species is used, density of stocking, the level and type of feeding, and yield. In contrast to pond culture, the more recently developed, high-density, raceway culture of shrimp is unquestionably intensive. Production from extensive, semi-extensive, and intensive culture systems differs by orders of magnitude. All three culture systems are currently operating in the United States.

The undomesticated nature of cultured populations, the diversity of species and husbandry systems used to farm these animals, and the vertical integration of the industry such that the culturist is breeder, grower, and marketer are major reasons a breeding program for marine shrimp cannot simply mimic programs for genetic improvement of terrestrial animal breeding.

Systems That Warrant Genetic Improvement

Extensive shrimp culture as practiced in most tropical areas or in the fallow coastal rice fields of South Carolina does not seem to justify genetic improvement. Yields from these systems could perhaps be more readily increased through the application of improved pond management practices, but even this may not be economically feasible. More importantly, because extensive systems often communicate with native habitat, efforts to improve yields by stocking selectively bred shrimp would be diluted by immigration of wild larvae and would, in addition, carry the unevaluated risk of tampering with the genetic structure of natural populations. Extensive pond culture of marine shrimp in tropical countries appears to be evolving toward the semiextensive level with increasing use of hatcheries and pond management. While genetic improvement in these semiextensive systems is probably not warranted today, it may be mandated by future developments.

Semiextensive and intensive marine shrimp culture systems in the United States, on the other hand, do appear to warrant the development of breeding programs because: (1) they are capital intensive businesses that are sensitive to fluctuations in costs of production; (2) they can be mathematically described so that the economic importance of changes in management or in biological traits can be precisely evaluated; (3) they are built largely on nonindigenous species so that brood stock must be maintained to produce seed; and (4) they rely on brood stocks kept as closed or nearly closed populations.

Dangers and Opportunities of Closed Populations

Domestication Selection

Closed breeding populations have advantages and disadvantages. They provide for genetic improvement of stocks either through natural selection or selective breeding, but they carry the risks of genetic deterioration in yield or reproductive performance because of inbreeding or conflicts between artificial and natural selection. As emphasized by Doyle (1983), selection for domestication may be intense when cultured populations are first isolated from their wild relatives. Domestication selection is most likely at work in closed marine shrimp populations that have been established by the culture industry. The consequences of domestication selection are not easily predicted as both the dynamic state of a newly isolated gene pool under intense selective pressures and the constantly improving husbandry practices of the culturist together make up a co-evolving system that is far from equilibrium. Yields or reproductive performance should increase through domestication selection (Doyle and Hunte 1980). Several culturists at the workshop reported their impressions that performance of closed populations was improving. What part of this improvement is genetic and what part is the result of improved husbandry is unknown. The shrimp farmer must guard against genetic deterioration of a closed population. A particularly insidious potential cause of deterioration can arise from the opposition between goals of natural selection and goals of an unwitting breeder. For example, deterioration of reproductive performance of brood stock has been documented in Indian carps as the result of artificial selection for large body size (Eknath and Doyle 1985).

Inbreeding and Effective Population Size

Inbreeding, which can arise either from nonrandom matings among related individuals or from restrictions of population size, is also a potential cause of declining performance in closed populations. Lowered performance may be caused by the expression of recessive lethal or semilethal genes that are brought together in homozygous condition in the inbred individuals, by a metabolic or physiological inferiority of homozygotes relative to heterozygotes (as inferred for oysters [Singh and Zouros 1981; Foltz, Newkirk, and Zouros 1983; Koehn and Shumway 1982]), or by genetic drift in small populations which allows the fixation of inferior genes or resists the directional forces of artificial selection. Thus the extent to which nonrandom consanguinous matings and small population sizes reduce genetic variance in closed commercial shrimp populations needs to be evaluated. The large fecundities of marine shrimp (up to 100,000 or 200,000 eggs per spawn) create the potential for inbreeding because a few females can produce enough seed to stock an entire commercial growout facility. Moreover, lack of pedigree information for individual shrimp in production systems (see below) leads to a high probability that siblings are chosen as brood stock.

At the workshop, representatives of commercial shrimp farms provided information on the number of brood stock used in maintaining populations that have been closed or partially isolated for about three generations (Table 1). Because of the importance of effective

TABLE 1. GENETICALLY EFFECTIVE POPULATION SIZES OF TWO REPRESENTATIVE POPULATIONS OF MARINE SHRIMP IN THE U.S. COMMERCIAL CULTURE INDUSTRY

Culture system	Intensive Raceway	Semiextensive pond
Location	Hawaii	Texas
Species cultured	*P. stylirostris*	*P. vannamei, P. stylirostris*
Source of stock	Mexico	Panama?
No. of generations isolated	~3	~3
No. of male brood stock	5–20	100–500
No. of female brood stock	40–60	400–700
Effective no. of brood stock (N)*	18–60	320–1,167
Genetically effective no. (N_e)†		
If $V_k = 5.0$	11–35	183–667
If $V_k = 50$	1–4.2	22–82
If $V_k = 100$	—	12–46
Rate of introduction from wild per generation	10%	5%

*Calculated using equation 1
†Calculated using effective number of brood stock, N, and equation 2

population size to the genetics of these cultured populations, we estimate genetically effective numbers (N_e) for these populations (Crow and Kimura 1970).

The first restriction on population size comes from the use of unequal numbers of males and females in maturation/mating tanks, the effect of which is given by:

$$N = 4MF/(M + F) \quad (1)$$

where M and F are the numbers of males and females that actually contribute offspring to the next generation of breeders. Because commercial culturists often use fewer males than females in maturation tanks, the effective number of brood stock is much less than the sum of $M + F$ and ranges from 18 to 60 in the intensively cultured population to about 300 to 1,000 for the semiextensively cultured population. Thus, inequality in sex ratio probably does not significantly constrain the effective sizes of closed commercial populations.

Unequal contribution by brood stock to the next generation is perhaps a more serious threat to the maintenance of sizeable closed populations. If we assume the size of the closed breeding population to be stable, then each female must leave two offspring on average to replace herself and her mate. Variation in the number of offspring per female, k, however, can reduce the population size as follows:

$$N_e = (4N - 2)/(V_k + 2) \tag{2}$$

where N is the effective number of brood stock calculated from equation 1 and V_k is the variance in the number of a female's offspring that reach reproductive maturity and are included in the brood stock of the next generation. $N_e = N$ when there is random sampling of gametes and V_k is the binomial variance, $2(N - 1)/N$. For the Ns calculated above, the binomial variance is approximately 2.0. However, the large fecundities of marine shrimp, in contrast to domestic farm animals, make it numerically possible for V_k to be many times — even orders of magnitude — larger than 2.0. In the most extreme case, one female may contribute all the shrimp that are selected for brood stock in the next generation so that the effective population size is closer to two rather than hundreds, as might be thought.

Such a case has recently been confirmed for a population of *P. japonicus* maintained by 300 brood stock of each sex since the second generation after introduction into Italy from Japan. Using electrophoretic methods to quantify genetic variability, Sbordoni, LaRosa, Mattoccia, Sbordoni, and DeMatthaeis (1987) have documented a decline in variation over seven generations that is as extreme as that expected in a population having an N_e between two and four. A parallel decline in the hatching success of this stock gives further evidence of inbreeding depression. Moreover, both Sbordoni et al. (1987) and Laubier, Pasteur, and Moriyasu (1984) have independently reported significant fluctuations in the allelic frequencies of different lots of postlarvae obtained from Japanese hatcheries, indicating that even these very sophisticated shrimp hatcheries are not immune to the problem of sampling errors in broodstock performance.

How variable are the reproductive contributions of marine shrimp in commercial and genetic breeding facilities? Kawagashi, McGovern, Pavel, Ashmore, and Carpenter (1986) estimate that 25% of the females in one commercial maturation facility contribute well over 50% of the eggs spawned. Consequently, it is important for commercial culturists to be aware of individual contributions of brood stock by isolating spawning females in separate hatching tanks. On the male side, no data exist on the variance in the number of females inseminated by individual males in maturation tanks, but the worst case of one male servicing all spawners was judged to be possible by the culturists attending the workshop. Tagging and direct

observation are needed to assess variance in male reproductive success. Finally, inequality in reproductive contribution of brood stock is not limited to events in the maturation/ spawning facility but may be compounded through interbrood competition in the hatchery or nursery and nonrandom distribution of broods in growout ponds.

We have no estimates of the variance in offspring per female, V_k, in closed commercial populations of marine shrimp, but using hypothetical values of 5.0, 50, and 100 for V_k and the values of effective broodstock numbers, N calculated from equation 1, we find genetically effective population sizes can be much smaller than N even when variance in reproductive success is only moderately large (Table 1). Compare these estimates with the recommendation that N_e can be no less than 50 breeding pairs in order to slow the rate of inbreeding (Kincaid 1983). The rate of inbreeding in the intensively cultured population of *P. stylirostris* would almost certainly hamper breeding efforts. Even the potentially larger, semiextensively cultured population may not be large enough to avoid substantial inbreeding. Occasional introduction of wild shrimp to commercial breeding populations could mitigate the rate of inbreeding, but it might also retard the rate of domestication selection. Whatever its ultimate consequence, the actual rate at which wild genes are introduced into commercial populations will probably be as difficult to ascertain as the reproductive success of the individual captive brood stock.

GENETIC IMPROVEMENT PROGRAM FOR MARINE SHRIMP

A Commercial Shrimp Breeding Program

Commercial Breeding versus Genetics Research

Commercial breeding must be distinguished from research. The former is done for the purpose of improving yields and lowering costs of production while the latter is designed to gain knowledge necessary to develop breeding technologies. Commercial breeding must be cost-effective, while research may sometimes be purposively cost-ineffective as, for example, in an experiment in which high- and low-yielding lines are selected in order to gain knowledge about the genetics of yield from information on the symmetry of response to bidirectional selection. In the second part of this section the components of a commercial breeding program for marine shrimp are described. Many of the actions that ought to be taken by shrimp breeders appear at this time to be impossible or very costly due to lack of knowledge or technology (Table 2). In the second section, the research program required to supply the information and tools needed for commercial breeding actions is described.

Components of a Shrimp Breeding Program

The breeding program described here is patterned after the discussion of Harris et al. (1984) and Shultz (1986b) with modifications to accommodate the unique characteristics of shrimp, as compared to domesticated livestock. Steps in the breeding program need not be sequential but may overlap in time.

TABLE 2. COMMERCIAL PRIORITY AND RESEARCH FEASIBILITY FOR COMPONENTS OF A MARINE SHRIMP BREEDING PROGRAM AND RESEARCH PROGRAM MANDATES

Steps or Components in a Marine Shrimp Breeding Program	Status in Shrimp Programs	Commercial Priority	Degree of Difficulty	Constraints, Comments
1. Establish Breeding Goals				
Bioeconomic model	Simple descriptors only	Very high	Low	Should be researched immediately
Nutritional traits	Three levels	High	Moderate	Have to consider three energy levels in ponds
Carcass traits	Acceptable	Low at present	Low	Favorable traits already exist
Disease resistance	IHHN virus	Low	High	Try to solve by management/ quarantine
Environmental tolerances	Temperate; salinity	High	Moderate	Notable lack of facilities
Fecundity	Maintain	High	Low	Monitor for inbreeding effects
Mortality	High	Low	High	Problems solvable by management
Sex determination	Mechanisms unknown	Moderate	Moderate	Monosex culture may be important
2. Choose and Develop Stocks				
Domestication	Short domestic history	High	High	Difficult without concentration of effort, and facilities
Test wild stocks	Many species	High	Low	Moderate level of facilities needed to begin testing
Inbred stocks	None	Moderate	Moderate	Needed for research
Natural service mating	Mass mating only	High	High	High priority for "one-on-one" mating capability
Artificial insemination	Some progress	High	Moderate	Needed for other breeding program components

Table 2 — *Continued*

Steps or Components in a Marine Shrimp Breeding Program	Status in Shrimp Programs	Commercial Priority	Degree of Difficulty	Constraints, Comments
Gamete manipulation	Some work done	High	Moderate	High potential, should be researched immediately
3. Design an Animal Evaluation System				
Measurability of all relevant stages and traits	All stages can be measured	Moderate	Low	—
Experimental technology	Not developed	High	Moderate	Lack of facilities and experimental know how
4. Estimate Genetic Parameters				
Variances	No estimates	High	Moderate	Lack of facilities to do proper testing
Correlations	No estimates	High	Low	Lack of facilities to do proper testing
5. Develop Selection Criteria and Methods				
Multiple criteria selection indexing	None	Low	Low	Long-term goal only
Single criteria selection	Possible	High	High	Can be done with proper facilities
6. Design a Mating System				
Family selection	Possible	Unknown	Low	Depends on genetic test results
Individual selection	Possible	Unknown	Low	Depends on genetic test results
Line breeding	Possible	Unknown	High	Depends on genetic test results
Crossbreeding	Possible	Unknown	High	Depends on genetic test results
Avoidance of inbreeding	Possible	High	Low	Should be practiced now

1. Establish breeding goals

This action, which needs to be taken in close conjunction with step 3 (designing an animal evaluation system), is described by Harris et al. (1984) as the stating of ". . . a mathematical function or set of functions that describe the contributions of various aspects of the system . . . to its productive efficiency."

Participants in both the plenary and industry panel sessions readily identified marine shrimp breeding goals in qualitative terms, but quantitative descriptions of the economic value of breeding for those goals could not be given. Bioeconomic models of aquaculture systems, such as the one developed by Griffin, Grant, Brick, and Hanson (1984) for penaeid shrimp culture in Texas, are a start at the required quantitative statements of breeding goals. The economic value of modifying particular biological characteristics through selective breeding can be judged in the context of the economics of the entire production system by analyzing the sensitivity of production costs to changes in the variables in the models. This also requires knowledge of genetic variance components that determine response to selection, hence the potential cost of improvement (Allen, Botsford, Schuur, and Johnson 1984).

The form of a quantitative statement of breeding goals can be on two levels of complexity. The simplest level focuses on one "production unit," described by Harris et al. (1984) for most cases in terrestrial agriculture, as a single animal and its offspring or a similar unit encompassing parents and sibs. The more complex level encompasses all production units in all production sectors as well as the cost-benefit analysis of the breeding program and its evaluation and modification. This illustrates another dissimilarity between terrestrial and aquatic animal production systems. The production unit in aquaculture is not a dam and her progeny but a husbandry unit, such as a pond or raceway. As discussed later, this difference forces the marine shrimp breeder to adopt more stringent inventory management methods than are currently practiced.

Lacking quantitative statements of breeding goals, workshop participants discussed qualitative goals for production unit performance. The industry panel was emphatic that final (harvest) performance should be the focus of breeding programs. The academic panel, on the other hand, pointed out the necessity of monitoring reproductive and survival traits for signs of inbreeding depression or negatively correlated responses to artificial selection for increased yield. Performances in mating and spawning, larval rearing, nursery, and early juvenile growth ought to be objects of genetic selection programs only in so far as they affect the final product sold to market. For example, selection for increased larval growth rate would not be desirable unless there was a high correlation between larval and adult growth. If such a high correlation was found (under a program designed to address step 4, estimation of selection parameters and economic weights) then the cost/benefit ratio of selecting for early performance would be much lower than selecting for late (final production) performance. In beef cattle, for example, there is a high genetic correlation between slaughter weight and weaning weight, so that selection can be directed at the latter. Indeed, it would be desirable to establish a crustacean analog of "weaning weight" upon which to select.

Growth rate per se (biomass added per unit time) should not be the only production trait considered. Botsford and Gossard (1978) show that, if selection for increased growth rate increases metabolic rates proportionately, increases in feed and water quality management costs, at least in an intensive aquaculture system, can offset much of the apparent economic gain of the breeding program. Unfortunately, metabolic rates and nutritional efficiencies are much more difficult to measure in aquacultural systems than in agricultural systems. Nutritional performance traits in detritivorous pond-reared marine shrimp must take into account the relative roles of nutrition derived directly from applied feeds and from natural productivity stimulated either by feed application or by endogenous nutrients and energy fluxing through the pond ecosystem. Of course this would not be true of raceway reared shrimp in which genetic improvement of nutritional efficiency might resemble that practiced for agricultural systems. In neither intensive nor extensive aquacultural systems has efficiency of weight gain been precisely measured.

Carcass quality evaluation in marine shrimp presents no unusual problems. In fact, as brought out in the industry panel, extensive measurements of the ratio of nonedible to edible parts (i.e., the so-called "head-to-tail" ratio) have shown little significant phenotypic variance, hence little hope of changing this ratio through genetic selection (Lester 1983). However, the genetic basis of this important trait has not been studied, so the possibility of genetic improvement cannot be ruled out.

"Fat-to-lean" characteristics are important in meat animal breeding. For example, low back fat thickness in hogs (Gray, Tribble, Day, and Lasley 1968) and marbling scores indicative of favorable interstitial fat content and distribution in beef cattle (Cundiff, Chambers, Stephens, and Willham 1964) are traits that have been improved with genetic selection. Marine shrimp carcasses already have excellent fat-to-lean characteristics, but they are moderately high in cholesterol compared with other meats. The average person's cholesterol intake from shrimp is still far below that of other meats, but this may change as total per capita intake of shrimp rises due, ironically, to consumers' perceptions that seafood is healthier than red meat. Reducing postharvest spoilage, may also be important. Perhaps there is genetic variation in individual spoilage rates which could be used in a selection program. Shrimp postharvest handling, shipping, and freezing technology are satisfactory to ensure product quality, but new markets may be developed and/or shipping costs lowered with increased resistance to spoilage.

There are several economically important diseases that afflict marine shrimp (Lightner 1983, 1984), most notably the infectious hypodermal hematopoietic necrosis (IHHN) virus which has caused massive mortalities in culture systems. Considering the severity of this disease and the possibility of controlled mating, at first glance it might seem logical to direct effort at developing an IHHN-resistant strain of marine shrimp. On closer examination, however, the path to this noble goal is technically more difficult and potentially more costly than breeding for other production traits. A prophylactic solution to this disease problem is likely to be far more cost efficient than a genetic solution. Most disease problems in agriculture are solved with medical technology (vaccines, antibiotics, etc.) rather than with the development of disease-resistant stocks. In marine shrimp, strict quarantine procedures

have greatly ameliorated the IHHN problem and improved management has reduced other disease problems.

Growth-tolerance characteristics, such as low temperature and salinity tolerances should likely be subjected to selection in semiextensive systems. "Temperature tolerance" refers to acceptable growth in ponds at suboptimal temperatures experienced in spring (generally March, April, and May) and fall (October and November) on the temperate U.S. mainland and in winter (December, January, February, and March) in Hawaii. Raceway-cultured shrimp are not subjected to significant, suboptimal temperature challenges, so a temperature-tolerance trait would probably not be an important object of selection in these systems. In selecting for suboptimal temperature tolerance, the breeder of semiextensively cultured shrimp should check for correlated responses in growth at optimal temperatures. A positive correlation would result in increased growth in early summer, allowing time for an earlier harvest and stocking of a second crop within the "window" of tolerable temperatures.

Successful reproductive performance of marine shrimp is a *sine qua non* for the existence of the commercial industry. Despite this, genetic improvement of reproductive performance may not be warranted because better husbandry methods are likely to improve this trait more readily in the foreseeable future. The fecundity of marine shrimp, like that of most aquatic organisms, is high compared to terrestrial animals. Consequently, there is no obvious mandate to breed for increased progeny numbers as there is, for example, with litter size in swine or calving rate in dairy cattle. However, variation in maturation and successful spawning, including variation in egg quality and nauplii production, as a function of maternal age and spawning frequency, are important traits to monitor for evidence of inbreeding depression. In these cases, selection may need to be directed not at improving these traits per se but at maintaining them at acceptable levels while selection for meat yield or efficacy of gain characteristics are carried out.

Emphasis on survival and mortality is much different in terrestrial agriculture than in aquaculture. In the former, mortality levels are low and not a serious problem. In aquaculture, however, mortalities are high but may not be a serious problem because of high fecundities. A 50% neonatal mortality (a common occurrence in aquaculture hatcheries) would be intolerable in uni- or multiparous farm animals. This is not to say that mortality problems do not occur in marine shrimp culture but only that their amelioration may be more readily accomplished by changes in management.

2. Choose and develop stocks

Major differences between agriculture and aquaculture are apparent in choosing a marine shrimp stock for genetic improvement. The domestic history of aquatic organisms is very short compared to that of terrestrial animals. Indeed, the wild relatives of aquacultured groups are extant and (with the exceptions of groups such as common carp, trout, and gold fish) are probably not genetically different from their cultured relatives. This situation can be useful in introducing new genetic variation into cultivars. In contrast, the ancestors of farmed livestock are for the most part, extinct. On the other hand, there are many intraspecific

genetic groups, described as strains, breeds, stocks, varieties, or lines, available in terrestrial agriculture. (There are more than 150 major beef cattle breeds in the United States and Canada alone — each with their own breed association [Warwick and Legates 1979]). No such diversity of identifiable stocks exists in aquaculture with the exception of ornamental goldfish and Japanese koi carp (Axelrod 1973). The marine shrimp culture industry has chosen only two species on the basis of preliminary comparative testing of available species. While the breeding program should concentrate on these, periodic retesting of alternative species or geographic populations would seem warranted, especially since husbandry methods are steadily evolving.

3. Design an animal evaluation system

The proper measurement and evaluation of biological characteristics relevant to genetic improvement programs will be done in close conjunction with step 4 and may, in fact, be done simultaneously. Of primary concern is the evaluation of the capacity for growth. Growth in aquatic animals is indeterminant and influenced by environmental conditions (temperature, water quality, intrapopulational density, and behavioral interactions within the social hierarchy) and by system energy factors (natural and applied feeds and dissolved nutrients) to a far greater degree than in terrestrial animals. A basic problem in evaluating the growth capacity of marine shrimp is the measurement of growth in individuals of known parentage. Progeny groups must be distinguished within pond and raceway systems which will represent a departure from the current practice of treating the pond or the raceway as the unit of production.

4. Estimate genetic parameters

The purpose of estimating genetic parameters is to evaluate the potential of alternative selective mating schemes. These parameters fall under the categories of:

1. phenotypic and genotypic variances
2. heritabilities
3. phenotypic and genotypic covariances between traits
4. genotype-environment interactions
5. inbreeding levels (coefficients)

For terrestrial agriculture many genetic parameters can simply be extracted from the literature (Francoise, Fogt, and Nolan 1973; Kinney 1969; Woldehawariat, Talamantes, Petty, and Cartwright 1977; Blake and McDaniel 1978). No such information is available for marine shrimp, so genetic testing has to be conducted *de novo*. However, as pointed out in the workshop discussion, parameter estimation should not be carried out for its own sake but should clearly be done in relationship to a well justified breeding plan.

5. Develop selection criteria and methods

A commercial breeding program must consider simultaneously several traits, their correlated responses, and adjustment factors (e.g., age of dam effects). To do this, an index of the desired composite phenotype must be developed as a linear function of economically weighted individual phenotypes. The determination of the appropriate economic weighting is conducted as part of the bioeconomic evaluation of the breeding goals (step 1). Neither phenotypic correlations among traits nor economic weightings have been determined for cultured marine shrimp.

Methods of selection include family selection, mass (individual) selection, line breeding, and cross breeding. Decisions about which method of selection will yield the most rapid response in shrimp breeding must be made based on results from steps 3 and 4.

6. Design a mating system

The mating system design in a commercial breeding program is chosen on the basis of genetic variation of individual traits, their selection response, and correlated responses, as well as on the basis of the concern for maintaining numerically healthy genetically effective population sizes. As pointed out by Harris et al. (1984), "Designing the mating scheme includes deciding among inbreeding, assortative mating, or random mating strategies. Inherent in these decisions are the specification of the mating ratio of females to males and the number of breeding seasons to be used for selected individuals . . . the primary goal of designing breeding population sizes should be to maintain a population large enough to sustain sufficient genetic variability for long-term response to selection. Adequate population size is also necessary for stable responses and for supporting the expansion system specified. . ."

We have already shown that existing closed or semi-isolated commercial populations of marine shrimp may be too small to avoid inbreeding. The first action a shrimp breeder can take to increase effective population size is simply to tag and track brood stock in maturation tanks so that the number of males and females effectively contributing to successful spawnings can be observed. Next, females must be isolated in separate spawning tanks so that individual contributions to total naupliar production can be estimated. Isolation of spawning females also provides the breeder with an important opportunity to increase effective population size. Theoretically, if variance in offspring number per female, V_k in equation 2, is zero, the genetically effective population size is nearly twice the effective number of brood stock maintained, i.e., $N_e=2N-1$. This means upper and lower limits on individual egg production should be set so that numbers of nauplii contributed per female to the brood stock of the next generation are made as equal as practical. Finally, progeny groups must be tracked through the production cycle so as to randomize the selection of the next generation of parents and to avoid maximally the mating of relatives (Kimura and Crow 1963). Interestingly, another way the breeder can increase effective population size per unit time is to increase the

generation length of brood stock (Lande and Barroclough 1987). Brood stock should not be discarded after first spawning but kept as long as reproductive performance remains acceptable.

Critical Areas for Genetics Research

Development of Technology and Brood Stocks

General considerations

Most biological characteristics of marine shrimp that seem important to production are measurable or quantitative traits. Experimental methodologies for analyzing the genetic bases of such traits, for predicting their responses to selection, and for practicing selective breeding are well described (Falconer 1981; Mather and Jinks 1982). Although the specifics of quantitative trait measurement and data analysis can be quite complex, the designs of classical mating experiments themselves are straightforward. In one common design, for example, gametes from a number of males and females are combined in all possible pairwise crosses, producing several full-sib families within paternal and maternal half-sib family groups. As long as these family groups are reared in common or replicated environments, the theoretical genetic relatedness within and between these family groups allows statistical partitioning of the variance of any measurable trait into various genetical and environmental causal components of variance. It is the knowledge of these components that allows the design of appropriate selection methods and the prediction of responses. The important point about these basic experimental designs is that once methods for carrying out such crosses are in place as many traits as possible can and should be measured during all life stages of rearing the progenies. This not only maximizes the amount of information gained from each experiment but also allows estimation and partitioning of the covariances among traits.

A top priority in a genetics research program for marine shrimp must be the development of systems and methods for making experimental crosses and evaluating their results (Table 2). This means the development of both complete reproductive control, so that crosses can be made at the proper time, and husbandry methods, so that commonality or sufficient replication of environments experienced by the genetic groups being tested, can be ensured. Then, it is simply a matter of applying the basic methodology in a logical series of experiments aimed at elucidating all the genetic parameters of interest. Only in this way will many of the pressing constraints on the development of commercial shrimp breeding be alleviated.

Lack of experimental "know how" and tools for carrying out such genetic evaluation experiments stands out in general as an obvious difference between agriculture and aquaculture. As mentioned earlier, because the production unit in terrestrial agriculture is often the dam and her offspring, pedigree information and control is readily attainable. This is not so in aquaculture because mixed populations are the units of production. Mass spawning and batch rearing of larvae, postlarval juveniles, and adults are normal industry practice. For the marine shrimp breeder or research geneticist, isolation of spawning females and progenies,

or better yet their tagging so that identities are kept in common environments, will be necessary to achieve the distinction of parentage required for genetic testing in commercial-scale husbandry systems.

Tagging

Tagging of larval marine shrimp in hatchery and nursery systems can be achieved through use of electrophoretically detectable protein variants (Hedgecock, Shleser, and Nelson 1976; Hedgecock 1977; Moav, Brody, Wohlfarth, and Hulata 1978; Lester 1983). Brood stock carrying rare combinations of protein variants can be collected in mass screening programs and used to generate biochemically tagged progeny groups that can be mixed in larval tanks and nursery ponds. Zacarias (1986) has demonstrated the usefulness of this approach in studying the problem of heterogeneous individual growth rates in freshwater prawns. We note here that electrophoretic markers are also useful monitors of increased homozygosity due to inbreeding and of the purity of genetic groups (Hedgecock 1977; Moav et al. 1978; Sbordoni et al. 1987).

Physical tagging of postlarval juveniles in growout systems and of brood stock in maturation facilities is also possible. The most sophisticated of these tags are the passive induced transponder (PIT) tags which can encode substantial amounts of individual identification data on an implanted memory chip and report these data when energized to transpond its contents. Such tags would be especially useful to keep track of individual brood stock and their performances in shrimp maturation facilities. The problem of identifying individual male contributions to fertilizations in mass mating tanks might even be solved by use of transponding tags activated by physical contact at copulation. PIT tags have been successfully implanted into sub-adult freshwater prawns. Color-coded streamer tags on progenies would allow mixed-group testing in raceways and ponds. Also, the availability of computer-based, image analysis technology allows, at sampling or harvest, rapid recording of identity at the same time that length measurements are digitized and stored in data bases.

Artificial fertilization and mating synchrony

Until artificial fertilization methods are available, another important requirement for genetic testing of shrimp will be synchrony among spawning parents in order to avoid confounding of family performance with differences in stocking times. Perfect synchrony is unrealistic, but we need to know how much variation in spawning time can be tolerated in making experimental crosses with natural service matings. For freshwater prawns, Malecha, Masuno, and Onizuka (1984) found no effect of growth rate for postlarval progeny groups hatched over a 3-day period. Similar broodstock husbandry methods will need to be developed for experimental crosses of marine shrimp.

Correcting for differences in initial size and competition

Another problem faced in comparisons of genetic groups in aquaculture systems is the confounding of family differences in mean weight at harvest with differences in initial

mean family weights at the time of stocking. Methods such as communal testing (Wohlfarth and Moav 1985) or size grading of families before stocking (Wohlfarth and Moav 1972) may need to be developed for marine shrimp in order to correct for this effect. Likewise, magnification of intergroup differences, through the intense competitive interactions that are characteristic of aquaculture systems (Wohlfarth and Moav 1985), will necessitate estimation of correction factors for scaling appropriately individual weight gains in mixed group testing.

Reproduction

Variance in maturation and spawning

The commercial shrimp industry has adopted broodstock management techniques that provide sufficient nauplii to meet production requirements. However, several problems remain:

1. The percentage of successfully spawning females in a broodstock pool is low.
2. Successive spawns from an individual female diminish in quality in successive generations.
3. Spawning parents contribute very unevenly to naupliar production.
4. There is large variation in total numbers of eggs among spawns.

As in the case of disease resistance, work on solutions to these problems should focus on, but not necessarily be limited to, nongenetic means. Basic research on the endocrinology, physiology, nutrition, and behavior of sexual maturation in marine shrimp needs to be done before genetic analysis and breeding for reproductive traits will be fruitful or even possible. However, it is important to quantify, with the aid of appropriate individual identification of brood stock and progenies, variation in reproductive performance. As discussed earlier, it is especially important to measure the actual number of parents and their numerical contributions to each generation so that V_k and N_e can be estimated. Likewise, measurement of individual performances in repeated maturation and spawning cycles is important for two reasons. First, repeated use of brood stock is a component of variation in reproductive success that needs to be evaluated. Second, it is important to monitor reproductive output for signs of reduced performance owing either to inbreeding depression or correlated response to selection during the growout phase of the life cycle. Study of the repeatability of reproductive performance for individuals should help assess the amount of environmental variation in maturation and spawning.

Measurement of reproductive performance is not overly complicated. Records on individual spawns, the numbers of eggs, and the early survival of nauplii need to be kept. Techniques for determining subtle biochemical differences among spawns would be useful in assessing egg "quality." Identified offspring of brood stock need to be reared to reproductive maturity so that parent-offspring correlations in maturation and spawning can be determined. Computer-based data management of broodstock inventory would be essential to the success of this program.

Gamete manipulation

In most cases the differences between agriculture and aquaculture systems with respect to life cycle control, husbandry, and selective breeding are stacked in favor of the livestock farmer. In the area of gamete manipulation, however, aquaculture may have the edge. Higher female fecundities and greater access to gametes in aquatic animals, including marine shrimp, facilitate artificial insemination, *in vitro* fertilization, and manipulation of chromosome sets as discussed in the next section.

The so-called open thelycum marine shrimp species such as *P. vannamei* and *P. stylirostris* are especially amenable to collection and manipulation of gametes. Spermatophores are readily obtained from males by electro-ejaculation (Sandifer and Lynn 1980), and eggs are naturally shed freely into the sea by female shrimp. Artificial insemination in open thelycum penaeid shrimp has been demonstrated (Persyn 1977) and used in successful artificial interspecific hybridization (Lawrence, Bray, and Lester 1983; Bray, Lawrence, Smith, and Lester 1986). *In vitro* fertilization has been demonstrated for *P. aztecus* by Clark, Talbot, Neal, Mock, and Salser (1973) whose work has stimulated a great deal of interest in the unique biochemistry and morphology of shrimp gametes. Applied to a genetics research program, methods for collecting, handling, and fertilizing marine shrimp gametes would facilitate the simultaneous pairwise crossing of a large number of males and females in the classical mating experiments described above. Cryopreservation of spermatophores would allow even more flexibility in making such crosses and offers the hope of repeated testing of sires in different seasons or in combination with different maternal groups.

Ploidy manipulation

At spawning, the ova of penaeid shrimp are in the metaphase stage of the first meiotic division. Upon contact with seawater, the egg is activated and initiates the completion meiosis. The first and the second meiotic divisions are completed within about 20 and 40 minutes, respectively, whether fertilization has occurred or not (Clark, Yudin, Griffin, and Shigekawa 1984). First cleavage of the zygote occurs about 90 minutes after spawning; unfertilized eggs show abnormal cleavages and are inviable.

Access to shrimp eggs during meiosis and first cleavage provides an opportunity, unmatched in animal agriculture, for manipulation of the number of chromosome sets or ploidy in individuals. Such manipulations have become quite important in fish and shellfish research and breeding programs, owing to dramatic consequences upon fertility, sex ratio, inbreeding, and the ability to map genes (Purdom 1983; Allen 1987). Manipulation of ploidy is achieved by blocking either of the meiotic divisions or the first cleavage so that two sets of maternal chromosomes are retained in the zygote. These cell divisions are inhibited by either physical (temperature shock, pressure) or chemical (cytochalasin, colchicine) treatments that suppress either cytokinesis (polar body formation) or karyokinesis (chromosome spindle activity). If an egg so treated has been normally fertilized, the resulting zygote is triploid. Since penaeid ova are activated upon contact with seawater, sperm is not required to initiate the fertilization reaction and subsequent cell division. Thus, in the absence of

sperm, successful inhibition of an early cell division should produce a parthenogenetic diploid zygote which is expected to be viable and to develop normally. If fertilized with an inactivated (by UV irradiation, for example) sperm, the egg would develop normally as a gynogenetic diploid zygote.

Because triploid animals tend to be sterile, induction of triploidy has become an important breeding strategy for those aquatic species that show marked reductions either in growth rate or carcass quality upon sexual maturity (Allen 1987; Bye and Lincoln 1986). Such reductions are not observed in sexually mature marine shrimp, but the growth capacity of sterile shrimp is of interest in light of the fact that mature females attain larger sizes than mature males.

Induced gynogenesis or parthenogenesis appears to have potential in marine shrimp breeding for production of monosex populations and accelerated development of inbred lines for research. If there is a chromosomal mechanism of sex determination in marine shrimp and the female is the homogametic sex, then gyno- or parthenogenetic shrimp should all be female. Because females can grow to larger, premium-priced sizes, all-female production may have some advantage in commercial culture. On the other hand, gyno- or parthenogenetic diploids, having only one parent, are more highly inbred than their normal, sexually produced counterparts. The amount of inbreeding depends upon which cell division is inhibited in restoring diploidy to the egg or zygote. Maternal heterozygosity (*H*) is retained at loci in a meiotic parthenote as a function of their recombinational distance, *c*, from the centromere. Expected heterozygosities for the artificial parthenotes made by inhibiting meiosis I and meiosis II are $H(1-{}^{c}/_{2})$ and $c\,H$, respectively (Allendorf and Leary 1984). Inhibition of first cleavage, however, results in the retention of two identical sets of chromosomes and the creation thereby of a 100 percent homozygous, inbred individual. If cryopreservation of gametes, followed by sex reversal and self-fertilization is possible, pure clones can be developed from first cleavage gynogenetic diploids as demonstrated for the zebrafish (Streisinger, Walker, Dowe, Knauber, and Singer 1981). Because of the tremendous usefulness of pure clones for experimental biology, research on induction of gynogenesis at first cleavage and on mechanisms of sex determination and methods of sex reversal are clearly of top priority in a marine shrimp genetics research program (Table 2).

Development and Growth

Correlations of growth among life stages

Traits related to growth are obviously of direct relevance to the genetic improvement of production. In order to select successfully for more rapid growth without harming, through negatively correlated responses, other important characteristics such as reproductive performance, the shrimp breeder needs to know the kinds and magnitudes of genetic variance in traits related to growth and the covariances among different traits and life stages. Estimation of these genetic parameters is accomplished simply by measuring appropriate variables, such as tail counts, at stocking, at sampling, and at harvest, for family groups produced in controlled experimental crosses as discussed above.

Tolerance to low temperature and salinity

Genetic evaluation of the temperature-dependence of growth, specifically the maintenance of good growth at suboptimal temperatures, presents interesting challenges. First, there is negative environmental correlation between the life stages affected by suboptimal growth temperatures in the two-crop annual production cycle at temperate localities. Low temperatures in these localities are experienced by the early juvenile stages of the first crop stocked but by the late adult stages of the second crop. If there is positive genetic correlation between early and late growth-temperature tolerances, selection for rapid juvenile growth at suboptimal temperatures will also confer rapid growth upon the adults harvested in fall. If not, breeding of early and late low-temperature tolerant stocks may be needed. Low-temperature tolerant stocks developed primarily for temperate culture systems might also prove useful in subtropical localities such as Hawaii. An important objective of the genetics research program, then, is the determination of variance in growth at suboptimal and optimal temperatures and at early and late stages in the growout cycle. This objective embodies a second challenge, providing low and optimal temperatures simultaneously for experimental comparisons of genetic groups and measurement of variance components. This problem is discussed below in the context of the facilities needed to carry out this important objective. Genetic evaluation of variance in growth at low salinities would present similar challenges to the design of experiments.

Carcass traits

Without knowledge of the phenotypic and genotypic variances of meat quality we cannot assess possibilities for genetic improvement of carcass traits. The genetic evaluation of carcass and spoilage characteristics can be done as part of the evaluation of production performance. One simply has to ensure the proper identification and handling of genetic groups in order to complete the appropriate analysis. Carcass quality evaluation should be a part of any genetic assessment of adult performance.

Disease resistance

Resistance to diseases such as IHHN virus is technically difficult to evaluate. First of all, a strictly quarantined facility completely separate from other commercial and research facilities would have to be utilized. Second, in the absence of cultured cell lines, the disease would have to be maintained in infected animals that may be difficult to culture. Lastly, the desirable phenotype (survival to disease challenge) is a binary character (survival or mortality) which is statistically more cumbersome to deal with than a metrical trait, requiring larger family sizes and more families. For all of these reasons the cost of estimating genetic parameters associated with disease resistance would be much higher than the costs associated with research on other production traits. Moreover, we noted above that the marine shrimp breeder would be wise to seek nongenetic remedies to disease problems. A top priority in finding solutions to the disease problems of cultured penaeid shrimp is the development of tissue culture methods and cell lines that can be used to study disease mechanisms and prophylaxis.

Metabolic efficiency

In terrestrial animals efficiency of weight gain is frequently the focus of breeding programs because it is an important component of production cost and can be measured precisely in individual production units. Metabolic efficiency is undoubtedly a significant component in aquatic animal production as well and, as pointed out earlier, needs at least to be monitored for changes induced by selection on other traits such as growth rate. However, food conversion efficiency is difficult to assess in benthic detritivores such as marine shrimp. The role of "natural productivity" in meeting shrimp nutritional requirements in ponds is exceedingly difficult to evaluate, and even in laboratory aquaria, food conversion efficiency and energy budgets are difficult to measure because of technical problems imposed by the aquatic medium.

Systems Analysis and General Considerations

Bioeconomic modeling

A first step in a commercial breeding program is to develop a quantitative, mathematical description of the production unit in terms of the biological and physical variables affecting cost of production. With such a model, the relative importance of direct or indirect change in these variables can be evaluated so that economic weights can be assigned to all traits toward which breeding might be directed. The relative economic weight given to each trait may be defined as the amount by which the cost of production may be expected to decrease for each unit improvement in that trait (Hazel 1943). The bioeconomic model given by Griffin et al. (1984) is a logical starting point for conducting a sensitivity analysis of the relative economic gains expected from biological changes that might be possible through selective breeding of marine shrimp.

Inter- and intraspecific comparisons

As noted in the second section, the U.S. marine shrimp culture industry has focused primarily upon two species, *P. vannamei* and *P. stylirostris*. This choice was made after preliminary comparisons among several New World penaeids showed that these species had generally higher survivals in all phases of culture and that they could be brought into sexual maturation fairly readily. By now husbandry of these species has been refined so that potential rivals might not compare favorably under specialized industry culture practices. Moreover, experience with disease introductions has had a chilling effect on further testing of alternative species. Because of the chance that other species might ultimately yield more than the present cultivars or that their genetic resources might eventually prove useful when incorporated into the chosen species, industry representatives at the workshop acknowledged the need for a research program in interspecific comparisons. This would have to be carried out in a fully quarantined facility in which side by side comparisons of standard cultivars and exotics could be made.

There is good opportunity to collect, evaluate, and possibly develop intraspecific genetic groups of several of the commercially important species. Most of these have geographically wide distributions. From the standpoint of looking for favorable growth responses to suboptimal temperatures, species with broad latitudinal ranges may exhibit suitable variation in physiological responses. There has been speculation that populations of *P. stylirostris* from Mexico, Central America, and South America differ in reproductive and growth characteristics, Lester (1983) did not find significant differentiation of allelic frequencies among these localities for three allozyme loci, but did find a difference in general protein phenotype between northern Gulf of California and southern collections. These results are consistent with the generally low geographic differentiation in allelic frequencies observed in studies of other species (Lester 1979; Mulley and Latter 1981a, 1981b). Nevertheless, controlled production trials are the only way to evaluate geographic variation in economically important quantitative traits, which can occur despite allozyme similarity.

ENABLING A MARINE SHRIMP GENETIC IMPROVEMENT PROGRAM

Needs for Facilities

There are a number of high priority genetic research program tasks that can be accomplished with present knowledge but there is a lack of suitable facilities in which to carry the tasks out (Table 2). Notable in this regard are tasks relating to breeding goals (temperature and low-salinity tolerances), genetic testing, and animal evaluation. The term "facilities" is used here to denote "bricks-and-mortar" infrastructure, not scientific equipment which might also be needed to carry out specific research tasks.

Workshop participants were polled to discover which, if any, of the current public sector facilities could be used for genetics research and a stock center. Table 3 summarizes the results of this poll. Of all the facilities with outdoor earthen ponds (Waddell Center, Texas A&M, University of Hawaii [UH], Hawaii Institute of Marine Biology [HIMB], and the Oceanic Institute [OI]), only theWaddell Center has sufficient numbers of ponds for genetics research. Other stations are not yet built (University of Texas, Port Aransas), have heavy commitments to other research projects (Texas A&M, Corpus Christi), or have limited numbers of ponds available (UH-HIMB, OI). The UH College of Tropical Agriculture and Human Resources facility has no ponds, only wet labs, a hatchery, and broodstock facilities.

Certainly genetics research in such areas as gamete manipulation and gynogenesis can be carried out in existing facilities as can the development of tagging technologies and even some nutritional testing using aquaria, tanks, and in-pond cage systems. However, the heart of a genetic research program — the testing and development of research stocks, the development of animal evaluation systems, and the estimation of genetic parameters and selection experiments — cannot be accomplished with the currently available facilities because:

1. There are not enough small (1/8 acre) ponds for genetic testing and stock holding.
2. There are no facilities for raceway testing.
3. There are no hatchery facilities for generating separate progeny groups and evaluating individual reproductive characteristics.

A minimum facility for genetics research and stock evaluation is described in the appendix.

TABLE 3. SUMMARY DESCRIPTION OF EXISTING EXPERIMENT STATION FACILITIES WITHIN THE SEA GRANT NETWORK THAT MIGHT BE USED IN MARINE SHRIMP GENETICS RESEARCH

Name/Source*	Location	Parent Institution	Facilities/Program	% Usable for Genetic Research
Waddell Center *Dr. Sandifer*	S. Carolina	Marine Resources Research Institute	4 species; fish, mollusks & shrimp; 12:1/4 acre, 6:6, 3:1 1/4; 12 outdoor tanks; hatchery, 10,000 ft.^{2} building	25%
Shrimp Maturation Project *Mr. Bill Bray*	Corpus Christi, Texas	Texas A&M University	18 1/4 & 1 2-acre pond planned: 6 20-acre ponds	Unknown, other uses
No name *Dr. Bright*	Port Aransas	University of Texas	New facility to be built	Unknown
Shrimp Aquaculture Project *Dr. Fast*	Oahu, Hawaii	Hawaii Inst. of Marine Biology, University of Hawaii	22 acres; hatchery; 12 ponds:1/4-acre; 1 pond:1-acre; 9-10 yrs. left; hatchery 20 outdoor tanks; option on 6 more acres; some problems with seawater quality	Unknown, other uses
Oceanic Institute *Dr. Ivy*	Oahu, Hawaii	Oceanic Institute	Full hatchery, 8 ponds 1/4-acre; 4 ponds 1/2-acre; 12 outdoor "Taiwanese" ponds	Unknown, other uses
Aquaculture Research *Dr. Malecha*	Oahu, Hawaii	College of Tropical Agriculture and Human Resources	4,000 ft^2 brood stock & hatchery; water tables, outdoor ponds	50%

*Workshop participant providing information

A number of experiments must be carried out simultaneously at a research facility if full use is to be made of hatchery and nursery system capacities and if the facility is to accommodate more than one research project at a time. Table 4 presents estimates of the minimum number of growout units needed for conducting five separate genetic research activities directed at posthatchery, growout performance traits: genetic selection, parameter estimation, animal evaluation system development, and stock comparisons. The experimental growout units are small earthen ponds (approximately 200 to 400 m^2) and raceways (1 m x 2 m x 10 m). Larger ponds needed for line expansion, scale-up testing, and in-pond cage testing of diets or genetic groups are also listed.

Two major, long-term genetic research projects are envisioned to take place — selection and stock development — requiring a total of approximately 14 acres (see "Appendix"). This is an extremely modest facility by any standard.

TABLE 4. ESTIMATE OF THE NUMBER OF EXPERIMENTAL UNITS NEEDED IN A GENETIC RESEARCH FACILITY AND STOCK CENTER

Genetic Research Activity	Experimental Group	No. Groups	No. Subgroups	No. Replicates	No. Ponds	No. Raceways	Duration
Selection (growth)	Control line	2	2	4	16	16	Long term
	Selected line	2	2	4	16	16	Long term
Variance Estimation	Half sib families	~50	Mixed testing	—	12	—	Short term
Covariance/ Correlation Analysis	Half sib families	~50	Mixed testing	—	12	16	Short term
Determinations of Scale	General groups	3	2	~3	12	12	Short term
Stock Development	Species	4	10	2	24	16	Long term
	Intraspecific groups	6	2	2	24	6	Long term
	Inbred lines	Mixed testing	—	3	3	—	Long term

Public Agency Support of Research

A work group comprised of the aquaculture coordinator from the National Sea Grant Program and representatives of four state Sea Grant College programs convened to discuss the role Sea Grant might play in fostering the development and initiation of a national effort in marine shrimp genetics and breeding. Eight points were considered.

Commitment to the Long Term Required by a Genetics Program

By its nature, genetics research requires the passage of generations to complete; moreover, the stocks generated by this research accrue value with each generation. The question of how such long-term commitments to projects and to the maintenance of stocks could be made by public support agencies that by law cannot make such commitments and whose typical grant cycles run 1, 2, or 3 years was thus raised. Sea Grant representatives agreed that grant cycles of 4 years for marine shrimp genetics projects would be entertained.

Coordination Among State Sea Grant Programs

Differences among the various state Sea Grant College programs with respect to deadlines and fiscal years would make cooperation among researchers from different states difficult. Sea Grant representatives agreed to entertain off-cycle submission of proposals if such problems were to arise.

National versus Local Sea Grant Priorities

Researchers expressed concern that the lack of new funds for a national Sea Grant effort in marine shrimp breeding and domestication might result in conflicts between local and national priorities. In some cases, an investigator proposing a shrimp project addressing a national need might compete against himself if he were also proposing a nonshrimp project addressing state needs. Sea Grant representatives agreed that without new funds this concern was real and suggested marine shrimp proposals be submitted through those states in which marine shrimp research was a local priority. This would seem to discourage the writing of Sea Grant proposals by competent investigators in states not having an important marine shrimp culture industry.

Use of This Report as Justification

Sea Grant representatives agreed that this report, if accepted, would serve as a planning document that could be specifically cited by investigators as justification or rationale for proposals relating to marine shrimp breeding and domestication. The converse use of this document by Sea Grant reviewers, program managers, and program monitors to match the content of new proposals against the list of research needs stated herein was judged to be somewhat risky. Good, innovative ideas in areas untouched by this report might be

ignored to the detriment of the marine shrimp genetics program. We emphasize that the research priorities stated in this report reflect the current states of the industry and knowledge; these priorities will require updating periodically.

Coordination Among Agencies

Competitive grants in aquaculture submitted to U.S. Department of Agriculture (USDA) are already cross-reviewed by the National Office of Sea Grant.

Coordination With Industry

Future meetings or workshops like the one held in La Jolla would help keep the industry abreast of research results and the academic scientists abreast of the industry's accomplishments and needs for improvement. Such meetings could perhaps be added onto the program for the annual meeting of the World Aquaculture Society or other such professional gatherings.

Coordination of Industry, University, and State

Close working ties among industry, university, and state sectors within state boundaries are essential to the success of a national effort in marine shrimp domestication and breeding. Such cooperation has begun in South Carolina and Texas and is imminent in Hawaii.

Sharing of Graduate Students Among Cooperating Universities

Allowing graduate students access to facilities available in other states and at other universities was judged to be important in fostering cooperation among academic scientists and in providing the best possible education for young scientists who will be the cornerstone of future efforts in marine shrimp domestication.

Industry Support and Guidance

In terrestrial agriculture, animal breeding is conducted by commercial breeders as a business distinct from the production sector of the industry. Land grant college university research, especially that conducted in agricultural experiment stations, supports industry breeding by providing new technologies and procedures. Such a division of labor between public and private efforts is not likely to obtain in the genetic improvement of marine shrimp because of the vertical integration of the culture industry and the undomesticated status of the animals themselves, as pointed out in the second and third section. Domestication selection is likely to take place wherever closed populations are kept, but the research needed to estimate critical genetic parameters allowing choice of breeding strategies and the initial testing of breeding methods will probably only be possible in the public sector.

Industry representatives at the workshop were thus highly supportive of efforts to initiate a genetics research program in the public sector. They believe that the program ought to be aimed, on the one hand, at providing the basic knowledge and tools needed for marine shrimp breeding and, on the other hand, at demonstrating at least one bona fide example of genetic improvement in a production trait. Emphasis should be on the commercially important species, not on animal models. Under these broad conditions, industry support could be expected on three levels: (1) in-kind support of genetic research on farms and in commercial hatcheries in the forms of space, facilities use, and, in some cases, technical support; (2) direct lobbying support to funding agencies on behalf of researchers; and (3) seed money to be used as matching funds to demonstrate concrete industry support of research projects as well as to purchase equipment, defray operational expenses, and support graduate students.

A continued voice in the future direction of marine shrimp genetics research was sought by industry representatives. Industry guidance could be solicited at periodic workshops such as discussed in the preceding part of this section.

CONCLUSIONS

The consensus reached by participants in the Sea Grant workshop on marine shrimp genetics is summarized in the following five points:

1. Increasing yield or efficiency of production must be the focus of a national research program on marine shrimp breeding. The industry panel in particular called for one clear demonstration of a bona fide genetic improvement in the production of a commercially cultivated species. In order to meet this goal, a facility is needed for the scientific production of pedigreed marine shrimp populations. In the absence of facilities to do production research, laboratory studies of gamete and chromosome set manipulation may provide powerful genetic tools for future production research.
2. Quantitative descriptions of the production systems and the economic values of breeding goals, including the costs of achieving those goals, are needed in order to guide the specific directions and objectives of breeding research.
3. While the focus must be on production, it is nevertheless very important to monitor reproductive and survival traits for signs of inbreeding depression. It will be necessary to develop methods for measuring reproductive performance and for quantifying individual broodstock contributions to future generations, so that populations of sufficient size to maintain genetic variability are propagated.
4. More species and strains of marine shrimp need to be collected and evaluated in careful yield comparisons with the small number of species that have come to dominate the marine shrimp culture industry. Again, there is need for a facility in which to conduct such trials under quarantine so that exotic diseases and pests will not be introduced into existing commercial facilities.

5. The longest term commitment to genetics research on the part of public funding agencies such as Sea Grant is a 4-year funding cycle. Coordination of different state Sea Grant College programs and new funding for a national shrimp program separate from individual state programs are desirable.

While these points of consensus were fairly easy to reach, the enabling and funding of a national research program in the aquacultural genetics of marine shrimp pose much more difficult problems. At present, opportunities to do the critically needed research described in this report are, unfortunately, extremely limited. There are three main difficulties.

First and foremost, there is no facility anywhere in the United States where the genetics of shrimp production can be scientifically studied. This became clear from a polling of workshop participants regarding facilities known or available to them (Table 3). Research on the quantitative genetics of marine shrimp production — research that must be the heart of a program to explore the potential for shrimp breeding — cannot be done without a facility dedicated to replicated production trials of pedigreed genetic groups.

Second, the marine shrimp culture industry in the United States does not appear to have the economic status to warrant government funding of the requisite research station. This point was made especially by Dr. Ben Ribelin, who along with others argued that a national program should make do with what is presently available until industry gets on firmer footing. We concur that tough questions about the economic value of the U.S. shrimp aquaculture industry will require satisfactory answers if the cost of a national research program in shrimp breeding is to be rationalized. We do not agree, however, with the "make-do" sentiment. The tools that need to be developed for shrimp breeding are those enabling measurement of the production characteristics of marine shrimp. These tools cannot be developed in a laboratory; they can only be developed in a production setting. The demonstration of genetic improvement that Dr. Ribelin and other industry participants called for assumes a background of scientific information that can only be obtained by making controlled crosses and experimental production trials. No shrimp farm, especially the marginally economic ones operating in the United States at present, can apparently sustain this type of research and development effort in its production ponds.

What can be done with existing facilities in parallel with industry development probably does not require a national program. Scientists now working with shrimp will continue to propose laboratory-scale research to Sea Grant, USDA, and other agencies, whether there is a national program or not. How laboratory research results are to be translated into experimental breeding programs and eventually into increased commercial production is the gap that will remain in the absence of an organized national research program in the aquacultural genetics of marine shrimp.

Third, there is no new Sea Grant funding available for a national research effort in shrimp genetics. This lack of new funds may result in conflicts between local and national priorities. An investigator proposing a shrimp project addressing a national need, for example, might compete against him- or herself if he/she were also proposing a nonshrimp

project addressing a state need. Sea Grant representatives agreed that this concern was real and suggested marine shrimp proposals be submitted through those states in which marine shrimp research was a local priority. This would seem to discourage the writing of Sea Grant proposals by competent investigators in states not having an important marine shrimp culture industry.

The technological and scientific challenges involved in domestication and breeding of marine shrimp are not insurmountable. Despite the differences between agriculture and aquaculture that have been stressed in this report, the well known successes of agricultural genetics, the promising initial results in the breeding of fish such as salmon and carp, and the general validity and broad applicability of genetic principles assure us that marine shrimp will almost certainly respond to appropriate efforts at domestication. Prospects for domestication and breeding of marine shrimp are good; the path ahead appears uncertain more for political and economical rather than for biological reasons.

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APPENDIX

A MINIMUM FACILITY FOR GENETICS RESEARCH AND STOCK DEVELOPMENT

Pond Facilities

The pond component of a minimum genetics research and stock facility for marine shrimp would consist of a number of small ponds needed to house, in replicated fashion, the various lines and genetic groups to be developed. As mentioned in the main text, two major long-term genetic research projects are envisioned to take place at a genetics research facility: selection and stock development. The baseline numbers of growout units needed for these two activities are estimated to be 32 ponds and 38 raceways. In addition to these two long-term projects, short-term projects, involving either variance estimation, covariance analysis, or the development of animal growout evaluation methods, will probably take place at any given time.

The following is an example of the type of design criteria that could be part of a marine shrimp genetics selection program. Figure 1 shows a hypothetical selection scheme using two selected populations and a control line. This scheme has been proposed for freshwater prawns but can be used as an example for marine shrimp.

Variation among ponds in mean size is a source of experimental error which affects the assessment of genetic response. It is the breeder's task to design an experiment so this variation does not mask the genetic response. Suppose previous experience in yield trials conducted in ponds similar to the ones that are proposed for the selection experiment showed that mature populations of animals grow to a mean size of 17 g with a standard deviation of 1.58 g among ponds. If we conservatively over-estimate the among-pond standard deviation to be 2.0 g in the selection experiment depicted in Figure 1, then the standard error of a difference between lines with 8 ponds/line is about 0.5 g. Thus the minimum difference in mean weight between two groups of 8 ponds that will be statistically different is 1.96 g. Suppose the within-pond standard deviation of weight to be 8.5 g in previous yield trials, for a coefficient of variation of about 50%. Suppose also the percentage of selected females to be approximately 5% (as shown in Figure 1) and the mean weight of these animals to be 30 g. Thus, the selection differential will be approximately 13 g, and the selection intensity in standard deviation, i, is 1.53. Realized selection response, R, can then be predicted using: $R = (1/2)ih\,\sigma$, where 8.5 g = standard deviation of the trait frequency distribution. R in this case comes out to 1.63 g in one growth cycle conservatively assuming $h^2 = .25$. (Malecha et al. [1984] estimated female juvenile freshwater prawn $h^2 = .35 \pm 0.15$.) Over three selection cycles, then, we expect a mean response of 4.89 g, which is well above the minimum detectable difference of 1.96 g. Note that the ability to detect a genetic response is sensitive to h^2, i, the frequency distribution of the trait, and the number of ponds used in housing the lines. The number of ponds needed to detect a genetic response above the "background noise" of among pond variation in size is modest, eight ponds per line, or a total of 24 ponds housing two selection lines and a control line.

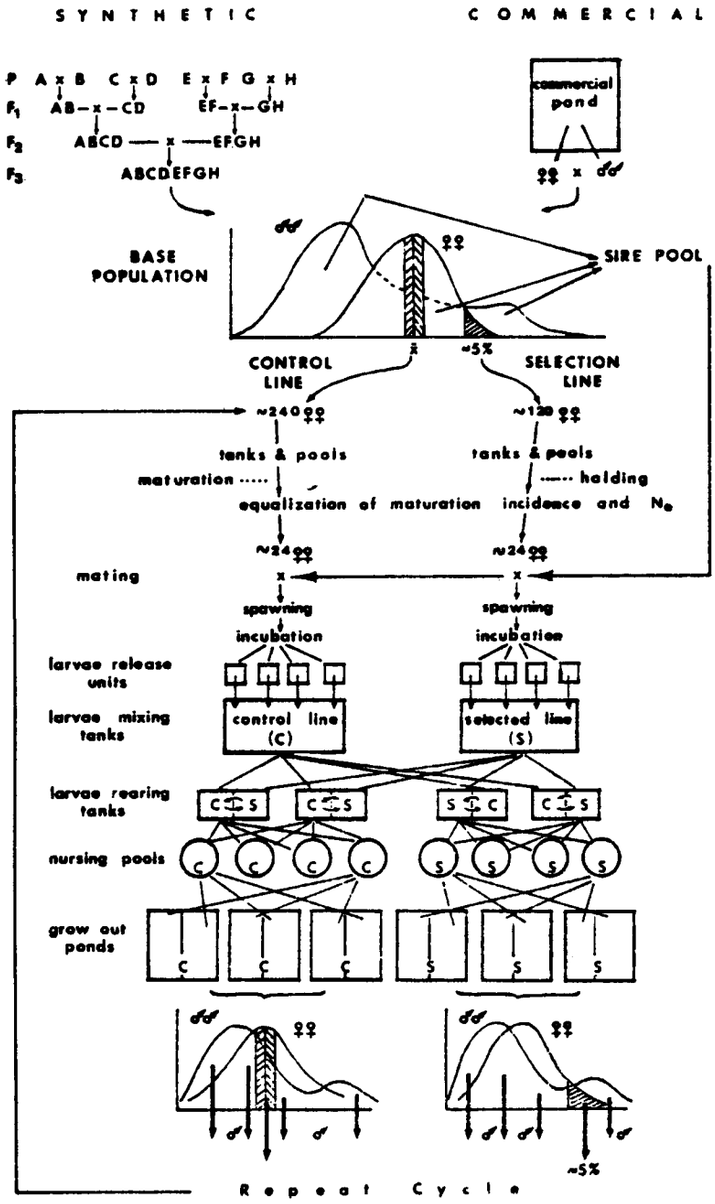


Figure 1. General scenario for proposed selection. Selection will be carried out within both a commercial and synthetic population although only one flow diagram is depicted. Space limitations do not allow depiction of all larval-release units, larval-rearing tanks, and ponds. Dispersal patterns of larvae to nursery pools and of juveniles from the latter to ponds is shown for only two cases within each line.

Hatchery Facilities

The broodstock, maturation, hatchery, and nursery components of the minimum genetics research facility include areas and tanks for maturation and spawning, algae production, larval rearing, and a postlarval (PL-30) nursery. Assuming (1) that larvae for selection and stock development experiments would have to be reared perhaps once per year, allowing for full maturation of the previous generation, and (2) that sequential short-term genetic research projects would require larvae every 4 months, then, at stocking densities of 20 PLs/m^2, no more than 128,000 PLs would be needed at any time for the experiments. At a production rate of 40 PLs/liter of final working volume, a 3,200-liter hatchery is needed. Approximately 32 100-liter tanks would be needed for the separate rearing of family groups or stocks. The physical plant needed to house a 3,200-liter hatchery is so modest that its capacity could, for little additional cost, be doubled to support additional research projects.

Assuming a hatchery of 64 100-liter larval rearing tanks, 6 1,000-liter tanks for producing larger batches, and work space (tank support, aisleways, etc.) of 2 m^2/100-liter tank and 5 m^2/1,000-liter tank, a total area of about 160 m^2 is required plus about 10% for contingency.

The space needed for various hatchery activities or research functions can be calculated easily by assuming a certain ratio of the space occupied by the larval rearing area to that occupied by the activity. The following is a list of common hatchery activity/work area items that have been standardized to 100 m^2 of larvae rearing activity:

	m^2
reservoirs	100
larval rearing	100
maturation	50
algae culture	10
laboratory	10
spawning	10
office/conference	6
power/electrical	6
tools/storage	2
toilet/shower	2

Construction costs for a facility can be roughly estimated using figures for similar agricultural buildings (King 1985). Construction costs for a dairy barn, for example, run between approximately $15 and $35 per square foot.

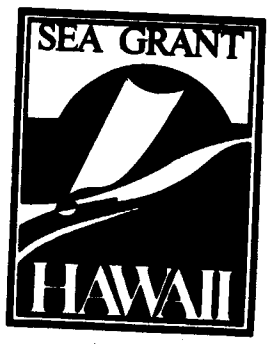
For initial planning purposes the space needed to house maturation tanks is roughly equal to the space occupied by the larval rearing tanks in a commercial hatchery. This is because the larval rearing tanks are similar to the maturation tanks and mixed batch culture of individual spawns is used. In a genetics research facility, on the other hand, larvae of many families (i.e., spawns from each individual female) have to be reared separately. Therefore,

many more spawning females are needed for the same number of PLs. The ratio of maturation tank work space to larval rearing tank work space will be greater than in a commercial hatchery. This work space can be estimated as follows. Assume: (1) a spawning tank stocking density of 10 females/m^2; (2) 8% of the females spawn per night over a 7-day (i.e., night) period, the maximum allowable time span to achieve "synchrony" of larval development among families; (3) approximately 50 females are required for a genetic experiment; and (4) each maturation tank is approximately 7 m^2 of bottom surface area (3 m in diameter). This leads to an estimate of a broodstock pool of 625 females occupying about 63 $m^2$of tank bottom area or 7 tanks. Allowing for a 10% work access area of approximately 7 m^2, then 70 m^2 are needed for the maturation area.

Raceways

In addition to the hatchery and broodstock facilities described above there are specific needs for selection experiments under intensive, raceway culture and for evaluating the genetic and phenotypic covariances in early and late growth rates as a function of temperature (identified as a high priority research task). To do this a genetic group will have to be divided into two parts and simultaneously one part tested under an early, cool — late, warm temperature regime, the other part under an early, warm — late, cool temperature regime. The only practical way to achieve this temperature control is in indoor temperature-controlled raceways. It is estimated that 48 raceways are needed, including 32 for a selection experiment. If each raceway has a surface area of 10 m^2 then 480 m^2 are needed for these containers. With a 10% access area, this amounts to a total of 528 m^2 for the raceway growout area.

Unless fresh seawater can be obtained directly, the minimum reservoir tank volume should equal the final working volume of all larval rearing, maturation, and raceway tanks, assuming an exchange of 100% per day. Ideally this exchange rate volume should be backed up with at least two volumes of reservoir capacity for sanitation (e.g., chlorination, dechlorination, sedimentation, and filtration pass through). Therefore under ideal circumstances reservoir capacity should be three times that of the working volume of all tanks.



University of Hawaii
Sea Grant College Program
1000 Pope Road, Room 220
Honolulu, Hawaii 96822