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ON THE SELECTION OF AQUACULTURE SPECIES: A CASE STUDY OF MARINE MOLLUSCS

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ABSTRACT

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An overview of marine mollusc culture in the Pacific Ocean reveals a rich variety of species in culture, physical environments where culture is effected, and technological, social, and economic backgrounds of the participating individuals. Despite this variety a few basic criteria have, until recently, dictated which molluscan species are prime candidates for aquaculture. It is the purpose of this article to illustrate how innovative thinking has influenced the historical development of mollusc culture and how advancing culture technology has influenced, and potentially will influence, the future choice of prime aquaculture species.

The criteria for selection of aquaculture species, first documented by Fan Lee nearly 2500 years ago in a treatise devoted to pond culture of freshwater fishes, stated that high priority should be given to species that grow rapidly, are tasty, not cannibalistic, hardy, and inexpensive to culture. It was not until the twentieth century that more intensive or extensive culture efforts made apparent the need to append this list to include adequate availability of seed from natural sources and good market value of final product. Two somewhat unrelated efforts were, however, to provide additional options for present and future efforts in molluscan culture. Both efforts gained momentum during the early decades of this century.

The first effort was the establishment of a reproducing population of *Crassostrea gigas* on the northwest coast of the North American continent through active introduction of breeding stock. The second effort was the development of controlled or manipulated environment hatcheries for seed production, mostly of oysters and mostly on the U.S. east coast. In combination these resulted in the aquaculturist being able to choose a candidate species from a global rather than local endemic pool and to uncouple the problem of seed or juvenile stock availability from natural biological fluctuations and seasonality.

We are now able to raise and maintain, through one or more generations, species that have only a marginal rating by Lee's original criteria, but that command high market prices from natural fisheries. A dichotomy in future development is evident. Where the primary stimulus is large volume production for consumption purposes, through a combination of intensive juvenile production and extensive grow-out methods, an appended listing of Lee's criteria is applicable irrespective of the economic and social background of the group being served. In contrast, where the primary stimlus is economic, and focuses on the culture of one of the aforementioned marginally appropriate but highly priced species, then equal or greater consideration must be given to the biological, engineering, and financial limitations of culturing large numbers of seed to adult size in a controlled environment.

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INTRODUCTION

The theme of this issue of *Aquaculture* is innovation in mollusc cultivation. I will illustrate how innovative thinking has influenced the historical development of mollusc culture and how advancing culture technology has influenced, and potentially will influence, choice of prime aquaculture species.

HISTORICAL PERSPECTIVE

The first documentation of criteria for the selection of aquaculture species was that of Fan Lee in about 500 B.C. in his treatise on the pond culture of the common carp, *Cyprinus carpio*, in China. Lee described a monoculture regime which provided animal protein in a subsistence-level economy. His criteria were that prime species were tasty, hardy, not cannibalistic, inexpensive to culture, and grew rapidly. Further application of Lee's criteria in selecting new aquaculture species was not required until approximately 618 A.D. when polyculture of grass carp (*Ctenopharyngodon idellus*), silver carp (*Hypophthalmichthys molitrix*), bighead carp (*Aristichthys nobilis*), and mud carp (*Cirrhinus molitorella*) was initiated. Not discussed by Lee was the requirement for a plentiful supply of juveniles. This was not a major problem with carp, which breed actively in culture ponds. With this addition, Lee's criteria are directly and equally applicable to subsistence economies, including much of the Pacific region, even today.

A survey of commonly cultured marine molluscs illustrates their fitness to Lee's criteria. Not mentioned in Lee's criteria are several particular attributes of marine molluscs which further enhance their suitability. Most cultured molluscs are herbivorous (low in the food chain) and, especially the planktotrophic species, harvest a resource that is directly unavailable to man. In certain physical regimes, such as raft or string culture of mussels or oysters in deep estuaries with good tidal exchange, the natural primary productivity of a large area can be harvested conveniently by one localized grazer, especially if the latter is distributed through the water column (see Ryther, 1969, for comments on potential production of planktotrophic molluscs in a temperate estuary, and Bardach *et al.*, 1972, for comments on productivity of raft culture systems). Temperate estuarine or intertidal regions are generally high-stress environments experiencing excesses of temperature, salinity, and even dessication on daily, tidal, and seasonal time scales. It is, therefore, not surprising to find that many prime mollusc aquaculture species (e.g., members of the genera *Ostrea, Crassostrea*, and *Mytilus*) originate from these regions and are noted for their ability to withstand stress in culture. Enormous fecundity is also a common feature of cultured molluscs (see Galtsoff, 1964; Cole, 1941; Walne, 1964); however, as Brooks (1890) noted, even enormous fecundity cannot offset the wastage of eggs at spawning, losses during larval life and early postsettlement, and, most of all, continued fishing pressure.

Culture of marine molluscs has, like pond culture of fishes, a considerable history. Perhaps the first effort to enhance natural oyster production is that reported by Plinius, who described how a Roman knight, Sergius Orata, working in Lake Avermis noted that *Ostrea edulis* juveniles had preferred substrates for settlement. By providing supplementary substrate, in this case brushwood of the mastic tree (*Pistacea lentiscus*) and the evergreen oak (*Quercus ilex*), Orata was able to increase spat settlement and subsequent production. This simple, innovative action initiated a method of oyster culture that is still used today for *O. edulis* in Norway and Yugoslavia (Korringa, 1976a), for *Crassostrea rhizophorae* in Cuba and throughout Latin America (Nikolic *et al.*, 1976), and *C. tulipa* in Sierra Leone, West Africa (Kamara, 1982).

Oyster culture in the Pacific probably began in earnest in the seventeenth century; however, shell mounds indicate the importance of harvested shellfish prior to that date (Korringa, 1976b). Again, initial efforts at enhancing natural production were stimulated by observation of settlement of *C. gigas* on bamboo fish weirs. Implanting bamboo sticks specifically for collection of oysters was undertaken. Later generations of oyster culturists included the use of shell strings for the same purpose, a practice still evident today.

Enhancement activity based on observation rather than experimentation or even a basic understanding of life history was a continuing practice until the late nineteenth century when several landmark investigations were made. In 1879, working at Crisfield, Maryland, Brooks successfully cultured the larvae of *C. virginica*. His methods were closely observed by Winslow, who, in 1880 while stationed in Cadiz, subsequently used them to culture the larvae of *C. angulata*. Brooks (1890) commented on the decline of the Chesapeake Bay oyster fishery due to continued heavy fishing pressure and the prospects for revitalizing the oyster industry. He stated that the only true remedy was to encourage planting of oysters in native waters. Driven by this goal he made pioneering studies of settlement of larvae on old oyster shell (thereby elegantly demonstrating the biological basis for the practice of planting cultch that had been effected, with some debate, in New York waters since the early 1850s). Work by Coste and DeBon in France (at the order of Napoleon) had also focused attention on provision of suitable substrate. Their work was continued by Kimmerer (see Orton, 1937, p. 123), who subsequently developed the lime-coated tile as a spat collector that allowed removal of juvenile oysters. In 1882, M. Bouchon-Brandeley succeeded in combining enclosure of spawning *C. angulata* with tile spat-collection techniques to effect the first production of oyster spat suitable for planting.

The work of Brooks, Winslow, Kimmerer, and Bouchon-Brandeley had set the stage for efforts to mass produce and metamorphose oyster larvae for subsequent field planting. The bivalve hatchery business was born.

THE DEVELOPMENT OF MODERN BIVALVE HATCHERIES

Under natural conditions bivalve molluscs experience massive mortalities during the first few weeks of larval and postlarval development. These losses are balanced by high fecundity of breeding females. Bivalve hatcheries are designed to both exploit this high fecundity and minimize early life mortality. The evolution of modern hatchery practice during the twentieth century may be viewed as a continuing process of identifying constrictions to this objective and sequentially overcoming them.

The early efforts of Wells and Glancy, working at the New York Conservation Commission, utilized forced blooming of natural phytoplankton in seawater that had previously been passed through a continuous centrifuge. Larvae reared in such a food regime were subsequently metamorphosed on an oyster-shell cultch. Their technique was gradually improved upon during the following decades by the workers at the Milford Laboratory, predominantly under the direction of Victor Loosanoff. In Europe, work on the rearing of *Ostrea edulis* was also progressing. Working at Conwy, Cole (1937) developed the approach of Bouchon-Brandeley, holding ripe *O. edulis* in large concrete tanks and, during both conditioning and larval development, maintaining a phytoplankton bloom by the addition of nutrients (minced crab!). Larval oysters were allowed to metamorphose on tiles and were subsequently transferred to on-growing sites around Britain (see Walne, 1974, for a general history of culture of *O. edulis* in the United Kingdom).

In providing greater control of the culture process, continuing work in the 1960s and 1970s by Walne in the United Kingdom, and Loosanoff and co-workers at Milford also added increasing complexity. Broodstock conditioning allowed extension of the natural spawning season; the isolation, culture, and evaluation of many phytoplankton species offered increased larval growth rates and percentage of larvae metamorphosing, and improved water-treatment systems afforded greater control of microbial infections. An example of the resultant complexity and capital-intensive nature of modern hatchery operation is illustrated by Dupuy *et al.* (1977). Greater control of culture has been offered as a positive characteristic for inducing investment from the business community, where stability of return is highly regarded. Unfortunately, the stability record of complex "controlled" hatcheries is to date not as unblemished as we would have hoped for. Despite the fact that significant problems remain in modern hatchery development, the cumulative product of hatchery-related research to date has given mollusc aquaculturists three options for future effort which would otherwise have been generally unavailable. These options are to choose appropriate technology for transfer to potential sites and economic climates elsewhere in the world, to use the present technology as a basis for culture of new species, and to operate outside of the time constrictions of natural spawning seasons.

APPROPRIATE TECHNOLOGY AND SPECIES SELECTION IN THE PACIFIC

In the Pacific there exists both a large range in climate and environment, varying from continental extremes of temperature on the western Pacific Rim, to maritime on the Eastern Rim, and from nutrient-depauperate tropical and subtropical islands to nutrient-rich coastal upwelling regions. There exists a similar range in social and economic climates. Where subsistence-level economies are beginning to advance, the transfer of highly sophisticated technology is quite obviously inappropriate. If local stock-enhancement techniques cannot supply present demand and hatchery production of endemic species is considered beneficial, low-technology hatcheries may offer considerable promise. The protocol described by Castagna and Kraeuter (1981), essentially a modified Well-Glancy method, may be appropriate here. Alternatively, if the social and economic pressures demand a rapid response (e.g., months) of the order that cannot be adequately served by construction of a hatchery, importation of seed may be considered. Ironically the development of hatchery technology and modern air transport is now such that it is often as easy, if not easier, to obtain large quantities of seed of nonindigenous rather than indigenous species. Indeed, recent movements of seed of *Crassostrea gigas* outside of its natural range and throughout the Pacific have been extensive (see Bourne, 1978). It is improbable that Lee ever considered the application of his criteria to a global rather than local pool of potential aquaculture species. This option is, however, a very real one to present-day aquaculturists.

The movement of marine mollusc species, particularly oysters, around the world for culture purposes has been extensive in the last century. Reviews of these movements, associated accidental introductions of pest species, and recent summaries of national and international guidelines to control such movements are given in Elton (1958) and Mann (1978, 1984).

An excellent example of selecting a prime mariculture species to fit an available growing environment was that of the importation of *C. gigas* by oriental immigrants to the Pacific Northwest of the United States during the first two decades of this century. Establishment of an actively breeding stock was hindered by substantial losses during transit and low water temperatures in receiving waters (see Quayle, 1969; Bourne, 1978; Chew, 1978). Breeding stocks were eventually established in Samish Bay, Washington and Pendrell Sound, British Columbia and subsequently in many other localities. The North American industry for *C. gigas* is now self-sufficient in seed production but the time required to reach this status has been considerable. In contrast, modern hatchery technology has allowed rapid establishment of *C. gigas* fisheries elsewhere in the world (see Mann, 1978, 1984), including several that are totally dependent upon hatchery seed (e.g., the United Kingdom, see Walne and Helm, 1978). The latter represent a marked contrast to Lee's original pond system which emphasized simplicity and natural reproduction.

Any program involving hatchery production or importation of juvenile forms must also consider means of growing those juveniles to marketable size. A special publication of the European Mariculture Society (Claus *et al.*, 1981) addresses this subject. Predator control is a necessity. Contributions by M. Castagna and K.K. Chew in this issue of *Aquaculture* describe recent advances in protection of infaunal species. Similar studies have been effected with the epifaunal *C. gigas* (Walne and Davies, 1977). Effective techniques are often site and species specific. Simple enclosures, such as "French" fences in northern Europe, are useful where swimming predators are few but inadequate where predation by swimming crabs and fish (e.g., *Holorhinus californicus*, the bat ray fish in the northwest United States) occurs. Suspended culture in lantern nets, on ropes, shellstrings, or even sticks, may alleviate attack from benthic predators such as starfish and predatory gastropods but may also present added cost in antifouling treatment or potential conflict with navigation channels. Unlike hatchery operations, field grow-out is, at best, a marginally controlled operation and a subject deserving of future attention.

FUTURE EFFORTS AND RESEARCH DIRECTIVES

Continuing and worthy development goals in hatchery programs devoted primarily to improving overall system stability and predictability include: conditioning and spawning regimes for broodstock (see Helm *et al.*, 1973; Morse *et al.*, 1977; Mann, 1979a,b; Lannan, 1980; Morse, this issue of *Aquaculture*, and Muranaka and Lannan, this issue of *Aquaculture*); provision of a formulated, stable diet as an alternative to cultured phytoplankton (see Langdon, 1980 and this issue of *Aquaculture*); development of methods to rapidly and simply assess larval health (Gallager and Mann, 1981); controlled induction of metamorphosis (Morse *et al.*, 1979; this issue of *Aquaculture*); simplifying system design (for example the recent replacement of mesh trays with upwelling sites in culture of postmetamorphic forms); and reducing microbial infections (Blogaslawski, 1984). The efforts are driven by two forms of economic incentive: they are identified problem areas which will give the greatest economic return on the development cost, and they promote an image of stability and prosperity to the business investor. Improving, rather than stabilizing, system performance is the primary incentive for expanding research efforts to include genetic engineering (increasing performance through active manipulation — see Morse, this issue of *Aquaculture*), tissue culture (replacing broodstock with defined gamete production systems — an obvious progression from the work of Lubet *et al.*, 1978), and selective breeding (increasing mean performance by selecting from presently available pools — see Newkirk, 1980; and Hershberger and Perdue, this issue of *Aquaculture*).

In the face of these developments, are Lee's original criteria of any current value? The answer lies in the stimulus for culture activity. In subsistence-level or low-technology economies efforts will still be limited to hardy, preferably native species with easily available seed sources. Extensive grow-out is compatible with this technology and Lee's criteria still apply. In high-technology economies, however, the stimulus to production is often primarily or exclusively economic. It is, therefore, not surprising to see efforts to develop culture techniques for species whose prime attribute is high market price. Rather than seeing the identification of a prime aquaculture species (by Lee's criteria) stimulate an appropriate culture technology for that species, we see the cumulative wealth of aquaculture technology for many species encourage efforts with species that may only be mediocre fits to Lee's criteria. The change is subtle but very significant.

An example illustrates this problem. Abalones command high market prices in Europe, North America, and the Orient. Most species are, however, slow growing. A commitment to growing these species, even at an accelerated rate, in closed environmentally controlled systems represents a long term venture in which return on capital investment can take a number of years. Creative marketing strategies, such as that to sell small abalones to the gourmet restaurant market (Chew, this issue of *Aquaculture*) rather than retain animals to a size comparable to naturally fished specimens, can reduce such economic pressures. Such strategies, however, serve only a small market and have limited potential for expansion. If large-scale, economically viable, closed-system culture of species that are only marginal fits to Lee's criteria is to be realized, the required advances will be predominantly in the area of engineering and water quality control rather than basic understanding of species biology (see, for example, contributions in Bolton, 1982, a description of closed system culture of bivalves). A comparison with the development of high-intensity terrestrial agriculture is tempting with concentrated effort being applied to inbred, highly productive strains that require continual care and attention. Ironically such characteristics are almost diametrically opposed to those outlined by Fan Lee.

Innovative thinking and actions have, over historical time, allowed progression from mimicry of pure observation, through manipulative studies that have also provided considerable insight into the biology of cultured species, to the present capability to maintain species both far removed from their indigenous range and unconstricted by seasonal reproductive periodicity. The appropriate technology for any particular locality is still closely allied to the prevailing economic and social climate. Although the pool of potential aquaculture species is now global rather than local, the selection criteria for a species in any chosen locality are, with only a few notable exceptions, still as outlined by Fan Lee over 2500 years ago.

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