Asian Fisheries Society, 11(1998): 59-69
Asian Fisheries Society, Manila, Philippines
https://doi.org/10.33997/j.afs.1998.11.1.007

Review Article

Domestication of Crustaceans

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Abstract

At least 60 species of crustaceans are farmed experimentally or commercially, mostly in the tropics and subtropics where species maturation times are shorter than in temper-ate climates. Over 50 species are kept by aquarists, and several, especially Artemia spp., are widely used as live foods for rearing fish and aquatic invertebrates. However, there has been far less application of genetics in crustacean farming than in finfish and mollusc farming, and very few crustaceans can be regarded as domesticated. The exceptions are a few disease-resistant and selectively-bred strains of farmed penaeid shrimps, color variants of some freshwater crayfish, and selected strains of *Artemia franciscana*. This is likely to change, but efforts to domesticate crustacean species are often hampered by the technical challenges of closing complex life cycles and coping with aggressive behavior in captivity. This applies particularly to marine species such as lobsters and crabs.

The development of domesticated breeds can contribute to making crustacean farming more productive, more profitable and, when feasible, less environmentally damaging. New breeding goals are being set for farmed penaeid shrimps, e.g. faster growth, disease resistance and tolerance to environmental stress. It may also be preferable to breed in captivity some species of crustaceans for the aquarium trade, rather than exploiting wild populations. Realizing all these possibilities will require a major research effort.

Introduction

Crustaceans contributed about 5.4% by weight (5.9 million t) and 15% by value (16.8 billion US dollars) to the world's supply of aquatic produce (less seaweeds) in 1993 (FAO 1996, 1997). Of these totals, about 3.5 million t were from crustacean fisheries and 0.9 million t from aquaculture. Bardach et al. (1972) mentioned around 60 species of crustaceans that have been farmed experimentally or commercially. This total probably remains about the same. FAO (1995b) reported 38 different crustacean aquaculture species or species groups. The possibility of enhancing crustacean fisheries by stocking from hatcheries has also been investigated and a few operations have become established, e.g. *Penaeus chinensis* in the Yellow Sea (Liu 1990) and astacid crayfish in Europe (Holdich 1993). Crustaceans are also widely used in the aquarium trade and as live foods in hatcheries and aquaria.

To what extent can crustaceans be domesticated? It may be valid to assess the domestication of plants, invertebrates and lower vertebrates using the same criteria as for domestic animals. Darwin (1875) applied the concept and criteria to a wide range of plants and animals, including bees and goldfish, and stated when explaining natural selection:

"So it is with certain parts of or organs in the same individual animal or plant, for instance, the jaws and legs of a crab ...."

Crustaceans are a well defined group. Domestication is less strictly defined. The following definition, developed by plant geneticists, is appropriate to our use.

"Domestication - the evolution of plants or animals either naturally or through artificial selection, to forms more useful to man .... characteristics of domestication are frequently absent in wild-types of the organisms and may constitute a negative genetic load for survival in the wild state" (IBPGR 1991).

Natural selection acts on captive-bred populations in addition to any artificial selection or genetic manipulations that may be imposed. This is termed domestication selection (Doyle, 1983) and can be rapid. Aquatic organisms are usually highly fecund and their early life history stages often suffer large mortalities in the wild and when bred in captivity. This may lead to a rapid loss of genetic diversity and poses problems for scientists trying to conserve the diversity by ex situ genebanking. Cryopreservation of gametes and embryos would be a solution but has not yet been well developed for crustaceans (Subramoniam 1994; B. Harvey, pers. comm.).

Crustaceans in Research on Domestication

Captive breeding is a prerequisite to domestication. Many crustacean life cycles, particularly the larval stages, have been studied in the laboratory, some from as early as the last century (Provenzano 1985) to enable identification of their many zooplankton stages. However, such studies have been almost entirely for scientific purposes and not for domestication. Marine shrimp (*Penaeus japonicus*) were first spawned in captivity in Japan in 1933 (Hudinaga 1942; Shigueno 1975), but mating and spawning in captivity were not commonly achieved until the mid-1970s (Shigueno 1975). For some species, such as *Penaeus monodon*, which dominates world shrimp aquaculture production, captive breeding is readily performed but commercial production still relies largely on capturing broodstock from the wild.

Freshwater crustaceans are generally easier to breed in captivity than marine species, and some have figured in basic studies on domestic selection. *Gammarus lawrencianus*, an estuarine species, was selected for adaptation to a laboratory environment over about 26 generations, when it was used as a model species for crustacean genetic studies (Doyle and Hunte 1981). Under conditions that allowed constantly increasing population size, its intrinsic rate of population growth increased 1.7-fold. The authors interpreted these results as selection for Darwinian fitness to the controlled environment and concluded that a possible approach to genetic improvement of commercially important crustaceans (e.g. *Macrobrachium rosenbergii*) might be to 'domesticate' the stock through such selection to farm environments before attempting breeding programs as applied to livestock. They suggested that domestication could improve yields by about 300%. Doyle (1983) further discussed domestic selection in aquaculture, including the abovementioned study and others on crustaceans: for *Macrobrachium rosenbergii*, selection on growth associated with variable development rate and age-at-harvest; and for *Homarus* spp., selection on growth caused by size-selective mortality in juveniles. His conclusion, still ignored by many farmers, was that management procedures in aquaculture can bring about strong positive or negative genetic change, through selection.

The parthenogenetic waterflea, *Daphnia magna*, is used extensively around the world in bioassay work and clones have been developed to ensure comparable results (e.g. see Baird et al. 1990; Barber et al. 1990). This use of genetically identical individuals has its advantages, but there are also drawbacks due to loss of variability.

Crustaceans in Aquaculture

The First International Symposium on Genetics in Aquaculture (Wilkins and Gosling 1983), held in Galway, Scotland, in 1982, was a turning point in the application of genetics to aquaculture. Previously, many researchers, developers and donors had held that applying genetics to aquaculture would be too costly and time-consuming and that research to improve feeds, husbandry, reproductive performance and health were all much more important. This reflected an overall weakness of aquaculture science, compared to agronomy, and the very short history of captive breeding for some of the most prominent farmed aquatic species: for example, the Chinese and Indian carps had long been farmed on a massive scale, but had been bred in captivity only since the 1960s.

The Galway Symposium contained contributions that would change this reluctance to apply genetics in aquaculture (Pullin 1982), but this process took at least a decade, during which time those who pioneered new selective breeding programs, even on species for which captive breeding was easy and generation times short [e.g. the tilapias (Pullin and Capili 1987)], faced scepticism and limited funding support.

The application of genetics in crustacean aquaculture has been even harder. Malecha (1983) stated, at the Galway symposium, that farmed crustaceans were "undomesticated", that no selection had been done on them and that, among all groups of farmed aquatic organisms, they have had the least amount of genetic research applied to them. He summarized the low genetic variability found in studies on farmed crustaceans and their relatives. Lee and Wickins (1992) also reviewed this information, from which it was assumed that progress in domestication and selective breeding of crustaceans would be difficult and slow. This evidence and the apparent difficulties in rearing, maturing, and rematuring crustaceans in captivity to produce high quality progeny have discouraged would-be crustacean breeders.

In retrospect, there are lessons here for research prioritization: the prevailing conclusions of the period reflected a paucity of data, insufficient analysis of those at hand and the biases of past thinking. The data suggested very low genetic variability for crustaceans but, like the data from almost all population genetics research carried out on aquatic organisms, they referred only to neutral markers, i.e., those having no established relevance to commercial traits. The assumption that such low variability means little or no scope for selection is probably false.

Benzie *et al.* (1992) have now found significant structuring of *Penaeus monodon* populations across northern Australia and have challenged previous conclusions of low genetic variation among penaeids. Recent advances in the analysis of genetic markers in penaeid prawns now permit even more precise separation of wild stocks (Aubert and Lightner 1997), improved precision in quantifying responses to selection, establishing pedigrees, monitoring inbreeding and measuring heritability (De Tomas Kutz *et al.* 1997), and in elucidating the genetics of commercially important traits in farmed prawns (Moore *et al.* 1996; Whan *et al.* 1996; Alcivar-Warren 1997; Alcivar-Warren *et al.* 1997; Astrofsky *et al.* 1997).

The calls for selective breeding programs for crustaceans, - and there were a few even back at the Galway meeting (Gjedrem 1983; Lester 1983) - are now being heeded, not only because of a growing realization that well-planned selective breeding nearly always pays, but also because of problems, especially disease, facing the shrimp farming industry worldwide.

Tropical penaeid shrimps are the major target of this new thrust towards selective breeding. They are currently the most important farmed crustaceans (approximately 920,617 t in 1994) (FAO 1997). Their behavior and the fast generation times of tropical and sub-tropical species pose fewer constraints to captive breeding and growout than, for example, marine crabs and lobsters. Gjedrem and Fimland (1995) summarized knowledge of the heritability of growth traits for penaeids and for *Macrobrachium rosenbergii*. Table 1 shows that progress towards the selective breeding of farmed crustaceans has been limited, but real. Given the economic incentives (e.g. to avoid massive production losses from disease caused by pathogens such as the IHHN virus) and the fast generation times of penaeids (most can breed after 3-6 months), future progress may be very rapid, at least, for those species which breed readily in captivity. A few farmed penaeids (the disease-resistant and growth enhanced strains referred to in Table 1) can be already considered domesticated and a few others are about to become so.

Crustaceans in Aquaria

Many crustacean species, including some commensals, are colorful and exciting additions to home or public aquaria. Table 2 lists some of the marine species that are commonly traded. Given the difficulties and costs of closing some crustacean life-cycles, most of these species will continue to be harvested from the wild as long as stocks last. There is also trade in freshwater lobsters (i.e., crayfish) and land hermit crabs as pets. *Artemia* spp., sometimes called

Table 1. Progress with and constraints to genetic selection in some cultured crustaceans.

Species/ Families	Status of hatchery technology/ captive breeding	Progress with selective breeding	Constraints to selective breeding	Reference(s)
Penaeus stylirostris	Commercial; about 23 generations in captivity in Tahiti and New Caledonia since 1980.	IHHN virus-resistant strain identified; other breeding goals pursued from 1992, including growth, tolerance to environmental stress and disease resistance	Narrow genetic base of captive stock; prior ad hoc selection for growth in the hatchery.	Bedier *et al.* (1996, 1997)
Penaeus vannamei	Commercial; captive breeding since 1980 in Texas.	Specific Pathogen Free (SPF) strains being sought; some identified - e.g. IHHN virus-resistant strain from Mexico; other breeding goals, such as growth, to be targeted next; a research consortium in the USA has a breeding program aimed at reducing the US shrimp trade deficit Significant genetic variation in growth among families; growth heritable.	Quarantine protocols are crucial because wild strains are still being imported for testing.	Sunden and Davis (1991); Gjedrem and Fimland (1995); Pruder *et al.* (1996) Alcivar-Warren *et al.* (1997); Carr *et al.* (1997); De Tomas Kutz *et al.* (1997)
Penaeus monodon	Commercial; but wild-caught gravid females are still preferred to captive-matured females.	Not significant because of captive breeding constraints; but heritability of growth determined as 0.1 based on 18 half-sib families.	Reasons for lesser performance of captive mature breeders not known.	Benzie (1996)
Penaeus japonicus	Commercial; experimental captive spawning established since 1933.	Genetic drift (loss of heterozygosity) described after seven generations of captive breeding in Italy.	Possibly low levels of variability due to inbreeding.	Sbordoni *et al.* (1987)
	Commercial-scale selective breeding for growth commenced in 1993 in Australia.	Significant improvement in growth demonstrated in five generations of farmed stocks in Australia. Heritability for growth and response to selection determined in controlled conditions; DNA markers identified.	Recent farm and tank experiments demonstrate rapid and significant positive response to selection for improved growth.	Hetzel *et al.* (1997); Moore *et al.* (1997)
Marine lobster (*Nephropsidae panuliridae*)	Experimental	None	Poor larval survival; aggresive	Nash (1991)
Freshwater prawns (*Macrobrachium* spp.)	Commercial; captive breeding established since the 1960s.	None. Growth heritability for female juvenile *M. rosenbergii* 0.35 ± 0.15 not significant for males.	Large variability in growth performance, especially males which display two morphologically distinct forms (small orange claw and large blue claw).	Malecha *et al.* 1984; Brown (1991); Daniels *et al.* (1995)

Table 2. Marine crustaceans used in the aquarium trade [K. Davenport, Ornamental Fish Industry (U.K.), Ltd., pers. comm.].

Shrimps		Crabs		Lobsters	
Common Name	Scientific Name	Common Name	Scientific Name	Common Name	Scientific Name
Anemone	*Periclimenes* spp.	Anemone-Pink	*Neopetrolishes maculatus*	Blue	*Panulirus versicolor*
Boxing	*Stenopus hispidus*	Anemone-Spotted	*Neopetrolisthes oshimai*	Common.	*Panulirus* sp.
Boxing-Pair	*Stenopus hispidus*	Arrowhead	*Stenorhynchus seticornis*	Pink	*Enoplometopus daumi*
Boxing-Rare	*Stenopus spp.*	Boxer	*Lybia* spp.	Scarlet	*Enoplometosus occidentalis*
Cave	*Stenopus pyrsonotus*	Decorator	*Libinia* spp.		
Cleaner	*Lysmata grabhami*	Decorator-Deepwater	*Stenorhynchus* sp.		
Crystal	*Periclimenes* spp.	Fiddler-Red	*Ucauca*		
Dancing	*Rhynchocinetes uritai*	Hermit-Common	*Clibinarius vittatus*		
Fire	*Lysmata debelius*	Hermit-Fancy Shell	*Clibinarius vittatus*		
Harlequin	*Hymenocara picta*	Hermit-Hawaiian Orange	*Dardanus megistos*		
Hawaiin-Big Eye	*Rhynchocinetes* sp.				
Hawaiin-Mosaic	*Saron marmoratus*	Hermit-Red Hairy	*Dardanus megistos*		
Jewel	*Saron* sp.	Hermit-Rock	*Pylopagurus* sp.		
Mantis	*Squilla* spp.	Hermit-Rock Red Leg	*Pylopagurus* sp.		
Mantis-Giant Green	*Squilla spp.*	Hermit-Rock White Claw	*Pylopagurus* sp		
Mosaic	*Saron inermis*				
Pistol	*Alpheus* spp.	Hermit-Tiger	*Aniculus maximus*		
Peppermint	*Lysmata rathbunae*	Horseshoe-Porcelain	*Porcellana* sp.		
Peppermint	*Lysmata californica*	Sally Light foot	*Peronon gibbesi*		
Purple Leg	*Saron rectirostris*				
Sexy	*Thor ambioensis*				

'sea monkeys', are sold as pets and as educational tools: they can be used to demonstrate reactions to light.

Some pet crustaceans are expensive. Hermit crabs have been sold in major department stores in Seoul, Korea for US$20-30 each. The crustacean 'sell' can also be highly imaginative. Aquarium shops in Manila, Philippines, sell the red swamp crayfish (*Procambarus clarkii*) with the slogans "Share your good tidings with a live Fortune Lobster" and "Fortune Lobster owners believe that an alert Fortune Lobster with 'Open Claws' helps them 'GRAB' all the 'Good Opportunities' coming their way." This species is also on sale in the UK as the 'Red Lobster' at up to 12 Pounds Sterling per individual. Such crayfish are easy to breed in captivity as, unlike their marine counterparts, they do not have larval stages but hatch as miniature crayfish. Color varieties of *Procambarus* spp. are often advertised for sale in aquarist magazines. Apart from these, can any of the crustaceans used by aquarists be considered as domesticated? The authors do not think so as there are no examples that can compare to domesticated finfish varieties such as goldfish and guppies.

Unfortunately, introductions and transfers of crustaceans for aquaculture and the aquarium trade are rarely preceded by appraisals of the environmental impacts that might occur if the animals escape or are released. The repercussions can be serious (Holdich 1988). Attempts to eradicate *Procambarus clarkii* can devastate wildlife (Mackenzie 1986). This species is also a known vector for the crayfish plague fungus (Dieguez-Uribeondo and Söderhäll 1993). Mikkola (1994) has warned against using *Procambarus clarkii* and *Cherax* spp. in southern Africa. *Procambarus clarkii* was brought to the Philippines by entrepreneurs who also imported the golden snail (*Pomacea* sp.), a pest that subsequently infested 400,000 ha. of ricefields (Acosta and Pullin 1991). The recent export of the Australian native red-claw crayfish (*Cherax quadricarinatus*) to countries such as Equador (Romero 1997; Romero and Murillo 1997) provides a good example of introducing an exotic species without sufficient consideration of the possible ecological consequences.

Crustaceans as food organisms in aquaculture and aquaria

Crustaceans are used worldwide as live foods for rearing fish and invertebrates. The main examples are the cladocerans (e.g. *Daphnia* and *Moina* spp.) in freshwater and, in brackish- and marine waters, *Artemia* spp. and a growing number of copepod species: the use of *Tigriopus* sp. is well established and others are under research [(e.g. *Acartia plumosa* (Sunyoto et al. 1995)]. The use of Artemia dwarfs that of all other species (Van Stappen and Soorgeloos 1993) but the global supply of Artemia cysts has been in jeopardy since mid-1995 as a result of two consecutive bad harvests at the Great Salt Lake in Utah, the origin of over 80% of all Artemia cysts used in aquaculture. Cysts from several sources in Russia and China are now entering the market. The annual consumption of cysts in aquaculture is somewhere between 2,000 and 3,000 t: it was close to or above 3,000 t in previous years but is now around 2,000 t because of the shortage. In terms of value, this industry is worth over US$100 million annually (P. Sorgeloos, pers. comm.).

Most of the various strains of Artemia cysts supplied for aquaculture are collected from salt flats and are not domesticated. Moreover, tailoring the polyunsaturated fatty acid profiles of Artemia (Leger and Sorgeloos 1985) to the nutritional requirements of farmed aquatic organisms has relied largely on feeding microencapsulated diets to nauplii, rather than on genetic approaches.It is, however, possible to consider a few Artemia stocks as domesticated. These include the selected strains of *Artemia franciscana* that are cultured in artisanal saltworks, mainly in Vietnam and, to lesser extents in, for example, Madagascar and Peru. These operations yield top quality Artemia cysts (small size, high HUFA content) and are prized as starter feeds in marine fish (and sometimes shrimp) larviculture. They command a very high price (over US$100 per kg) and only small quantities are at present available: just over 10 $t \cdot yr^{-1}$ (P. Sorgeloos, pers. comm.)

The Future

With the domestication of most farmed aquatic organisms still just beginning, the crustaceans present special challenges and great potential. They command high prices worldwide but hardly any are domesticated. A few farmed penaeids are on the road to domestication and, for these, future progress is likely to be rapid given their economic value, short generation time and lack of aggressive behavior.

Domestication of crustaceans will require thorough evaluation of their genetic resources; closing complex life-cycles for captive breeding, rematuration and production of high quality progeny in captivity; engineering ways around the problems of aggression and cannibalism, especially during moulting; reducing the generation times of long-lived species such as crayfish, lobsters and crabs; and ensuring adequate nutrition and health in captivity. The domestication of crustaceans and their wider use by humans must also avoid adverse environmental and social impacts. Further progress will depend on adequate resources for the necessary research and the choice of appropriate strategies. If these are done, the domestication and selective breeding of crustaceans can have a major impact on the productivity and sustainability of crustacean aquaculture.

Acknowledgments

The authors wish to thank those who contributed information for the preparation of this paper, especially Keith Davenport, Ornamental Fish Industry (U.K.); Dr. David Holdich (University of Nottingham); Dr. Patrick Sorgeloos, Director, Artemia Reference Center, Ghent; and Dr. Brian Harvey, World Fisheries Trust, Victoria, B.C.

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Manuscript received 26 January 1998; Accepted 5 March 1998.