Asian Fisheries Science **14**(2001): 121-142
ISSN: 0116-6514
https://doi.org/10.33997/j.afs.2001.14.2.003

Proceedings of the International Forum on the Culture of Portunid Crabs

Asian Fisheries Society, Manila, Philippines

Choosing Tropical Portunid Species for Culture, Domestication and Stock Enhancement in the Indo-Pacific

M.J. WILLIAMS[1] and J.H. PRIMAVERA[2]

[1]*ICLARM – The World Fish Center*
PO Box 500, GPO 10670
Penang, Malaysia

[2]*Aquaculture Department*
Southeast Asian Fisheries Development Center
Tigbauan, Iloilo, Philippines

Abstract

Large and long-term investments in research, development and technology verification are required for the successful culture, domestication and coastal stock enhancement of any species, including crabs. As more species options are sought for culture, the choice of candidate species could be guided by *ex-ante* assessments to help identify suitable species and anticipate future constraints and opportunities. Focusing on tropical Indo-West Pacific Portunidae, we propose multiple criteria for domestication and stock enhancement that include life cycle, diet and feed conversion efficiency, behavior, disease resistance, growth rate, marketability, farming systems, profitability and environmental impact. The chief candidate species (four species of *Scylla*, *Portunus pelagicus, P. sanguinolentus,* and *Charybdis feriatus*) are considered against the criteria. Experience in the stock enhancement of *P. trituberculatus,* a subtropical portunid, is reviewed. We conclude that full domestication will not occur in the next 5 to 10 years and that the main constraints to be overcome are the aggressive behavior of the crabs, their carnivorous diet and competition for suitable coastal farm sites. We also recommend considering the tropical *Portunus* and *Charybdis* species examined here as additional or alternative options to the *Scylla* species. Stock enhancement may be feasible in some locations, provided suitable fisheries management and industry institutions are created.

Introduction

Several large tropical species of the swimming crabs, family Portunidae, are prized as food and considered candidate species for aquaculture. The culture of the mud crab *Scylla serrata* dates back to 1890 in Guangdong, China (Shen and Lai 1994). Since the 1970s, steady interest has been shown in the culture of *Scylla* species in tropical Asia, mainly in the farming of wild juveniles and socio-economic studies. As hatchery production of *Scylla* species becomes a reality, greater investments will be made in research, development and technology verification, and new challenges in farming, such as disease and potential environmental problems will ensue. To make such investments efficient and effective, examining the portunid species to domesticate or enhance stock could serve as an *ex-ante* guide to identifying future constraints and opportunities and filling knowledge gaps.

In the present paper, the species considered are *S. serrata, S. olivacea, S. tranquebarica, S. paramamosain, P. pelagicus, P. sanguinolentus,* and *C. feriatus*. One temperate species, *P. trituberculatus* is also considered as a model species for stock enhancement using three decades of stock enhancement experience in Japan.

This paper suggests a set of species selection criteria for domestication and stock enhancement and applies the criteria to tropical portunid crabs. Some critical gaps are caused by the uncertain taxonomy of the genus *Scylla*, dating back to the 1940s when Estampador (1949) described three species and one variety. This taxonomy was later revised by Stephenson and Campbell (1960), who recognized only one species of *Scylla*, namely *S. serrata*, and by Keenan et al. (1998) who divided the genus *Scylla* into four separate species based on allozyme electrophoresis and mtDNA sequencing. However, Ronquillo et al. (1999) claim that the morphology of the neotypes designated by Keenan et al. (1998) are not consistent with the holotypes described for *C. serratus* by Forsskal, *C. olivaceus* by Herbst, and *S. serrata* var. *paramamosain* by Estampador (1949). Knowledge on biological and aquaculture systems for the other large portunids is also scant.

Reviewing the domestication[1] of crustaceans using a strict definition, Pullin et al. (1998) noted that less progress had been made in closing the life cycles of crustacea than for any other major aquatic taxa, probably due to their complex life cycles and aggressive behavior. Full domestication is not possible unless life cycles can be closed in captivity.

An Overview of Criteria for Selection

A set of criteria for selecting species for domestication and stock enhancement synthesized from the works of Bardach et al. (1972), Blankenship and Leber (1995), Ross and Beveridge (1995), Munro and Bell (1997) and Travis et al. (1998) has been adapted (Table 1). Encompassing biological, aquaculture, environmental, social and economic factors, we use the criteria to review the suitability for full culture and/or stock enhancement of the *Scylla* species and *P. pelagicus, P. sanguinolentus* and *C. feriatus*. Stock enhancement of *P. trituberculatus* in Japan is also reviewed, especially the occurrence of diseases during hatchery rearing.

---

[1]*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).*

Scylla species

Most of the articles reviewed below were written before revision of the genus (Keenan et al. 1998), therefore the original species names of *Scylla* as they appear in the literature are retained.

LIFE CYCLE/REPRODUCTION IN CAPTIVITY

The most common criteria for sexual maturity in *S. serrata* are the presence of mature abdomen form and mature ovaries for females, and the presence of sperm in sperm ducts and mating scars for males (Robertson and Kruger 1994). In general, there is a trend towards smaller sizes at maturity in the lower latitudes with recent reports of a minimum carapace width (CW) of 90 mm for ovigerous mud crab from Indonesia (Poovichiranon 1992) and Malaysia (Marichamy 1996). A female mud crab

Table 1. Criteria for selection of Portunid species for domestication and stock enhancement. Criteria marked "E" are considered essential and those marked "D" are desirable or relative.

Domestication[1 2]	Stock Enhancementf[3 4 5]
1. Closed life cycle. Reproduction in captivity achievable biologically, technically and economically. Preferably young age at maturity. (E)	1. Captive breeding achievable. Age at maturity not critical since breeders are taken from the wild and do not need to be held in captivity. (E)
2. Diet such that feeds, will be available in suitable quantity and quality. Herbivores and autotrophs are more economical to feed than omnivores or carnivores. (E)	2. Suitable natural feed available in the target ecosystem. (D)
3. Behavior, including social, mating and migratory behavior, permits culture and confinement. (E)	3. Behavior permits handling for breeding. (E)
4. Resistant to diseases. *A priori*, disease susceptibility is difficult to determine since risks usually increase with time, as culture intensifies and as the number of pathogens to which the species is exposed increases. (E)	4. Diseases in the hatchery are manageable and methods can be found to minimize the risk of transferring diseases to wild stock. (E)
5. Species has good growth and large size. Price, market and nutritional value may be quite independent of size but faster growing species usually give better returns than slower growers. (E)	5. Species has good growth and large size unless use and value dictates otherwise. (D)
6. One or more products from the species has good market demand. One species may have many different products and markets. (E)	6. Market or use demand is strong, e.g. for recreational fishing, commercial fishing, conservation, cultural value. (E)
7. Feasible farming systems exist or can be created. Farming systems and the natural, financial, human and knowledge resources required should be kept in the forefront when selecting species. (E)	7. Suitable natural ecosystems exist, including habitats, food/prey, and a balance with predators. An essential part of the system is a species management plan. (E)
8. Profitable enterprises. Costs of production and prices provide a good rate of return. The faster the original investment is recouped, the more attractive will be the enterprise. Rates of risk and perceived risk are low, especially if small scale and poor operators are to be attracted. Labor needs preferably low especially in countries with high labor costs. (D)	8. Costs and benefits, financial, conservation and other enhancement program are as such to make the investment attractive to the government, private and community groups involved. The enhancement program should be monitored to gauge its effectiveness against the objectives. (E)
9. Farming causes minimal or positive environmental impacts, including on biodiversity, genetics of wild populations and on the capture fishery of the species. (E)	9. Should have a positive environmental and biodiversity impact. Genetic resource management should be a prime consideration of the enhancement program. (E)

[1]Bardach, et al 1972
[2]Ross, L.G. and M.C.M Beveridge 1995
[3]Blankenship, H.L. and K. M. Leber 1995
[4]Travis,J. F.C., Coleman C.B., Grimes D. Conover, T.M. Bert & M. Tringali 1998
[5]Munro, J.L. and J.D. Bell 1997

can release 0.5 to 4 million eggs in one spawning (Chen 1990, Latiff and Musa 1995).

Closing of the life cycle of *S. serrata* was first documented by Ong (1964). In contrast to some *Portunus* species, larval rearing in *Scylla* remains a bottleneck. The best survival rates from zoea I (Z_I) to crab I (C_I) from experimental studies are 1% (Ong 1964), 4% (du Plessis 1971), 15% (Marichamy and Rajapackiam 1992), 26% using a recirculating system by Heasman and Fielder (1983) and up to 80% (Mann et al., this volume). For large-scale rearing, Quinitio et al. (this volume) obtained a mean survival rate of 3% from Z_1 to 3 to 5 day old megalopa for *S. serrata* and 24.3% to megalopa for *S. tranquebarica* (Yamaguchi 1991). Cannibalism, particularly at the megalopa and crab stages, is the main cause of mortality (Heasman and Fielder 1983, Jamari 1992, Latiff and Musa 1995).

Recent trials have shown that megalops stocked in net cages inside earthen ponds attain 35 to 50% survival and a 3 g body weight after 30 days (Rodriguez et al., this volume).

FEED/FOOD ITEMS

S. serrata juveniles are omnivores that feed primarily on crustaceans and the subadults are carnivores that prey on bivalves (Jayamanne and Jinadasa 1991). The ability of adult mud crabs to feed on a wide size-range of prey is a major factor in their widespread distribution in the Indo-West Pacific region (Hill 1979a). Their feeding behavior and dexterity of the mouthparts enable mud crabs to feed on a variety of large, hard-shelled mollusks and crustaceans (Heasman and Fielder 1978, Williams 1978).

Food items used in mud crab culture include raw (trash) fish, shrimp, crabs, clams, mussel, snails, filamentous algae, 'waste' materials such as kitchen leftovers, bones, animal hide and entrails, fish offal, and shrimp heads (Pagcatipunan 1972, Prinpanapong and Youngwanichsaed 1992, Samarasinghe et al. 1992). These food items reduce operational costs and recycle otherwise low value items (see *Environmental Impacts*).

Larval feeds include microalgae (e.g. *Skeletonema*) and zooplankton (e.g. rotifer and *Artemia*) for the zoea and megalopa stages, and unprocessed wet feeds (e.g. clam meat), and pellets for the early crab instars (Ong 1964, Jamari 1992, Shen and Lai 1994).

BEHAVIOR IN CAPTIVITY

Mud crabs undergo five larval molts before the crab stage, and 15 to 17 more for the juveniles (Heasman and Fielder 1978). Asynchronous molting produces newly-molted individuals in the megalopa, juvenile and adult stages vulnerable to attack by hard-shelled and healthier crabs. Decreasing stocking densities and providing shelters in larval tanks and ponds help reduce cannibalism (Chen 1990, Liong 1992, Marichamy and Rajapackiam 1992) (see *Farming Systems*).

Scylla species bury in soft mud or construct burrows in firm mud (Macnae 1968, Hill 1978), hence the common name 'mud crab'. Since burrows may weaken or destroy the dikes of culture ponds, fences are installed to prevent crab burrowing and escape. *S. serrata* were observed to move at an average speed of 461 m nightly (Hill 1978) and mean displacement of recaptured *S. serrata* was 58.6 to 111.6 m (Robertson and Piper 1991).

DISEASE SUSCEPTIBILITY

Devastating fungal *Lagenidum* spp. infections of *Scylla* larvae and control of infection using treflan, malachite green and formalin have been reported by Bian et al. (1979) and Lio-Po et al. (1982). *Vibrio harveyi* was more pathogenic compared to other luminous bacteria, causing mass deaths among crab larvae (Parenrengi et al. 1993). Mortality may be due to bacterial infection in early larval stages and cannibalism among megalopa and crab stages (Boer et al. 1993). External incubation exposes the eggs to bacteria, fungi and ectoparasites.

The low incidence of diseases in *S. serrata* in the growout phase may be due to low stoking densities. Bacterial populations have been found in lesions on the carapace of wild mud crabs from Queensland, Australia (Walker 1998) and in crabs dying from 'Orange crab' disease in floating net cages (Chong and Mee (1986). *S. serrata* and *P. pelagicus* infected with White Spot Syndrome Virus isolates from infected *P. monodon* by means of injection exhibited mortality, but not immersed crabs (Supamattaya et al. 1998).

GROWTH RATES

Among the four *Scylla* species, *S. serrata* has the highest growth rates, attaining maximum male sizes of 250 to 280 mm CW and 2 to 3 kg BW, compared to 200 mm CW for *S. paramamosain* and *S. tranquebarica*, and 180 mm CW for *S. olivacea* (Carpenter and Niem 1998). Growth rate of *S. serrata* in the wild is rapid in the first 12 to 15 mo reaching 80 to 160 mm CW, then slows to a maximum of 140 to 180 mm CW in year 3 (Hill 1975).

Harvest sizes start at 150 g BW for local markets and 250 g for export. Mud crabs show great variability in size and growth rates, especially when juveniles of diferent sizes are stocked (Varikul et al. 1971, Samarasinghe et al. 1992, Macintosh et al. 1993).

MARKETS

Scylla spp. and other portunid crabs may be sold live (as crablets or adults), processed (chilled, frozen, canned meat), or as byproducts (e.g., shells for chitosan extraction). Mud crabs are a highly prized delicacy in both local and export markets throughout Asia and Australia. Export markets with Chinese communities (e.g., Singapore) and local luxury restaurants and hotels offer higher prices for large, high quality crabs and leave small and watery (post-moult) crabs to local consumers (Jayamanne 1992, Kathirvel and Srinivasagam 1992). These specialized Southeast Asian markets for live crabs may be easily saturated, highlighting the need to diversify products and markets.

Commercial mud crab enterprises generally specialize in three end-products: 1) short-term (<1 mo) fattening of male/female crabs and egg development of female crabs, 2) long-term (>1 mo) grow-out of meat crabs, and 3) soft-shelled crabs (Macintosh et al. 1993, Cholik 1999, Hoang 1998).

Local prices vary with season, size, sex and gonad maturity, the highest of which are the mature females with ripe eggs while the lowest priced are the spawned females and watery crabs. Export categories are also based on size.

FARMING SYSTEMS

Mud crab culture has evolved from low-density pond polyculture with fish (Robles 1983) using wild seeds introduced tidally or intentionally, to monoculture in smaller ponds, pens and cages (Varikul et al. 1971, Cholik and Hanafi 1992) and more recently to integrated mangrove-crab systems (Liong 1993, Primavera and Triño 1999).

Ponds – Fattening or grow-out ponds from 0.25 ha up to 1 ha in size may be earthen, concrete or brick. Fences to prevent escapes are made of bamboo, asbestos sheets, asphalt felt, plastic cloth, and polyethylene netting (Baliao 1983, Liong 1995, Rattanachote and Dangwatanakul 1992). Shelters are provided by building trenches, canals, islands and by stocking seaweeds in the pond (Liong 1993, 1995). Larger crabs are selectively harvested starting at 2 to 3 mo. Yields are 400 to 600 kg crab + 300 to 600 kg fish$\cdot$ha^{-1} crop^{-1} for polyculture (Lijauco et al. 1980, Baliao 1983) and 1 to 2.4 t$\cdot$ha$^{-1}\cdot$ crop^{-1} for monoculture (Agbayani et al. 1990, Marichamy 1996).

Cages and pens – Pens and floating cages made of bamboo, polyethylene netting and galvanized wire netting are set in coastal waters, shallow lagoons and ponds (Cholik and Hanafi 1992, Liong 1993, 1995). Grow-out cages of 3 x 3 x 2 m in Malaysia are stocked at 30 to 60 kg$\cdot$cage^{-1} (Liong 1992). Crabs for fattening in Indonesia are stocked in 2 x 1.5 x 1 m at 70 to 110$\cdot$cage^{-1} or in individual compartments in 2 x 0.5 x 2 m cages, while 4 x 4 x 2.5 m bamboo pens are stocked at 100 crabs$\cdot$pen^{-1} (Cholik and Hanafi 1992).

Mangrove pens – Crab culture can be integrated with conservation of existing mangroves or rehabilitation of degraded areas (Primavera 1995, Primavera and Triño 1999, Overton and Macintosh 1997). Small (160 to 1,200 m^2) and bigger (2,000 m^2) pens are rectangular, square or irregular in shape. The pen area is enclosed by a net set on stakes of wood, bamboo or *nibong* palm embedded in the substrate, or by bamboo slats. Canals to hold water during the low tide occupy 20 to 30% of total pen area; optional gates provide better water exchange (Chang Wei Say and Ikhwanuddin 1999, Triño et al. 1999b). The natural mounds constructed by the mud crab are retained (Primavera and Triño 1999).

PROFITABILITY OF ENTERPRISES

The culture of mud crab for egg development, fattening, or grow-out is highly profitable, perhaps because risks are minimal at low densities and small scale that characterize most enterprises.

Net income of P58,585 $ha^{-1}·yr^{-1}$ to P164,730 $ha^{-1}·yr^{-1}$ (1992, US$1 = Phil. P26), return on investment (ROI) of 49 to 66%, and payback period of 1.17 to 2 yr for culture ponds are reported by Samonte and Agbayani (1992) and Baliao et al. (1999a). Pens earn a monthly income of RM424 (1992-1993, US$ = RM 0.40) in Malaysia (Say and Ikhwanuddin 1999) and a yearly profit of P55,080 (1999, US$1 = Phil.P38), 60% ROI and 1.4 yr payback period in the Philippines (Baliao et al. 1999b).

Environmental impacts

The main impacts of mud crab farming arise from wild seed collection and the use of raw (trash) fish. As culture area and/or stocking densities increase, demand increases for low-value fish which are important protein sources for lower income coastal communities in Southeast Asia.

As long as hatchery production for *Scylla* is unreliable, excessive harvesting of wild seed may deplete wild crab fisheries and affect local populations. Recently established farms that specialize in high value, soft-shelled crabs require use of wild seed (because of higher mortality rates) and present a net loss because meat weight is gained (Overton and Macintosh 1997). Since newly-molted crabs can be frozen, this industry will open a niche similar to frozen shrimp enabling market expansion beyond Southeast Asia (see *Markets*) but also increasing pressure on natural stocks. Nevertheless, mud crab culture can be more environment-friendly than conventional fish or shrimp farming through polyculture with fish, shrimp and seaweed and retention of mangrove trees to provide shelter from heat and unfavorable water conditions.

Portunus species and Charybdis feriatus

The culture and potential culture characteristics of the large *Portunus* species (*P. pelagicus* and *P. sanguinolentus), C. feriatus* and the more temperate *P. trituberculatus* are evaluated here against the criteria, for stock enhancement potential.

LIFE CYCLE/REPRODUCTION IN CAPTIVITY

After their eggs hatch, *P. pelagicus* and *P. trituberculatus* generally pass through four zoeal stages and a megalopa (Motoh et al. 1978, Shinkarenko 1979, Sun Yingmin and Yan Yu 1984, Cowan 1984). However, Jose et al. (1996) reported five zoeal stages in *P. pelagicus* in Mandapam, southern India. The larval stages of *P. sanguinolentus* have not been described although Naidu (1955) described the first zoeal stage from one specimen in India. The eggs hatched into early first zoea stage, whereas those of *P. (Neptunus) pelagicus* were described by the same author as hatching into the prezoea stage. Subsequent studies on the larval development of *P. pelagicus* did not make this distinction.

The duration of larval stages is fairly consistent for each species, at 3 to 4 days each for the zoeal stages of *P. trituberculatus* and 5 to 7 days for the megalopa (Cowan 1984, Sun Yingmin and Yan Yu 1984) at 20 to 25°C. Unlike the three *Portunus* species, *C. feriatus* has six zoeal stages before it molts to megalopa (Motoh and Villaluz 1976).

Data on size at sexual maturity and fecundity for the *Portunus* species and *C. feriatus* (Table 2) are available. Most tropical and temperate populations of the species have ovigerous females all year round, with some seasons showing peak activity. Temperate populations are more seasonal. At present stock levels, ovigerous and mated females are common for all species.

Fecundity is high in all species and all can produce multiple batches of eggs (at least four) from a single mating in a single season. However, Cowan (1984) reports that most hatcheries use only the larvae from the first or first two spawnings, as quality and quantity of eggs deteriorate with successive batches.

In all species, fecundity increases with crab size. Large (1 kg) *P. trituberculatus* females can produce three million eggs (Cowan 1984). Large (>150 mm CW) *P. pelagicus* in Australia may produce over two million eggs (Kailola et al. 1993). More than 1.3 million eggs were recorded from slightly smaller females of *P. pelagicus* in the Philippines (Ingles and Braum 1989).

The life cycle does not appear to have been closed for any of the four species. In Japan, *P. trituberculatus* spawners are caught from the wild either before or after egg-extrusion (Cowan 1984) and monitored carefully until spawning.

In mass rearing of *P. trituberculatus* in Japan, Cowan (1984) and Morioka et al. (1988) report high variability in mortality from first zoeal stage to first to fourth crab stages, based on unpublished reports and hatchery records. Estimates were from 1% to 43% on average across batches, with individual batches having up to 71% survival (quoted in Cowan 1984). Morioka et al. (1988) report possible higher mortality in the 3rd and 4th zoeal stages but this could not be confirmed as a general feature.

Water quality (temperature, salinity, nutrient and hygiene) is a significant factor in larval survival (Motoh et al. 1978).

Larval feeds for *P. trituberculatus* are rotifer (*Brachionus plicatilis)*, brine shrimp *(Artemia salina*) nauplii and hashed krill *(Euphausia pacifica)* under experimental conditions (Morioka et al. 1988). Cowan (1984) described hatchery feeding regimens consisting of the same feed items as well as soy cake, blended fish, clam mince (*Tapes philippinarum),* shrimp mince and artificial feeds. The minces and artificial feeds tended to be used in the megalopa and first crab stages.

Portunus pelagicus larvae fed on *Artemia* nauplii (Shinkarenko 1979), *B. plicatilis,* egg and mussel in suspension and *Tetraselmis sp*. (Raman et al. 1987), mixed phytoplankton (*Chaetoceros spp.* and *Chlorella*), rotifer and freshly hatched *Artemia* nauplii (Jose et al. 1996). Algae alone did not assist larval culture, but *B. plicatilis* was sufficient for survival through all larval stages. *Artemia* enhanced the development from the fourth zoeal stage to the megalopa.

Table 2. Size at first sexual maturity and fecundity in *Portunus trituberculatus, P. pelagicus, P. sanguinolentus* and *Charybdis feriatus*

Country	Size (CW in mm)[Sex/method for determining maturation –see key below] Min	Mean/Range	Fecundity	Reference
P. trituberculatus				
Japan		[F/-](wt/gms): 400/700/1,000	$1x10^6/2x^6/3x10^6$	Cowan (1984)
P. pelagicus				
Philippines, Ragay Gulf	102.0 (M/C) 94.0 (F/C, E)	96.4 (M/H) 106.0 (F/H)	— 142×10^3 - $1{,}132 \times 10^3$ eggs depending on crab size	Ingles and Braum 1989
Philippines, Bantayan, Cebu		96.0 (M/H) 106.0 (F/H)	— 498×10^3 - 44.6×10^9 (*sic*) or 5×10^3 - 13×10^3 eggs·gm^{-1} body wt	Ingles 1996
Australia		(M/E) 85-157 Peel-Harvey Inlet, W. Aust.;≥80 Gulf of Carpentaria; 82, 95-150 Moreton Bay; Qld, 105-140 S. Australia (F/E) 68, Gulf of Carpentaria; 82, Moreton Bay; 96, S. Australia; 120-127, W. Australia		Kailola et al. 1993 (review article)
India, South W.		85-90 (M/AP) 80-90 (F/AA)		Sukumaran and Neelakantan 1996
India, Karnatak	81-85 (F/AA,O)	-	-	Jacob et al. 1990
Egypt	100 (F/E)	-	-	Razek 1987
P. sanguinolentus				
India, Southwest coast		85-90 (M/AP) 80-90 (F/AA)	-	Sukumaran and Neelakantan 1996
India, Kakinada Reg.	36 (CL)(F/E) 26 (CL)(F/P)	(36-72 CL) (F/E)	420×10^3-$1{,}150 \times 10^3$ eggs for females 50 - 70 mm CL	Devi 1985
India, Karnatak	81-85 (F/AP,O)			Jacob et al. 1990
India, South Kanara Coast	78 (F/E)	78-143 (F/E)	300×10^3 eggs for crab 87 mm; 700×10^3 for crab 113 mm	Sukurman et al 1986
C. feriatus				
India, Cochin, Kerala	66 (F/E)	-	52×10^3 to 309×10^3, depending on size of crab	Padayatti 1990

Key: Sex: M - male, F - female

Method for determining maturity: H = Hiatt growth diagram, prepubertal molt estimate; C = observed copulation; E = egg-bearing; AP = allometric growth, chela propodus (males); AA = a llometric growth, abdomen (females), O = ovary development, P = pubertal

Yang et al. (1994 – quoted in Kumar 1997) found that high nitrogen levels in the rearing water reduced the larval survival of *P. trituberculatus*.

In all species, lack of synchronization in larval growth rates and molting can lead to cannibalism during rearing (Cowan 1984, Raman et al. 1987, Jose et al. 1996,) and therefore the larvae from each female are usually reared separately (Cowan 1984).

FEED/DIET

Results from studies on the natural diet of *P. pelagicus* and *P. trituberculatus* indicated that they are opportunistic carnivores, feeding on sessile invertebrates and other available feed (Patel et al. 1979, Williams 1982, Wassenberg and Hill 1987).

BEHAVIOR IN CAPTIVITY

Molting and aggressive behavior of these four species are similar to the *Scylla* species. In the wild, *P. pelagicus* buries in sand soon after molt to escape predation while still soft (Williams 1979).

For stock enhancement, suitable release sites and times would have to be determined based on seasonality, spatial and depth mediated migrations and temperature and salinity tolerances and preferences.

Two of the three *Portunus* species migrate during their life. Mature females tend to prefer deeper, more oceanic waters for spawning (see Kailola et al. 1993 for review of the biology of *P. pelagicus* in Australian waters, Ingles 1988 for this species in the Philippines and Sumpton et al. 1989 for Australian *P. sanguinolentus*). Shiota and Kitada (1992) reported that *P. trituberculatus* in the Seto Inland Sea of Japan did not move far from the tagging sites. The modal distance was between 10 and 20 km. Mated female crabs undertook a spawning migration to shallow waters of 10 m depth. Kurup et al. (1990) reported seasonal occurrences of *P. pelagicus* and *P. sanguinolentus* in a coastal lake in Kerala State, southern India. The presence of crabs was linked to higher salinities. *P. trituberculatus* hibernates in winter in depths between 20 to 30 km in the Seto Inland Sea, Japan (Shiota and Kitada 1992).

DISEASE SUSCEPTIBILITY

In the wild, adult *Portunus* species have been reported as bearing high infestation rates of sacculinid (rhizocephalan) parasites (Sumpton et al. 1989 for *P. pelagicus* in Queensland, Australia, Srinivasagam 1982 for *P. sanguinolentus* in Pulicat Lake in India, and Devi 1985 for *C. feriatus (cruciata)* in Kakinada Region, India). These parasites have serious impacts on the growth, appearance and marketability of the crabs and completely castrate the host crabs. Sacculinids are unlikely to infest cultured species but may establish in stock enhanced fisheries. Other ecto-parasites reported on crabs are barnacles (stalked and acorn), colonial ciliates and hydrozoans (Devi 1985).

In the wild, adults are unlikely to suffer major disease problems although environmental pollution and the impacts of red tides will be constraints in some inshore areas. In stock enhancement, the larval stages in hatcheries could be the most susceptible to diseases.

In Japan, *P. trituberculatus* is susceptible to disease during larval rearing, notably from a *Vibrio* sp. specific to crabs (Muroga et al. 1994). Since 1985, hatcheries have reported larval losses, including catastrophic mortalities, due to pathogens of several types, like fungi in eggs and larvae (Yasonobu et al. 1997, Hamasaki and Hatai 1993).

In Taiwan, wild-caught specimens of *P. sanguinolentus, C. granulata* and *C. feriatus(a)* showed no signs of natural infections by the white spot baculovirus (WSBV) (Wang et al. 1998) which is a major cause of mortality in the farmed shrimp, *Penaeus monodon*. When captive specimens of crabs were fed with *P. monodon* heavily infected with WSBV, mortality among the experimental group of crabs was not significantly different to that of the controls. However, most of the living and dead crabs tested positive for WSBV, indicating that they could carry the virus which was detected in the gills, stomach, hepatopancreas, muscle and reproductive tissue of the crabs (Chang et al. 1998).

GROWTH RATES

All four portunids attain a large maximum size but their sizes and growth rates vary with locality (Table 3). Except for *C. feriatus* for which limited information suggests that males reach a larger maximum size than females (Padayatti 1990), both sexes appear to grow to about the same maximum size. In the wild, the sexes are often segregated by size and space as a result of the different seasonal migrations referred to above.

Most fisheries consist of individuals from one year class only, occasionally two if escapement is sufficient to permit this.

MARKETS

Landings of *P. pelagicus, P. sanguinolentus* and *C. feriatus* are not reported to species level for all countries. Total landings for these and other similar species were 71,319 tons in 1993 and 116,461 tons in 1996 (FAO FishStatPC 1998). China is the dominant producer of *P. trituberculatus*, reporting 283,394 tons in 1996. Japan reported 4,022 tons and South Korea 15,754 tons.

For Australian producers, export markets in Singapore, Kuala Lumpur, Hong Kong, South Korea, Taiwan and Japan of high quality, high value *P. pelagicus* are profitable (Stevens 1997). The Taiwanese and Japanese markets also have a demand for live crabs. However, profitability was based on wild caught crabs and not culture or stock enhanced crabs that would be more expensive to produce.

In contrast to *S. serrata,* none of the four species survive for long out of water, thus presenting transport challenges. All these species have lower

Table 3. Size and growth of *Portunus* and *Charybdis* species

Country	Sex	Maximum size **(CW/mm)**	**Growth Rate**	**No. of crab instars**	**References**
Portunus trituberculatus					
Japan, Osaka Bay	M, F	264	From eggs hatched July, C1 August, Instars 12-13 in November of following year	15	Ariyama 1992
Portunus pelagicus					
Egypt, Mediterranean coast	M, F	185	(a) For crabs 45-55 mm in September: September – December: 16.7 mm·mo^{-1}; December to April: 10.0 mm·mo^{-1} (to 135-145 mm modal size) (b) For crabs 65-85 mm in September: September – December: 15 mm·mo^{-1}; December – April: 5 mm·mo^{-1} (to 135-145 modal size)	-	Razek 1987
India, Kakinada Region	M, F	154	6.4 (M) and 6.8 9(F) mm·mo $^{-1}$ for crabs 41 – 81 mm CL between January and November		
India, Vembanad Lake, Kerala State	M,F	161	-	-	Kurup et al. 1990
Australia	M,F	218 but rarely more than 200 mm; in some regions (northern and southern ends of range in Australia), rarely >150 mm	Maximum age 4 years		Kailola et al. 1993 (review)
Philippines, Bantayan, Cebu	M, F	225 (estimated) 205 (observed)	-	-	Ingles 1996
Philippines, Ragay Gulf	M, F	176	-	19	Ingles 1988
Portunus sanguinolentus					
India, Kakinada Region	M, F	-	5 mm·mo^{-1} (M and F) CL from January to November for crabs 32-62 mm CL	-	Devi 1985
India, Vembanad Lake, Kerala State	M,F	134	-	-	Kurup et al. 1990
Charybdis feriatus					
India, Cochin, Kerala State	M,F	154 (M), 120 (F)	-	-	Padayatti (1990)

market value than *S. serrata* but demand is reported to be increasing in many countries such as India (Jose et al. 1996).

FARMING SYSTEMS

In Japan, the effectiveness of stock enhancement of *P. trituberculatus* is not verified since there is no reliable method to distinguish hatchery-reared crabs in the wild from those produced in nature (Cowan 1984, Yanagi 1997). In the Seto Inland Sea, numbers of adults captured after a suitable lag period do not bear any relationship to the numbers of juveniles released (Yanagi 1997). Kitada and Shiota (1990) showed that fishing mortality was high and natural mortality of adults was low. However, for a highly fecund species, this would not necessarily mean that the recruitment to the fishery is dependent on prior release of hatchery-reared juveniles.

In Japan, Cowan (1984) described how strategies such as the use of onshore tanks and semi-enclosed inshore net pens for the *P. trituberculatus* juveniles and the release of young to protected inshore habitats such as seagrass beds, artificial shelters and artificial tidal wetlands.The traditional Japanese system of coastal management by fishery cooperatives favors management of enhanced stocks. Similar locally managed and respected arrangements would need to be established for other countries. A suitable management regime must be able to control fishing mortality, regulate access to the resource, commission and maintain the hatchery. In many Asian countries such as the Philippines, the trend towards community based coastal resource management and marine protected areas could assist stock enhancement.

Hatcheries could be communally owned or commissioned since stock enhancement cannot be readily privatized. Although many Asian countries have marine hatcheries run by the governments or private sector, e.g. for shrimp culture, new institutional arrangements may be needed. Coastal water and habitat quality must be suitable for stock enhancement to work.

Farms, cages, pens and polyculture, species such as milkfish, shrimps and seaweed would need to be developed in the case of full aquaculture and domestication of the four species. Crab culture would then be competing for sites with other coastal aquaculture or integrating with other forms. The adoption of crab culture will depend on its profitability.

Soft shell crab production is already practiced for *Scylla* species in the Asian region as a luxury product and other portunids would certainly be suitable, with precautions on ensuring that the wild stocks are not overexploited.

PROFITABILITY OF ENTERPRISES

Few studies have been done on ROI. For *P. trituberculatus* in Japan, Cowan (1984) reported that the cost of juvenile crab production, reseeding and early stage maintenance were already close to being offset by the market value of crabs. Profitability estimates are derived differently for stock enhancement and aquaculture as, in each activity, capital investment, operational costs and benefits are each provided by different actors.

ENVIRONMENTAL IMPACTS

Aquaculture will potentially pollute coastal waters if intensified and/or if farms are inappropriately sited and managed. Cultured crabs could also cause genetic and disease problems for wild stocks when they escape.

If stock enhancement is to be contemplated, responsible stock enhancement is recommended (Blankenship and Leber 1995, FAO 1995).

Conclusions

Within the next 5 to 10 years, the culture of large tropical portunid species will develop only if a number of significant constraints that we have identified are addressed. In the longer term, additional constraints such as the species' carnivorous diet and the demands on good quality coastal space may present the most significant problems.

The present constraints arise from knowledge gaps and in the species' biological limitations (Table 4). Full domestication may not occur within the next 5 to 10 years. Indeed, whether the portunid species reviewed here do become fully domesticated will depend on the extent of and success with their culture and on managing broodstock. Responsible stock enhancement may be a more feasible alternative. We also conclude that those seeking to

Table 4. Scores of suitability (H=high, M=medium, L=low, U/K = unknown) against criteria for selection of Portunid species for domestication and stock enhancement. Criteria marked "E" are considered essential and those marked "D" are desirable or relative. Refer to Table 1 for full description of criteria.

	Scylla spp	*Portunus pelagicus*	*P. sanguinolentus*	*P. trituberculatus*	*Charybdis feriatus*
Domestication					
1. Closed life cycle: (E)	M	H	U/K	H	U/K
2. Diet: (E)	L	L	L	L	L
3. Behavior: (E)	M	M	M	M	M
4. Resistant to diseases: (E)	U/K	U/K	U/K	M	U/K
5. Species has good growth: (E)	H	H	H	H	H
6. Good market demand: (E)	H	M	M	H	H
7. Feasible farming systems: (E)	H	U/K	U/K	U/K	U/K
8. Profitable enterprises: (D)	H	M	U/K	U/K	U/K
9. Environmental impacts: (E)	M	U/K	U/K	U/K	U/K
Stock Enhancement					
1. Captive breeding achievable: (E)	M	H	U/K	H	U/K
2. Suitable natural feed available: (D)	H	H	H	H	H
3. Behavior permits handling for breeding. (E)	M	M	M	M	M
4. Diseases resistance: (E)	U/K	U/K	U/K	M	U/K
5. Good growth and large size: (D)	H	H	H	H	H
6. Strong market: (E)	H	M	L	H	H
7. Suitable, managed natural ecosystems exist: (E)	M	M	M	H	M
8. Good cost/benefit outlook for enhancement system: (E)	U/K	U/K	U/K	U/K	U/K
9. Positive environmental and biodiversity impact: (E)	U/K	U/K	U/K	H	U/K

promote culture of portunids in the tropical Indo-West Pacific should look beyond just *Scylla* species and pay attention to some of the other large portunids

Table 5 summarizes the opportunities for, and constraints to, domestication presented by the major portunid species. On the positive side, all the species are large in size, fast-growing, highly fecund and widely distributed in nature. In addition, *Scylla* species have high market values for a variety of products. Inconsistent larval survival rates, in part due to cannibalism, remain a bottleneck for the species in contrast to well-developed hatchery technology for *P. trituberculatus*. Early signs are that *P. pelagicus* is easier to rear in hatcheries than the *Scylla* species. Basic knowledge of biology and ecology is lacking for the two tropical *Portunus* species and *C. feriatus*. Moreover, their market value is low because these marine species die soon after harvest unlike the *Scylla*, hence the need for research on product development. *C. feriatus,* however, has considerable potential as a market species if well promoted and presented. Since portunids are carnivorous, diet development must find alternatives to trash fish and fish meal-based pellets that compete with human food. Possible alternatives are low-value bivalves, agricultural by-products, and recycled ‘waste’ materials such as fish offal.

Scylla species could contribute more to maintaining the environment than the cultured fish and shrimps through integration with mangroves and reseeding of natural populations. Environment friendly farming

Table 5. Opportunities and constraints in aquaculture and stock enhancement programs of portunid species

	Opportunities	Constraints
All species	- good growth rate, large size, high fecundity	- cannibalism at all stages
Scylla species	- wide distribution - broodstock availability - few diseases in culture - eurythermal, euryhaline (culture) - long transport periods - high acceptability, good markets - varied products	- low survival of larvae - nursery techniques for megalopa, early crabs - refine polyculture techniques - develop integrated mangrove systems - grow-out feeds (trash feeds, trash fish substitutes)
Charybdis and *Portunus* spp.	- wide distribution - larvae reared readily	- limited knowledge of ecology and biology for restocking, - marketing methods need development since generally lower priced than *Scylla* - limited knowledge of feeds, all stages of juveniles
Charybdis feriatus	- marketable	- little known biology, ecology - rare species, broodstock availability -unknown grow-out conditions
Portunus pelagicus	- marketable, many products possible - plentiful species - available broodstock - wide distribution	-low market value - product development - coastal grow-out sites, technology (culture) - management of coastal fishing
Portunus sanguinolentus	-marketable	- oceanic conditions - rare species, broodstock availability
Portunus trituberculatus	- good market value, acceptability - well developed mass rearing technology	- disease control in mass larval culture - inshore pollution, red tide

systems have to be developed for the other species, along with incentives and regulations that support their sustainability. Institutions and mechanisms to ensure the sustainable management of coastal fisheries will be among the most challenging problems of stock enhancement, especially for the *Portunids* and *Charybdis* species that range widely in open coastal waters.

We suggest that any agency wishing to promote the development of culture of any of these portunid species undertake a careful analysis, based on investments in time and resources required as well as the likelihood and benefits of success. A plan should then be devised to systematically address the critical constraints, whether they arise from gaps in knowledge or from biology.

The present preliminary review for *Scylla* species indicates that research should focus on refining the new taxonomy of the genus (Le Vay, this volume) as a prerequisite to determine which species are being used. Secondly, research should address three of the main biological limitations, namely; low survival of larvae and early crab stages, the problem of cannibalism in all life stages, and the need for cost-effective feeds. Lastly, suitable and sustainable farming systems should be developed, while protecting natural stocks from over harvesting to assist culture. If culture of *Scylla* species proves to be feasible through alleviation of the biological and farming constraints, then market development, including development of value added products is a must.

For *P. pelagicus*, priority in research should be geared towards full development and technology verification for mass producing juveniles for pond culture or stock enhancement. In some localities, cryptic speciation may also occur and therefore taxonomic studies may be required (Bryars and Adams 1999). If culture is preferred to stock enhancement, then feasible and environmentally sustainable farming systems will need to be determined, mitigating the consequences of aggression and cannibalism and finding suitable feeds for this carnivorous species. Polyculture with compatible species should be considered. If stock enhancement is chosen, suitable coastal management and institutional arrangements for hatchery establishment and operations must be developed. To make either culture or stock enhancement financially viable, product development is required.

Presently, *P. sanguinolentus* seems an unlikely species for artificial propagation due to its more oceanic habit, lesser market profile and smaller size. *C. feriatus* has very good market potential but more knowledge is required of its basic biology and ecology.

Increasing demands on scarce research resources for aquaculture means that comprehensive desk reviews such as the one we have tried in this paper is required as a basis for determining whether to proceed with research investments for a species. All things being equal, the species is still sufficiently attractive, therefore knowledge gaps and limitations identified in our review could provide good guidance to research and development investors.

Acknowledgments

The authors thank Junemie Lebata and Jon Altamirano for preparing the tables and to Violeta Perez Corral for her assistance with the references.

References

Agbayani, R.F., D.D. Baliao, G.P.B. Samonte, R.E. Tumaliuan and R.D. Caturao. 1990. Economic feasibility analysis of the monoculture of mudcrab (*Scylla serrata*) Forsskal. Aquaculture 91: 223-231.

Ariyama, H. 1992. Molting and growth of the swimming crab *Portunus (Portunus) trituberculatus* reared in the laboratory. Nippon Suisan Gakkaishi 58:1799-1805.

Baliao, D.D. 1983. The culture of alimango and bangus in brackishwater ponds. Modern Fish Farming Special Issue: 1 – 7.

Baliao, D.D. 1997. Mudcrab, "alimango" production in brackishwater pond with milkfish. SEAFDEC Aquaculture Department, Tigbauan, Iloilo, 9 pp.

Baliao, D.D., M.A. de los Santos and N.M. Franco. 1999a. Mudcrab, *Scylla* spp, production in brackishwater ponds. Aquaculture Extension Manual No. 28. SEAFDEC Aquaculture Department, Iloilo, Philippines, 14 pp.

Baliao, D.D., M.A. de los Santos and N.M. Franco. 1999b. Pen culture of mudcrab in mangroves. Aquaculture Extension Manual No. 26. SEAFDEC Aquaculture Department, Iloilo, Philippines, 10 pp.

Bardach, J.E., J.H. Ryther and W.O. McLarney 1972. Aquaculture: The Farming and Husbandry of Freshwater and Marine Organisms, John Wiley and Sons, USA. 868 pp.

Bian, B.Z., K. Hatai, G.L. Po, C.R. Lavilla and S. Egusa. 1979. Studies on the fungal diseases in crustaceans. I. *Lagenidium scyllae* sp nov. isolated from cultivated ova and larvae of the mangrove crab (*Scylla serrata*). Transactions of Mycological Society of Japan 20: 115-124.

Blankenship H.L. and K.M. Leber 1995. A responsible approach to marine stock enhancement. American Fisheries Society Symposium 15:167-175.

Boer, D.R., Zafran, Parenrengi, A., and T. Ahmad. 1993. Preliminary study of luminescent disease in the larvae of mangrove crabs, *Scylla serrata*. Coastal Aquaculture Research Journal 9(3).

Bryars, S.R. and M. Adams 1999. An allozyme study of the blue swimmer crab, *Portunus pelagicus* (Crustacea: Portunuidae), in Australia: stock delineation in southern Australia and evidence for a cryptic species in northern waters. Marine Freshwater Research 50:15-26.

Carpenter, K.E. and V.H. Niem. 1998. The Living Marine Resources of the Western Central Pacific. Volume 2. Cephalopods, crustaceans, holuthurians and sharks. FAO Species Identification Guide for Fishery Purposes. FAO, Rome.

Chang, P.S., H.C. Chen and Y.C. Wang 1998. Detection of white spot syndrome associated baculovirus in experimentally infected wild shrimp, crab and lobsters by in site hybridization. Aquaculture 164:233-242.

Chang Wei Say, C. W. and A. M. Ikhwanuddin. 1999. Pen culture of mud crabs, genus *Scylla*, in the mangrove ecosystems of Sarawak, East Malaysia. In: Mud Crab Aquaculture and Biology (eds. C. P. Keenan and A. Blackshaw). Proceedings of an international scientific forum held in Darwin Australia, 21-24 April 1997. ACIAR Proceedings No. 78, pp. 83-94.

Chen, L.C. 1990. Mud crab culture. In: Aquaculture in Taiwan (ed. L. C. Chen), pp. 142-149. Fishing News Books.

Cholik, F. 1999. Review of mud crab culture research in Indonesia. In: Mud Crab Aquaculture and Biology (eds. C.P. Keenan and A. Blackshaw). Proceedings of an international scientific forum held in Darwin Australia, 21-24 April 1997. ACIAR Proceedings No. 78, pp. 14-20.

Cholik, F. and A. Hanafi. 1992. A review of the status of the mud crab (*Scylla* sp.) fishery and culture in Indonesia. In: The Mud Crab (ed. C.A. Angell), pp. 13-28. Proceedings of the Seminar on Mud Crab in Surat Thani, Thailand, 5-8 November 1991. Bay of Bengal Programme, Madras.

Chong, Y.C. and C.T. Mee. 1986. Septicemias of marine crabs and shrimp. In: Proceedings of the First Asian Fisheries Forum (eds. J.L. Maclean, L. B. Dizon and L.V. Hosillos) pp. 331-332. Asian Fisheries Society, Manila.

Cowan, L. 1984. Crab Farming in Japan, Taiwan and the Philippines. Inf. Ser. Dep. Primary Ind. Queensland, No. QI84009, 85 pp.

Devi, S.L. 1985. The fishery and biology of crabs of Kakinada Region. Indian Journal of Fisheries. 32:18-32

du Plessis, A. 1971. A preliminary investigation into the morphological characteristics, feeding, growth, reproduction and larval rearing of *Scylla serrata* Forskal (Decapoda: Portunidae), held in captivity. Fisheries Development Corporation of South Africa, Unpublished ms., 24 pp.

Estampador, E.P. 1949. *Scylla* (Crustacea: Portunidae) II. Comparative studies on spermatogenesis and oogenesis. Philippine Journal of Science 78(3): 301-346.

FAO 1995. Codes of Conduct for Responsible Fishing.

FAO. 1998. Aquaculture Production Statistics. FAO of the United Nations, Rome.

Hamasaki, K. and K. Hatai. 1993. Prevention and fungal infection in the eggs and larvae of the swimming crab *Portunus trituberculatus* and the mud crab *Scylla serrata* by bath treatment with formalin. Nippon Suisan Gakkaishi Bulletin 59:1067-1072 .

Heasman, M.P. and D.R. Fielder. 1978. The Mud Crab. Queensland Museum, Queensland, 15 pp.

Heasman, M.P. and D.R. Fielder. 1983. Laboratory spawning and mass rearing of the mangrove crab, *Scylla serrata* (Forskal), from the first zoea to first crab stage. Aquaculture 34: 303-316.

Hill, B.J. 1975. Abundance, breeding and growth of the crab *Scylla serrata* in two South African estuaries. Marine Biology 32:119-126

Hill, B.J. 1978. Activity, track and speed of movement of the crab *Scylla serrata* in an estuary. Marine Biology 47: 135-141.

Hill, B.J. 1979. Aspects of the feeding strategy of the predatory crab *Scylla serrata*. Marine Biology 55: 209-214.

Hoang, D.D. 1998. Description of mud crab (*Scylla* spp.) culture methods in Vietnam. In: Keenan, C.P. and Blackshaw, A. (eds.) Mud Crab Aquaculture and Biology. Proceedings of an international scie ntific forum held in Darwin Australia, 21-24 April 1997. ACIAR Proceedings No. 78, pp. 67-71.

IBPGR 1991. Elsevier's dictionary of plant genetic resources, compiled by the International Board for Genetic Resources. Elsevier Science Publisgers, Amsterdam.

Ingles, J.A. 1988. Management strategies for *Portunus pelagicus* fishery in Ragay Gulf, Philippines. Fisheries Research Journal of the Philippines 13:15-22.

Ingles, J.A. 1996. The crab fishery off Bantayan, Cebu, Philippines.A report submitted to the Philippine Council for Aquatic and Marine Research and Development. 34 pp.

Ingles, J. and E. Braum 1989. Reproduction and larval ecology of the blue swimming crab, *Portunus pelagicus* in Ragay Gulf, Philippines. Internationale Revue der Gesamten Hydrobiologie 5:471-490.

Jacob, R., P.N. Prasad and M.S. Kusuma. 1990. Maturity and dimensional studies in female crabs of *Portunus sanguinolentus* and *P. pelagicus* (Decapoda: Portunidae). Indian Journal of Marine Sciences 19:221-223.

Jamari, Z.B. 1992. Preliminary studies on rearing the larvae of the mud crab *(Scylla serrata*) in Malaysia. In: The Mud Crab (ed. C.A. Angell), pp. 143-147. Proceedings of the Seminar on Mud Crab in Surat Thani, Thailand, 5-8 November 1991. Bay of Bengal Programme, Madras.

Jayamanne, S.C. 1992. The mud crab fishery in Sri Lanka. In: The Mud Crab (C.A. Angell, ed.), pp. 41-48. Proceedings of the Seminar on Mud Crab in Surat Thani, Thailand, 5-8 November 1991. Bay of Bengal Programme, Madras.

Jayamanne, S.C. and J. Jinadasa. 1991. Food and feeding habits of the mud crab *Scylla serrata* Forskal inhabiting the Negombo Lagoon in the west coast of Sri Lanka. Vidyodaya Journal of Science 3(2): 61-70.

Jose, J., M.R. Arputharaj, A. Ramakrishnan and A. Viramani 1996. Larval rearing of the crab *Portunus pelagicus* (Crustacea, Portunidae) in hatchery at Mandapam Regional Centre of CMFRI. Marine Fisheries Information Service Technical Extension Series No. 143, pp 23-24.

Kailola, P., M. J. Williams, P. Stewart, R. Reichelt, A. McNee and C. Grieve 1993. *Australian Fisheries Resources*. Bureau of Resource Science and Fisheries Research and Development Corporation, 432 pp.

Kathirvel, M. and S. Srinivasagam. 1992. Resource and exploitation of mud crab *Scylla serrata* (Forsskal) in India. . In: The Mud Crab (ed. C.A. Angell), pp. 184-94. Proceedings of the Seminar on Mud Crab in Surat Thani, Thailand, 5-8 November 1991. Bay of Bengal Programme, Madras.

Keenan, C.P., P.J.F. Davie and D.L. Mann. 1998. A revision of the genus *Scylla* de Haan, 1833 (Crustacea: Decapoda: Brachyura: Portunidae). Raffles Bulletin of Zoology 46(1): 217-245.

Kitada, S. and K. Shiota. 1990. Estimation of mortality rates of female swimming crab *Portunus trituberculatus* from single release marking studies. Nippon Suisan Gakkaishi 56:1449-1453.

Kumar, M.S. (Ed.) 1997. Proceedings of the first National Workshop on Blue Swimmer Crab *Portunus pelagicus*. South Australian Aquatic Sciences Center, South Australian Research and Development Institute, West Beach, South Australia 7-8 May 1997. 129 pp.

Kurup, B.M., M.J. Sebastian, T.M. Sankaran and P. Rabindranath 1990. Fishery and biology of edible crabs in Vembanad Lake. Second Indian Fisheries Forum Proceedings, May 27-31, 1990, Mangalore, India. pp. 169-173.

Latiff, F.A. and C.U.C. Musa. 1995. The Biology of Mud Crab and its Hatchery Production. Buletin Perikanan. Department of Fisheries, Malaysia, 20 pp.

Le Vay, L. (in press, this volume) Ecology and management of mud crabs *Scylla* spp.

Lijauco, M.M., O.Q. Prospero and E.M. Rodriguez. 1980. Polyculture of milkfish (*Chanos chanos*) and mud crab (*Scylla serrata*) at two stocking densities. QRR 4(4): 19-23

Liong, P.C. 1992. The fattening and culture of the mud crab (*Scylla serrata*) in Malaysia. In: The Mud Crab (C.A. Angell, ed.), pp. 185-190. Proceedings of the Seminar on Mud Crab in Surat Thani, Thailand, 5-8 November 1991. Bay of Bengal Programme, Madras.

Liong, P.C. 1993. The culture and fattening of mud crabs. INFOFISH International 3: 46-49.

Liong, P.C. 1995. Crab culture - present status, future prospects. In: Aquaculture Towards the 21st Century (eds Nambiar, K.P.P. and T. Singh), pp. 4-11. Proceedings of the INFOFISH AQUATECH '94 Conference, Colombo Sri Lanka, 29-31 Aug. 1994. INFOFISH, Kuala Lumpur.

Lio-Po, G.D., Sanvictores, M.E.G., Baticados, M.C.L. and C.R. Lavilla. 1982. In vitro effect of fungicides on hyphal growth and sporogenesis of *Lagenidium* spp. isolated from *Penaeus monodon* larvae and *Scylla serrata* eggs. Journal of Fish Disease 5:97-112.

Macintosh, D.J., C. Thongkum, K. Swamy, C. Cheewasedtham and N. Paphavisit. 1993. Broodstock management and the potential to improve the exploitation of mangrove crabs, *Scylla serrata* (Forskal), through pond fattening in Ranong, Thailand. Aquaculture Fisheries Management 24: 261-269.

Macnae, W. 1968. Fauna and flora of mangrove swamps. Advances in Marine Biology 6: 73-270.

Mann, D.L., T. Asakawa, M. Pizzutto, C.P. Keenan and I.J. Brock. Investigation of an *Artemia*-based diet for larvae of the mud crab *Scylla serrata*. Asian Fisheries Science. This volume

Marichamy, R. 1996. Crab farming potential in India. In: Proceedings of the Seminar on Fisheries—a Multibillion Dollar Industry, pp. 115-122. Aquaculture Foundation of India and Fisheries Technocrat Forum, Madras.

Marichamy, R. and S. Rajapackiam. 1992. Experiments on larval rearing and seed production of the mud crab *Scylla serrata* (Forskal). In: The Mud Crab (ed. C.A. Angell), pp. 135-142. Proceedings of the Seminar on Mud Crab in Surat Thani, Thailand, 5-8 November 1991. Bay of Bengal Programme, Madras.

Moriaka, Y., C. Kitajima and G. Hayashida 1988. Oxygen consumption, growth and calculated food requirement of the swimming crab *Portunus trituberculatus* in its early developmental stage. Nippon Suisan Gakkaishi Bullettin of Japanese Society of Scientific Fisheries 54:1137-1141.

Motoh, H., D. de la Pena, M. Dimaano and E.Tampos. 1978. Peliminary report on the first production of the crab stages of alimasag, *Portunus pelagicus* (Linnaeus). Q. Res. Rep. Aquaculture Department Southeast Asian Fisheries Development Center 2, pp 16-21.

Motoh, H. and D.K. Villaluz 1976. Larvae of Decapod Crustacea of the Philippines – I The zoeal stages of a swimming crab, *Charybdis cruciata* (Herbst) reared in the laboratory. Bulletin of the Japanese Society of Scientific Fisheries 42 (5) 523-531.

Munro, J.L. and J.D. Bell. 1997. Enhancement of marine fishery resources. Reviews in Fisheries Science 5:185-222.

Muroga, K., K. Suzuki, K. Ishimaru and K. Mogami 1994. Vibriosis of swimming crab *Portunus trituberculatus* in larviculture. Journal of World Aquaculture Society 25(1):50-54.

Naidu, K.G.R.B. 1955. The early development of *Scylla serrata* (Forsk.) de Haan and *Neptunus sanguinolentus* (Herbst). Indian Journal of Fisheries 2:67-76.

Ong, K.S. 1964. Early development stages of *Scylla serrata* Forskal (Crustacea Portunidae), reared in the laboratory. Proceedings of the Indo-Pacific Fisheries Council 11(2): 135-146.

Overton, J.L. and D.J. Macintosh. 1997. Mud crab culture: prospects for the small-scale Asian farmer. INFOFISH International 5: 26-32.

Padayatti, P.S. 1990. Notes on population characteristics and reproductive biology of the portunid crab *Charybdis (Charybdis) feriatus* (Linnaeus) at Cochin. Indian Journal of Fisheries 37:155-158.

Pagcatipunan, R. 1972. Observations on the culture of alimango, *Scylla serrata* at Camarines Norte (Philippines). In: Coastal Aquaculture in the Indo-Pacific Region (ed. T.V.R. Pillay), pp. 362-365. Fishing News Books, United Kingdom.

Parenrengi, A., Zafran, D.R. Boer and I. Rusdi. 1993. Identification and pathogenicity of several *Vibrio* bacteria in mangrove crab larvae, *Scylla serrata*. Coastal Aquaculture Research Journal 9(3).

Patel, N.M., N.D. Chhaya, M. Bhaskaran. 1979. Stomach contents on *Portunus pelagicus* (Linn.) from AD net catches. Indian Journal of Marine Science 8:48-49.

Poovichiranon, S. 1992. Biological studies of the mudcrab *Scylla serrata* (Forskal) of the mangrove ecosystem in the Andaman Sea. In: The Mud Carb (ed..C.A. Angell, pp. 49-58 Proceedings of the Seminar on Mud Crab in Surat Thani, Thailand, 5-8 November 1991. Bay of Bengal Programme, Madras.

Primavera, J.H. 1995. Mangroves and brackishwater pond culture in the Philippines. Hydrobiologia 295: 303-309.

Primavera, J.H. and A.T. Trino. 1999. Mangrove-friendly aquaculture studies at the SEAFDEC Aquaculture Department. Seminar on Aquaculture Development in Southeast Asia, Iloilo City, 11-14 October 1999.

Prinpanapong, S. and T. Youngwanichsaed. 1992. Rearing of mud crab (*Scylla serrata*). In: The Mud Crab (ed. C.A. Angell), pp. 191-194. Proceedings of the Seminar on Mud Crab in Surat Thani, Thailand, 5-8 November 1991. Bay of Bengal Programme, Madras.

Pullin, R.S.V.P., M.J. Williams and N. Preston. 1998. Domestication in crustacea. Asian Fisheries Journal 11(1):56-69.

Quinitio, E.T., F.D. Parado-Estepa and O.M. Millamena. Seed production of mud crab *Scylla serrata* juveniles. This volume

Raman, K., S. Srinivasagam, C.P. Rangaswamy, S. Krishnan, K.O. Joseph and M. Sultana. 1987. A note on larval rearing of the edible crab, *Portunus pelagicus* Linnaeus, at Ennore Hatchery, Madras. Indian Journal of Fisheries. 34:128-131.

Rattanachote, A. and R. Dangwatanakul. 1992. Mud crab (*Scylla serrata* Forskal) fattening in Surat Thani province. In: The Mud Crab (ed. C.A. Angell), pp. 171-178. Proceedings of the Seminar on Mud Crab in Surat Thani, Thailand, 5-8 November 1991. Bay of Bengal Programme, Madras.

Razek, F.A.A. 1987. Crab fishery of the Egyptian waters with notes on the bionomics of *Portunus pelagicus* (L.). Acta Adriatica 28:143-154.

Robertson, W.D. and A. Kruger. 1994. Size at maturity mating and spawning in the portunid crab *Scylla serrata* (Forskal) in Natal, South Africa. Estuarine Coastal Shelf Science 39: 185-200.

Robertson,W.D. and S.E. Piper. 1991. Population estimates of the crab *Scylla serrata* (Forskal, 1755) (Decapoda: Portunidae) in two closed estuaries in Natal, South Africa, from mark-recapture methods. South African Journal of Marine Science 11: 193-202.

Robles, J. 1983. Further observations on crab (*alimango*) culture. Modern Fish Farming.

Rodriquez, E.M., E.T. Quinitio, F.D. Parado-Estepa and O.M. Millamena. Culture of *Scylla serrata* megalops in brackishwater ponds. Asian Fisheries Science. This volume

Ronquillo, J.D., Z.V. Pura and R. M. Traifalgar 1999. “Seedling” production and pond culture of hatchery-produced juveniles of the mud crab, *Scylla oceanica* Dana, 1852. In Crustaceans and the Biodiversity Issues (eds. F.R. Schram, J.B. Von and V. Kline), Proceedings of the Fourth International Crustacean Congress, Amsterdam, vol. 1: pp. 999-1011.

Ross, L.G. and M.C.M. Beveridge. 1995. Is a better strategy necessary for development of native species for aquaculture? A Mexican case study. Aquaculture Research 26:539-548.

Samarasinghe, R.P., D.Y. Fernando and O.S.S.C. de Silva. 1992. Pond culture of mud crab in Sri Lanka. In: The Mud Crab (ed. C.A. Angell), pp. 161-164. Proceedings of the Seminar on Mud Crab in Surat Thani, Thailand, 5-8 November 1991. Bay of Bengal Programme, Madras.

Samonte, G.P.B. and R.F. Agbayani. 1992. Pond culture of mud crab (*Scylla serrata*): an economic analysis. In: The Mud Crab (ed. C.A. Angell), pp. 225-234. Proceedings of the Seminar on Mud Crab in Surat Thani, Thailand, 5-8 November 1991. Bay of Bengal Programme, Madras.

Shen, Y. and Q. Lai. 1994. Present status of mangrove crab (*Scylla serrata* (Forskal)) culture in China. Naga, The ICLARM Quarterly January 1994: 28-29.

Shinkarenko, L. 1979. Development of the larval stages of the blue swimming crab *Portunus pelagicus* L. (Portunidae : Decapoda : Crustacea). Australian Journal of Marine and Freshwater Research 30: 485-503.

Shiota and Kitada 1992. The life history of the swimming crab in Hiuchi Nada, Seto Inland Sea estimated from marking experiments. Nippon Suisan Gakkaishi Bulletin of Japanese Society of Fisheries 58:2297-2302.

Srinivasagam, S. 1982. An instance of large scale parasitism of *Heterosaccus dollfusi* Boschma on the edible crab, *Portunus sanguinolentus* (Herbst) in Pulicat Lake. Journal of Inland Fisheries Society of India 14:88-90.

Srinivasagam, S. and M. Kathirvel. 1992. A review of experimental culture of the mud crab *Scylla serrata* Forskal in India. In: The Mud Crab (ed. C.A. Angell), pp. 195-203. Proceedings of the Seminar on Mud Crab in Surat Thani, Thailand, 5-8 November 1991. Bay of Bengal Programme, Madras.

Stephenson, W. and B. Campbell. 1960. The Australian portunids (Crustacea: Portunidae) IV: remaining genera. Australian Journal of Marine and Freshwater Research 11(1): 73-122.

Stevens, R. 1997. Improvement in post harvest handling and marketing strategy for blue crabs. In: Proceedings of the First National Workshop on Blue Swimmer Crab *Portunus pelagicus* (ed. M. Kumar) South Australian Aquatic Sciences Center, South Australian Research and Development Institute, West Beach, South Australia 7-8 May 1997, pp 57-75.

Sukumaran, K.K., K.Y. Telang and D. Thippeswamy. 1986. On the fishery and the biology of the crab *Portunus sanguinolentus* along the south Kanara coast. Indian Journal of Fisheries 33:188-200.

Sukumaran, K.K. and B. Neelakantan 1996. Relative growth and sexual maturity in the marine crabs, *Portunus (Portunus) sanguinolentus* (Herbst) and *Portunus (Portunus) pelagicus* (Linnaeus) along the southwest coast of India. Indian Journal of Fisheries 43:215-223.

Sumpton, W., G. Smith and M. Potter. 1989. Notes on the biology of the portunid crab, *Portunus sanguinolentus* (Herbst), in subtropical Queensland waters. Australian Journal Marine Freshwater Research 40:711-717.

Sun Yingmin and Yan Yu 1984. The larval development of *Portunus trituberculatus*. Journal of Fisheries of China 8:220-226.

Supamattaya, K. R.W. Hoffmannn, S. Boonyaratpalin and P. Kanchapanaphum. 1998. Experimental transmission of white spot syndrome virus (WSSV) from black tiger shrimp *Penaeus monodon* to sand crab *Portunus pelagicus*, mud crab *Scylla serrata* and *Krill autes* sp. Dis. Aqua. Org. 32 (2): 79-86.

Travis, J.F.C., C.B. Coleman, G.D. Conover, T.M. Bert, and M. Tringali. 1998. Critically assessing stock enhancement: an introduction to the Mote Symposium. Bulletin of Marine Science 62: 305-311

Triño, A.T., E.M. Rodriguez, E.B. Coniza and B.P. Juanga. 1999b. Mudcrab. Aquaculture Extension Manual No. 27. SEAFDEC Aquaculture Department, Iloilo, Philippines, 32 pp.

Triño, A.T., O.M. Millamena and C. Keenan. 1999a. Commercial evaluation of monosex pond culture of the mud crab *Scylla* species at three stocking densities in the Philippines. Aquaculture 174: 109-118.

Varikul, V., S. Phumiphol and M. Hongpromyart. 1971. Preliminary experiments in pond rearing and some biological studies of *Scylla serrata* (Forskal), pp. 366-374. In Pillay, T.V.R. (ed) Coastal Aquaculture in the Indo-Pacific Region. West Byfleet, Fishing News Books.

Walker, M.H. 1998. Mud Crab Necrosis Project, Summary Final Report. Central Queensland University, Queensland, Australia. 8 pp. + 3 tables, 16 figs.

Wang, Y.C., C.F. Lo, P.S. Chang and G.H. Kou. 1998. Experimental infection of white spot baculovirus in some cultured and wild decapods in Taiwan. Aquaculture 164:221-231.

Wassenberg, T. and B.J. Hill 1987. Feeding by the sand crab *Portunus pelagicus* on material discarded from prawn trawlers in Moreton Bay, Queensland. Marine Biology 95:387-393.

Williams, M. J. 1979. Feeding ecology and behavior of inter-tidal portunid crabs (Portunidae: Brachyura) in Moreton Bay. Doctor of Philosophy Thesis, University of Queensland. 265 pp.

Williams, M. J. 1982. Natural food and feeding in the commercial sand crab, *Portunus pelagicus* (Crustacea, Decapoda, Portunidae) in Moreton Bay, Queensland (Australia). Journal of Experimental Marine Biology and Ecology 59: 165-76.

Williams, M.J. 1978. Opening of bivalve shells by the mud crab *Scylla serrata* Forskal. Australian Journal of Marine Freshwater Research 29: 699-702.

Yamaguchi, M. 1991. Aquaculture in Tropical Seas. Midori Shobo, Tokyo. 360 pp.

Yanagi, T. 1997. the preservation and creation of fisheries grounds, pp. 97-119. In Okaichi, T. and T. Yanagi (eds). Sustainable Development in the Seto Island Sea, Japan-from the Viewpoint of Fisheries. Terra Publishing Co., Tokyo.

Yang, S.Y., S. Kabeta, O. Matsuda, and T. Yamamoto 1994. Variation of nitrogenous compounds in the mass-production ponds of swimming crab *Portunus trituberculatus* larvae with particular reference to the survival rate. Applied Biological Science. Seibutsu-Seisangaku-Kenkyu 33:29-35 (cited in Kumar 1997).

Yasonobu, H., H. Nagayama, K. Nakamura and K. Hatai 1997. Prevention of a fungal infection in the swimming crab *Portunus trituberculatus* larvae by high pH of rearing water. Nippon Suisan Gakkaishi 63:56-63 (abstract).