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Ecology and Management of Mud Crab *Scylla* spp.

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Abstract

The recent revision of the genus *Scylla* into four species provides a basis for the development of a better understanding of their ecology, population biology and the sustainable management of fisheries, as well as the selection of species for aquaculture. In many cases, previous studies of mud crab fisheries and ecology have reported the occurrence of more than one "type" of mud crab, but data for any one currently known species have rarely been recorded. Consequently, much of the biological and ecological data in the literature must be reviewed. This paper summarizes the current state of knowledge on mud crab ecology in relation to population biology and management, and discusses priorities for future research to support the development of sustainable mud crab aquaculture and fisheries.

Introduction

The mud crabs, *Scylla* spp., represent a valuable component of small-scale coastal fisheries in many countries in tropical and subtropical Asia, for which there has been a general trend of increased exploitation in recent years (Angell 1992; Keenan 1999). Unless effectively managed, it is likely that mud crab populations will experience increased fishing pressure, targeting all size-classes, from juveniles for pond culture to mature females for premium markets. Declining crab landings and smaller maximum sizes have been reported over the last two decades (Angell 1992).

Pond culture of mud crabs is presently dependent on wild-caught juveniles and, in some areas, further expansion of crab farming is now limited by fisheries for juveniles (Keenan 1999; Fortes 1999). Until hatchery production becomes economically viable, a strong interaction between management of natural populations and the potential for expansion of pond culture will continue. Furthermore, large mud crab populations are typically associated with well-established mangrove forests so that, aside from direct fishing pressure, loss of habitat represents a serious impact on mud crab populations. Clearly, the sustainable development of crab aquaculture will need to be closely integrated with fisheries and mangrove management.

It is beyond the scope of this paper to comprehensively review literature on the biology and ecology of mud crabs. However, in the context of the recent revision of the taxonomy of the genus (Keenan et al. 1998), it sets out to highlight areas where even basic biological information is lacking at the species level, especially when relevant to fisheries management and aquaculture.

Taxonomy

Until recently the taxonomic status of the genus *Scylla* has been considerably confused. Historically, several researchers have described the occurrence of more than one species. Estampador (1949a) revised the genus using burrowing habit, coloration, morphological characters and chromosome structure to recognize three species and one variety of *Scylla* in the Philippines: *S. oceanica*, *S. tranquebarica*, *S. serrata* and *S. serrata* var. *paramamosain*. This level of diversity within the genus was supported by Serene (1952, cited in Keenan et al. 1998) who recognized four forms of *Scylla* in specimens from Vietnam, based on spination and color. Kathirvel and Srinivasagam (1992a) reviewed the taxonomy of mud crabs in India, reporting the occurrence of at least three species of *Scylla*. On the other hand, the lack of certainty in species identification has also led many authors to follow Stephenson and Campbell (1960), who determined that there was insufficient evidence for the separation of species beyond the monospecific term *S. serrata* (Forskal).

More recently, morphometric and allozyme studies have indicated speciation within the genus (Fuseya and Watanabe 1996; Overton et al. 1997; Sugama and Hutapea 1999). This has been confirmed in the revision of the genus *Scylla* into four species, *S. serrata, S. tranquebarica, S. olivacea* and *S. paramamosain*, based on allozyme electrophoresis, mitochondrial DNA sequencing and morphometric analysis (Keenan et al. 1998). Furthermore, the latter study concluded that the four species could be separated on the basis of morphological characters; the shape of frontal teeth, spination on the carpus and propodus of cheliped and coloration. However, the individual characters are variable within species and need to be used in combination to avoid confusion. The ability to consistently distinguish the four species through external characters now provides a sound basis for a better understanding of mud crab biology, ecology and fisheries management.

Literatures related to mud crab fisheries and ecology show that in many cases the identity of the species studied remains uncertain, especially in areas where the occurrence of more than one "type" of mud crab is reported. This makes it difficult to draw general inferences from the literature and much of the biological and ecological data available will need to be reassessed once it can be ascribed to a particular species. In some cases, it may be possible to separate historical data in fisheries where local common names have distinguished sympatric species. This has been found to be the case, for example, with *S. olivacea* and *S. paramamosain*, that are known locally as "red" and "white" crabs in the Mekong Delta, Vietnam (Vu et al.

1998). The situation is less problematic in some regions, such as the east coasts of Africa and Australia, where it seems that only *S. serrata* occurs.

Distribution

Representatives of the genus *Scylla* are found across the Indo-West Pacific. While the full extent of the range for each species remains to be clarified, there are apparent differences in their distributions (Table 1). *S. serrata* has the widest distribution and is the only species so far recorded in the Western Indian Ocean, Japan and the South Pacific islands. *S. tranquebarica* and *S. olivacea* have distributions focused on the South China Sea, extending into the Indian Ocean and the western Pacific, while *S. paramamosain* appears to have a more limited distribution, being mostly restricted to the South China and Java Seas.

Habitat

Mud crabs are mostly found in estuarine and sheltered coastal habitats and, in general, large populations are usually associated with established mangroves, especially in estuaries. However, the conditions determining local distribution and abundance of the four mud crab species are likely to be complex. Hill (1975; 1978) and Hill et al. (1982) studied the abundance and distribution of *S. serrata* populations in South Africa (estuaries) and Australia (tidal flats) by mark-recapture. They found that distribution and abundance depend on the developmental stage; juveniles up to 8 cm carapace width were most abundant on intertidal flats, while subadult and adult crabs were more subtidal in habit. Chandrasekaran and Natarajan (1994) found that newly recruited juveniles prefer sheltered and shallow-water habitats amongst seagrasses, algae and mangrove roots. Le Vay et al. (in press) report that *S. paramamosain* juveniles (3 to 4 cm carapace width) are captured foraging on intertidal mudflats at night. Analysis of fisheries landing records indicates that estuarine mangroves and associated

Table 1. Distribution of *Scylla* species (Keenan et al.1998)

Species	Region
S. serrata	Indo-West Pacific: South Africa, Red Sea, Australia, Philippines, Pacific Islands (Fiji, Solomon Islands, New Caledonia, Western Samoa), Taiwan, Japan
S. paramamosain	South China Sea: Cambodia, Vietnam, Singapore, China, Taiwan, Hong Kong, Singapore; Java Sea: Kalimantan, Central Java
S. olivacea	Indian Ocean: Pakistan to Western Australia; South China Sea: Thailand, Singapore, Vietnam, Sarawak to southern China; Pacific Ocean: Philippines, Timor, Gulf of Carpentaria
S. tranquebarica	Indian Ocean: Pakistan to Malaysia; South China Sea: Sarawak, Singapore; Pacific Ocean: Philippines

mudflats in the Mekong Delta may act as a "nursery" for *S. paramamosain*, with a greater proportion of adult crabs in subtidal populations (Le Vay et al. in press).

Keenan et al. (1998) have suggested that the four *Scylla* species may have diverged in their preference or tolerance to salinity, at the larval or juvenile stages. They argue that *S. serrata,* is dominant in oceans with salinity above 34 ppt and in mangroves that are inundated with high salinity water for most of the year. The other species are more abundant in seas where salinity is generally below 33 ppt, and are able to colonize estuarine habitats in which periods of low salinity occur seasonally. Ecological studies have indicated apparent differences in salinity tolerance in juveniles between species. Chandrasekaran and Natarajan (1994) studied the seasonal abundance and distribution of mud crab juveniles (*Scylla* sp.unknown) in a mangrove system in Southeast India and found that abundance of juveniles was lowest in October, when the salinity was very low (1.5 to 2 ppt). Hill (1974) found that *S. serrata* juveniles can survive at 2 ppt, though high mortalities may occur in this species as a result of sudden salinity decreases associated with freshwater flooding (Hill 1979). *S. paramamosain* shows a preference for estuarine habitats, and catch-per-unit-effort data (CPUE) indicates stable populations despite extended periods of low salinity or even freshwater conditions through a large part of the year (Le Vay et al. in press).

Growth

Values for size-at-maturity in *Scylla* species show clear differences with latitude (Table 2). Larger size-at-maturity and maximum sizes are reported in *S. serrata* on the east coasts of Australia and South Africa than in most tropical *Scylla* populations. Quinn and Kojis (1987), Roberston and Kruger (1994) have suggested that size differences with latitude might reflect more rapid growth and earlier maturation at tropical temperatures, but it now seems that they represent differences in growth characteristics among species. Female *S. serrata* first reach maturity at about 12 cm carapace width and may reach a maximum of 24 cm, while the maturity molt in *S. paramamosain* is 8 to 9 cm carapace width with crabs reaching a maximum of 14 to 15 cm (Vu et al. 1998; Le Vay *et al.* in press). Species-specific difference in growth is supported by evidence from sympatric populations. Quinn and Kojis (1987) reported that females of two species of mud crab found in the same estuary in Papua New Guinea became sexually mature at different sizes, 10 cm and 12 cm carapace width. Similarly, in northern Queensland, *S. olivacea* co-exist at a relatively low abundance with *S. serrata,* but females rarely reach the minimum legal landing size (15 cm carapace width) for the crab fishery (D. Mann, *pers. comm.*). Thomas et al. (1987) studied growth characteristics from landings of two *Scylla* species co-occurring in Cochin and estimated that they would

reach asymptotic carapace widths at 36 cm and 16 cm. The larger species also exhibited markedly more rapid growth, that clearly has implications for both selection of species for culture (see Williams and Primavera, this volume) and optimization of culture conditions.

Reproduction

Maturation and spawning in *Scylla* species show that in nearly all cases reproduction is continuous through the year, with some seasonal peaks (Table 3). In tropical populations, a higher incidence of maturation in females appears to be associated with seasonal high rainfall, that may be related to periods of high productivity in coastal waters (Heasman et al. 1985). In sub-tropical climates, seasonality in reproduction is more strongly related to temperature and day-length, with a distinct peak spawning season in the summer when water temperatures are highest.

A universal phenomenon in *Scylla* populations appears to be offshore migration of females to spawn (Table 4). The distances migrated may vary between species and may also depend on environmental conditions. The presence of a high proportion of females with spent ovaries in coastal populations of *S. serrata* indicates that many are able to return to the coast after spawning (Heasman et al. 1985). As Heasman et al. (1985) point out, in some areas, conditions suitable for larval development may occur in inshore coastal waters. Thus, migration may be more a dispersal

Table 2. Size at maturity of *Scylla* species

Area	Species	Size at maturity	Source
Papua New Guinea	Not known	100 - 120 mm CW	Quinn and Kojis (1987)
India	Not known	85 - 129 mm	Kathirvel and Srinivasagam (1992b)
Sri Lanka	Not known	120 mm	Jayamanne (1992)
Thailand (Andaman Sea)	Not known	110 mm, maturity index value 0.88	Poovachiranon (1992)
Thailand (Ranong)	Not known	Majority at 100 - 115 mm	Macintosh et al. (1993)
South Africa	*S. serrata*	For females: 123 mm (50% of females mature) For males: 92 mm (50% of males mature)	Robertson and Kruger (1994)
South Africa	*S. serrata*	83 - 144 mm with age of 1 to 1.5 years	Hill (1975)
Australia	*S. serrata*	Females 128 mm, males 165 mm	Heasman et al. (1985)
Vietnam	*S. paramamosain*	Female maturity molt *circa* 80 mm	Vu Ngoc Ut et al. (1998)
Indonesia, North Java	*S. paramamosain*	Female maturity molt 80 - 90 mm	Le Vay *pers. obs.*

CW = Carapace width

Table 3. Seasonality in maturation in *Scylla* species

Area	Species	Season	Source
India	Not known	Year-round, peaks in April - June and September - February	Kathirvel and Srinivasagam (1992b)
Philippines	Not known	Year-round, peak in May - October	Arriola (1940); Estampador (1949b)
Papua New Guinea	Not known	Peak in April - June and September - October	Quinn and Kojis (1987)
Thailand (Andaman Sea)	Not known	Year-round, peak in maturity October - December	Poovichiranon (1992)
Thailand (Ranong)	Not known	Peak in maturity in September, main egg carrying and spawning period from July - December	Macintosh et al. (1991)
Vietnam	*S. paramamosain*	Year-round, September-October peak in mature females	Le Vay et al. (in press)
South Africa (Natal)	*S. serrata*	Spawning throughout the year, with a peak through the summer months	Roberston and Kruger (1994)
Australia (Queensland)	*S. serrata*	Peak mating activity in spring and early autumn; spawning only in summer (water temperature > 22ºC)	Heasman et al. (1985)

Table 4. Reports of spawning migration by female mud crabs

Area	Observation	Source
Philippines	Females migrate to the sea to spawn	Arriola (1940)
Malaysia	Berried females not found in brackish waters	Ong (1966)
Thailand (Andaman Sea)	Females found 15 to 84 nautical miles offshore, 97 to 200 m depth	Poovichiranon (1992)
S. Africa (Eastern Cape)	Females migrate out of estuaries after mating	Hill (1975)
Australia (Queensland)	Females migrate up to 65 km offshore	Hyland et al. (1984)
Australia	Mature females migrate to spawn at 10 to 60 m depth, 3 to 95 km offshore, return to coast after spawning	Hill (1994)
Vietnam	Mature females move from estuarine mangrove into subtidal fishery	Le Vay et al. (in press)

mechanism than a requirement to ensure optimal conditions for larval survival (Hill 1994). Few detailed studies of juvenile recruitment have been undertaken. In subtropical climates, juvenile recruitment follows the seasonal patterns for reproduction, being closely related to water temperature (Table 5). In tropical populations, juvenile abundance may be related to seasonal variation in rainfall and salinity (Poovichiranon 1992). However, despite seasonal peaks, size-frequency sampling, monitoring of megalopa in plankton surveys and CPUE analysis of hand-collection of crab seeds indicate that recruitment can be continuous throughout the year in both sub-tropical and tropical populations (Chandrasekan and Natajaran 1994; Forbes and Hay 1988; Robertson 1987; Robertson and Kruger 1994; Le Vay et al. in press).

Discussion

There is clearly a need for stock management in some mud crab fisheries, especially where there are no regulations limiting the collection of juveniles and mature crabs. However, in most cases, there has not been sufficient research on which to base management guidelines. Key areas for research include reproduction and recruitment, growth and mortality rates, migration, stock separation, and abundance specific

Table 5. Seasonality in recruitment in *Scylla* species

Area	Species	Observation	Source
India (Pichavaram)	Not known	Juveniles (2 to 3 cm) absent during low salinity period in monsoon (October - November), peak in post-monsoon dry season (January - February)	Chandrasekran and Natajaran (1994)
India	Not known	Peak availability of juveniles in December to October, throughout the year in some areas	Kathirvel and Srinivasagam (1992)
Thailand (Andaman Sea)	Not known	Year-round recruitment, based on size-frequency distribution	Poovichiranon (1992)
Vietnam (Mekong Delta)	*S. paramamosain*	Year-round recruitment into estuarine mangrove, measured as CPUE for juveniles and from size-frequency distribution	Le Vay et al. (in press)
S. Africa (Natal)	*S. serrata*	Year-round megalopa in plankton	Forbes and Hay (1988)
S. Africa (Natal)	*S. serrata*	Year round, with peak in juvenile numbers in May - December	Roberston (1987)

to habitat and life stage. For as long as pond culture of mud crabs is dependent on wild-caught seed, the requirements for sustainable development of crab culture and management of fisheries and mangrove habitats will remain closely interlinked. The development of commercially-viable hatchery techniques can play an important role in promoting both sustainable crab aquaculture and fisheries management. However, since hatchery production is being developed, it is important that efforts are made to rehabilitate and manage mangrove habitats and integrate sustainable development of pond culture with an assessment and management of the associated fisheries. As the high rate of cannibalism in juvenile crabs in intensive culture systems currently limits pond culture to relatively low densities (0.5 to 1.5 crabs·m^{-2}), the release of hatchery-reared juveniles is also a possible complementary approach to sustainable crab production from fisheries in sensitive habitats.

The migration of females to considerable distances offshore to spawn and planktonic larval development over several weeks suggests a potential for dispersal and recruitment between distant populations. The application of DNA techniques may also prove to be a very useful tool in differentiating populations. However, until such data are available, a less strict definition of stock identity is required in practical fishery management (Cobb and Caddy 1989), that should assume a high likelihood of distant recruitment. Available evidence for *S. serrata* suggests that apart from spawning migration, movement is limited and that post-recruitment populations

Table 6. Evidence for post-recruitment movement in *Scylla* species

Area	Species	Observation	Source
Caroline Islands	Not known	Little movement away from release point in mangrove channels	Perrine (1978) (cited in Hyland et al. 1984)
Sarawak	*S. olivacea*	Limited movement within mangrove	Ikhwanuddin and Oakley (1998)
	S. tranquebarica	More free-ranging movement	
South Africa	*S. serrata*	Displacement of up to 13 km within estuary, but movement mostly restricted to less than 1 km	Hill (1975)
Australia (Queensland)	*S. serrata*	Movement of up to 600 m over intertidal flats	Hill et al. (1982)
Australia (Queensland)	*S. serrata*	Mangrove channels; limited exchange with adjacent habitats Intertidal flats: free ranging movement, low net displacement (<10 km); very low exchange between populations in adjacent bays/estuaries	Hyland et al. (1984)

within bays and estuaries are, to a large extent, isolated (Hyland et al. 1984, see Table 6). This suggests that stock enhancement through release of hatchery-reared juveniles might support sustained increases in localized populations. On the other hand, telemetry studies indicate that some species may be more free-ranging than others (Ikhwanuddin and Oakley 1998), and these differences need to be investigated further. The successful enhancement of a fishery through release of hatchery-produced juveniles will be dependent on several factors. From the culture aspect, reliable and economic production of juveniles must be established, with a nursery phase to rear animals to a size suitable for release. Equally important is a good understanding of population dynamics to increase the likelihood of success (i.e. of released crabs surviving and entering the fishery in sufficient numbers to justify the cost of production). True stock enhancement, that is an increase in the spawning stock and consequent recruitment to a population, is always likely to be impossible to quantify. In order to monitor the short-term localized success of a release program, a reliable method for identifying released crabs returning to the fishery is required. Coded microwire tags (Jefferts et al. 1963) can be used to identify individuals or batches of animals and can be effectively applied in very small crabs (e.g. *S. paramamosain, circa* 15 mm carapace width) with little tag loss and no impairment of growth through multiple molts (Le Vay et al. 1998, 1999). Monitoring of landings of tagged crabs entering a commercial fishery will support cost-benefit analysis and can also provide estimates of mortality and the effects of size-at-release. Both trapping and tagging studies have been used to study abundance, growth and migration in mud crabs but sampling with traps is difficult due to selectivity that may introduce bias against juveniles and molting crabs, as well as trap-saturation and temperature dependant effects (Williams and Hill 1982; Robertson 1989). Consequently, application of mark-recapture techniques requires appropriate sampling methodologies for juveniles and adults (Fitz and Weigert 1992; van Montfrans et al. 1991). However, the technique may be very useful, as differences may emerge between species in terms of habitat preference, growth rates and range of migration that are directly relevant to the feasibility of any stock release program. Some factors, such as growth rate are also directly relevant to selection of species for culture (Williams and Primavera, this volume). CPUE data from trapping surveys can provide a measure of relative abundance (Robertson 1989) and, where standardized data are available, CPUE analysis from landings can be used in monitoring seasonal and longer-term changes in crab populations (Le Vay et al. in press).

All stock assessment techniques depend on the recognition and separation of the individual species. This brief review highlights the fact that there is considerable overlap in distributions of species and a severe lack of species-specific biological and ecological information. A priority area for research is the production of larval, juvenile and adult keys to facilitate standardized accurate species recording in ecological and fisheries studies. Accurate records are also needed for species used in larval culture, with

the establishment of temperature and salinity preferences for each stage of development and growth characteristics. These are directly relevant not only to the development of aquaculture techniques but also to an understanding of the ecological differences between species.

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