

# Use and exchange of genetic resources of penaeid shrimps for food and aquaculture

John A. H. Benzie

Environmental Research Institute, University College Cork, Cork, Ireland and Moana Technologies LLC, Kailua Kona, HI, USA

## Correspondence

John A. H. Benzie, Environmental Research Institute, University College Cork, Cork, Ireland.  
Email: j.benzie@ucc.ie

Received 27 October 2009; accepted 27 October 2009.

## Abstract

*Penaeus (Litopenaeus) vannamei* Boone, 1931 and *Penaeus monodon* Fabricius, 1798 provide 87% of the world's farmed marine shrimp, and 99% with another five species, *Penaeus (Fenneropenaeus) chinensis* (Osbeck, 1765), *Penaeus (Fenneropenaeus) indicus* Milne-Edwards, 1837, *Penaeus (Fenneropenaeus) merguensis* de Man, 1888, *Penaeus (Litopenaeus) stylirostris* Stimpson, 1874 and *Penaeus (Marsupenaeus) japonicus* Bate, 1888. Genetically improved strains have been traded for *P. chinensis*, *P. stylirostris*, *P. vannamei* and *P. monodon*, although closed populations have been developed for all seven species. To date, domesticated strains have played a dominant role in seed production for only *P. vannamei* and *P. stylirostris*. Extensive worldwide transfer of wild and/or domesticated stocks has occurred for these two species and for *P. monodon*, but the volume and extent of transfer of the other species is less. Genetic variation documented in wild stocks does not appear to be threatened, but variation within cultured stocks is often reduced relative to the wild and has affected performance in some (now mostly defunct) cultured populations. Hybridization is not effective in producing useful shrimp strains. There is no organized banking of penaeid shrimp genetic resources, either as live shrimp, frozen tissue, tissue or cell culture or DNA. Open access DNA sequences are available, although limited for most species. Significant expressed sequence tags and large insert libraries are available only for *P. vannamei* and *P. monodon*.

**Key words:** aquaculture, domestication, fisheries, genetic resources, penaeid shrimp, selective breeding.

## Introduction

Farmed shrimp constituted up to 70% of the shrimp sold on world markets in 2006 (FAO 2009) and provided more than 50% of world production for several years. Since shrimp farming was first developed on an industrial scale <40 years ago, this represents a remarkable rate of growth. From 1970 to 1990 the average annual growth in crustacean aquaculture (comprised largely of penaeid shrimp) was 24%, falling to 9% in the decade 1990–2000 and rising again to 16% between 2000 and 2006; an average annual growth rate of approximately 18% from 1970 to 2006. Although the total volume of crustaceans produced in 2006 was only 9% of aquaculture production, the value of that production was US\$17.95 billion (23% of the total in 2006) (FAO 2009). Shrimp therefore has one of the highest values per unit weight for

an aquaculture commodity. This is, on average, approximately 3.9-fold that of fish and 4.7-fold that of molluscs.

This stunning growth was built on increasing the area under cultivation and improving culture methods to increase yield per unit area. Key developments have included large-scale, larval-rearing technologies to provide post-larval shrimp to stock ponds, formulated feeds and pond-rearing technologies (Fast & Lester 1992; Pullin *et al.* 1998) (and see Rosenberry (2002) for an introduction to shrimp farming and a brief history of the industry). The industry relied for the first 20–30 years on wild genetic resources, but domesticated strains provide a more reliable supply of post-larvae and the opportunity to develop specific pathogen free (SPF) and genetically improved stocks. As these have been developed, genetically improved stocks have begun to play an increasingly



important role in seed supply. The penaeid species farmed are all tropical or subtropical, and are thus most economically produced in tropical or subtropical regions of the globe (Table 1). There is some farming outside this region in warm desert areas, and indoors in temperate regions, but the total tonnage produced outside the tropics is small. The principal regions of production are in

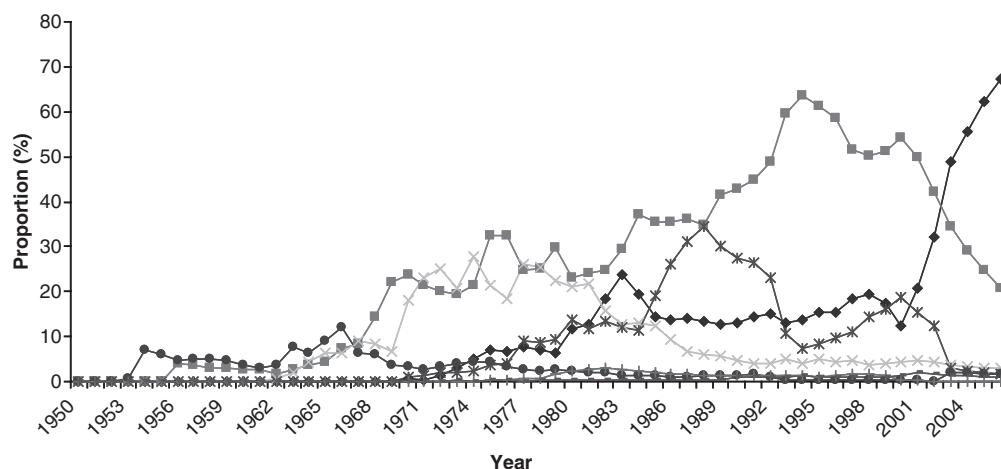
South, South-East and East Asia, Central and South America, with smaller amounts produced in the Middle East, the USA, Oceania and Africa (FAO 2009).

The proportion of world production provided by particular species has varied over time (Fig. 1), depending on the development of suitable production technologies, the geographic region being brought into aquaculture

**Table 1** Principal farmed shrimp species and the availability and use of domesticated strains

Species name (alternative common names)	Proportion (%) of world production 2005	Principal regions in which the species is farmed	Domesticated strains
<i>Penaeus</i> ( <i>Litopenaeus</i> ) <i>vannamei</i> (Pacific white shrimp, white-legged shrimp)	62	Central and South America, USA; East and South-East Asia; Middle East, minor in Africa	Developed. Available. 99% of production.
<i>Penaeus monodon</i> (Black tiger prawn, giant tiger prawn)	25	East, South-East and South Asia; Middle East, Oceania, minor in Africa	Developed. Available. Minor use to date.
<i>Penaeus</i> ( <i>Fenneropenaeus</i> ) <i>merguiensis</i> ( <i>Penaeus merguiensis</i> : Banana prawn)	3	South-East Asia; Australia	Developed. Locally available. Minor use to date.
<i>Penaeus</i> ( <i>Fenneropenaeus</i> ) <i>chinensis</i> ( <i>Penaeus chinensis</i> , <i>P. orientalis</i> : Fleshy prawn, Chinese white shrimp)	2	East Asia	Developed. Locally Available. Minor use to date.
<i>Penaeus</i> ( <i>Marsupenaeus</i> ) <i>japonicus</i> ( <i>Penaeus japonicus</i> : Kuruma prawn)	2	Japan and Australia, China, Vietnam	Developed. Locally Available. Minor use to date.
<i>Penaeus</i> ( <i>Litopenaeus</i> ) <i>stylirostris</i> ( <i>Penaeus stylirostris</i> : Blue shrimp)	<1	New Caledonia; minor in Central and South America	Developed. Available. 99% of production
<i>Penaeus</i> ( <i>Fenneropenaeus</i> ) <i>indicus</i> ( <i>Penaeus indicus</i> : Indian white shrimp)	1	Middle East, South and South-East Asia; East Africa	Developed. Private use. Minor use to date.
Unassigned penaeid	5		

Species names are from Pérez-Farfante and Kensley (1997). Production statistics are from the latest year (2005) for which consolidated data are available (FAO 2009). Refer to Figure 1 for changes in production volume over time.



**Figure 1** Changing proportion of the different species in world production of shrimp. *Penaeus japonicus* peaked in the late 1960s at approximately 10%, declining to <2% by the late 1970s; *Penaeus merguiensis* peaked at approximately 30% in the mid-1970s, declining to <5% by the late 1980s; *Penaeus chinensis* peaked in the late 1980s at approximately 35% and production since 2004 has been <3%. The two dominant species used today first appeared in significant volume in the early 1970s, both increasing their market share since then, with *Penaeus monodon* being dominant until the end of the 1990s, when the introduction of domesticated specific pathogen free strains of *Penaeus vannamei* in Asia, the traditional production area for *P. monodon*, resulted in a huge increase in the production of *P. vannamei*. (—◆—) *L. vannamei*; (---×---) *F. merguiensis*; (—●—) *M. japonicus*; (—▲—) *F. indicus*; (—■—) *P. monodon*; (---\*---) *F. chinensis* and (—+—) *L. stylirostris*.



production, the effects of disease and the relative profitability of different species. For example, the earliest development of large-scale larval rearing was in the 1930s in Japan using the kuruma prawn, *Penaeus (Marsupenaeus) japonicus* Bate, 1888 (see Table 1 for alternate scientific and common names) (Fast & Lester 1992; Liao & Chien 1994; Rosenberry 2002). Larger-scale industrial farming techniques were developed in the 1960s. However, the requirement of this species for an expensive high protein diet, and other cost factors, has seen other species used for high volume production, particularly *Penaeus (Litopenaeus) vannamei* Boone, 1931 in the Americas and *Penaeus monodon* Fabricius, 1798 in Asia, when techniques for their farming were introduced through the 1970s and 1980s (Fig. 1). *Penaeus japonicus* is a preferred species in the high-value Japanese market, but now supplies only 2% of the world market for shrimp.

Viral diseases have been spread by the relatively unrestricted transfer of stocks. As new diseases, or new strains of established diseases, decimated shrimp production in one region, production would shift to another region, or to another species. For example, although production of *Penaeus (Litopenaeus) stylirostris* Stimpson, 1874 was never large, it fell in the mid 1980s as a result of disease (Infectious Hypodermal and Hematopoietic Necrosis Virus [IHHNV] and Taura Syndrome Virus [TSV]) and production of *P. vannamei* increased. A domesticated IHHNV-resistant stock was developed in the French Pacific territories (Bedier *et al.* 1998). This was introduced under the name of 'supershrimp' to Central and South America, and to some Asian countries in the late 1990s (SEAFDEC 2005), but did not perform as expected, partly because of susceptibility to other diseases, such as white spot syndrome virus (WSSV). The availability of a domesticated strain of *P. vannamei* resistant to TSV meant that production of this species continued to rise. Production of *P. stylirostris* is now a very small proportion of the world volume. This species now supports an important niche production for a Pacific Island economy, where the diseases to which it is particularly sensitive do not exist. It is an example of an industry that now relies on a fully closed domesticated stock.

The dominant farmed species in Asia, responsible for the bulk of world industry value through much of the 1980s to the early 2000s, was *P. monodon*, largely because of its fast growth and robust pond performance. This was despite continued reliance on wild-caught broodstock, as *P. monodon* proved very difficult to reproduce in culture in the long term (Fast & Lester 1992). However, reduced returns for farmers resulting from slow-growth syndrome and losses to disease resulted in large-scale introduction of *P. vannamei* to Asia in the first decade of the 21st century (SEAFDEC 2005). The widespread availability of

SPF domesticated stock from several sources, underpinned by large corporate investment to assist widespread introduction in Asia, has seen *P. vannamei* assume the dominant position in world production today. It will be interesting to see the effect of the commercial introduction of a recently developed SPF, genetically improved strain of *P. monodon* that is now available (Argue *et al.* 2008; Benzie *et al.* 2008).

In the past 40 years, rearing technologies have been developed for approximately 20 penaeid species including, *Penaeus esculentus* Haswell, 1879, *P. penicillatus* Alcock, 1905, *P. plebejus* Hess, 1865, *P. semisulcatus* de Haan, 1844, *Penaeus (Farfantepenaeus) aztecus* Ives, 1891, *Penaeus (Farfantepenaeus) brasiliensis* Latreille, 1817, *Penaeus (Farfantepenaeus) californiensis* Holmes, 1900, *Penaeus (Farfantepenaeus) duorarum* Burkenroad, 1939, *Penaeus (Farfantepenaeus) notialis* Pérez Farfante, 1967, *Penaeus (Farfantepenaeus) paulensis* Pérez Farfante, 1967, *Penaeus (Farfantepenaeus) subtilis* Pérez Farfante, 1967, *Penaeus (Litopenaeus) occidentalis* (Streets, 1871), *Penaeus (Litopenaeus) setiferus* (Linnaeus, 1767), *Penaeus (Litopenaeus) schmitti* Burkenroad, 1938, *Metapenaeus affinis* Milne-Edwards, 1837, *Metapenaeus monoceros* Fabricius, 1798 and *Metapenaeus ensis* de Haan, 1844 (Fast & Lester 1992; Rosenberry 2002; Briggs *et al.* 2005), in addition to the main seven species farmed. Those species not assessed in the early phase of technology development during the 1970s were investigated in response to disease affecting established farmed species, usually in an attempt to replace production with a disease-tolerant species, or to make use of local biodiversity, or to develop a local niche product. Although a few of these species continue to be farmed locally, none has come to play a significant role in aquaculture production, collectively contributing <1% to world production. Seven penaeid species, *Penaeus (Fenneropenaeus) chinensis* (Osbeck, 1765), *Penaeus (Fenneropenaeus) indicus* Milne-Edwards, 1837, *Penaeus (Fenneropenaeus) merguensis* de Man, 1888, *Penaeus (Litopenaeus) stylirostris*, *Penaeus (Litopenaeus) vannamei*, *Penaeus (Marsupenaeus) japonicus* and *Penaeus monodon*, now provide 99% of the world's farmed marine shrimp (Table 1). Two species, *P. vannamei* and *P. monodon*, with particularly advantageous production characteristics contribute 87% of world production. Domesticated stocks are now available for the main farmed species and are playing an increasing role as a source of seed to farms.

Although significant research has been carried out in Asia (Rosenberry 2002), the development of the domesticated strains now on the market has been carried out disproportionately by institutions and companies outside the main producing regions (i.e. based in France, the USA and Australia) (Table 3). This is also true of much of the other molecular genetic resources being developed,



including genetic maps, expressed sequence tags (ESTs), gene sequences and the few DNA libraries for shrimp. Although limited in depth and extent, all of these genomic resources are derived from one or more of the seven principal farmed species.

### Genetic resources covered

Immortal cell culture is not available for penaeid shrimp (Crane & Benzie 1999; Crane & Williams 2002; Rosenberry 2002; Rinkevich 2005), and although sperm have been cryopreserved successfully, eggs and embryos have not (Bart *et al.* 2006). There is, therefore, no organized cell culture-based genetic resource for shrimp.

Although individual groups may hold frozen material, there is no organized gamete or tissue banking, or indeed DNA banking, for any penaeid shrimp species. None of these types of resource has appeared to play a significant role in the transfer or preservation of genetic material for shrimp species and will not be considered further.

Crosses between shrimp species have been experimental, largely unsuccessful, and have not resulted in the development of useful hybrids (Benzie *et al.* 2001). This approach has been largely abandoned and is not considered further.

Chromosomal manipulation has been used to develop triploid and tetraploid shrimp, but these have proved difficult to reproduce and do not necessarily grow faster than diploids and there is no practical application as yet (Xiang *et al.* 2006). Similarly, although some research has been carried out, technology for monosex culture has not been developed for penaeid shrimp (Moss *et al.* 2002). As neither of these approaches has produced significant genetic resources they are not considered in detail.

Direct gene transfer has proved technically difficult in shrimp (Benzie 1998; Preston *et al.* 2000). Although new approaches have allowed for improved transfer of DNA (Sun *et al.* 2005), continued technical issues and the unacceptability of genetically modified (GM) shrimp to consumers has inhibited work in this area. No developed GM resources are known and this type of genetic resource is not considered further.

Genomic work is still limited in shrimp, but first-order genetic maps, EST and gene sequences, and large insert DNA libraries are available for some of the main farmed species (Benzie 2005). Work is in progress towards developing physical maps and genome sequences for these species.

Therefore, this review will focus on the genetic resources available in live wild and domesticated populations of the main seven farmed species, the geographical transfers of these species and the genomic resources available for these species. None of the minor species that are not one of the principal seven farmed species is subject to a domestication programme or plays a role as an experimental model

organism or has an unusual wild population structure that would be useful to include in more detailed discussion.

### Variety of users and uses

Penaeid shrimp are grown principally for human consumption, although some shrimp and shrimp by-products may be used in aquaculture feeds. Farmers span the full range from local smallholders to large corporations with significant national or international operations, and use a range of farming techniques from extensive to intensive culture (see industry summaries in Kongkeo 1997, 2001; Rosenberry 2002; Limsuwan & Chanratchakool 2004). The vast majority of operators in Asia are smallholders, whereas larger corporations tend to dominate in South America. Shrimp are harvested, cleaned and sold as fresh frozen or cooked, either whole, shelled or tail only. There is significant local consumption, but most of the product is exported from the producing countries in Asia and South America to North America and Europe.

Although some companies have vertically integrated operations that include the collection or production of broodstock, hatchery production of post-larvae, pond grow-out and processing of the final product for wholesale or retail sales, the industry is composed of a range of companies that specialise in some of these activities. Typically, broodstock collection is undertaken by fishers and companies specialise in either hatchery production or farm grow-out, or post-harvest processing. There are a few specialist suppliers of domesticated, selectively bred stocks.

### Use and global exchange of shrimp genetic resources and their benefits

#### Use of shrimp genetic resources

With the exception of *P. vannamei* and *P. stylirostris*, most shrimp farming today still relies heavily on natural resources (Table 1 and references listed therein). Direct collection of post-larvae of *P. vannamei* and *P. stylirostris* from the wild was commonly used by farmers to stock their production ponds in the 1970s and 1980s (Fast & Lester 1992). This practice continued into the late 1990s in Ecuador, Guatemala and parts of Mexico. Similarly, wild capture of post-larvae using tidal flooding of extensively farmed ponds is still used in parts of Asia, such as Vietnam and India, to obtain *P. monodon* and *P. indicus* seed. This approach clearly accesses and impacts largely on local stocks, and in Bangladesh catching of wild shrimp larvae resulted in significant losses in other species in the bycatch in the early days of shrimp farming (Primavera 1998). Today, production from wild-caught larvae is limited and most post-larvae are now produced in hatcheries.



However, many hatcheries that collectively produce billions of post-larvae every year, still source the parents of this material from wild populations (Kongkeo 1997, 2001). Although the number of large adults required for the production of billions of larvae is much less (hundreds of thousands), the scale of the industry can impact on local populations. Since the 1980s hatcheries have sourced broodstock not only throughout their national area, but from throughout the natural range of the species in which they were interested. Economies of scale and the unpredictability of local supply have also led to hatcheries selling post-larvae to wherever they could. These practices have resulted in considerable transfer of genetic material throughout the geographical range of the species for which there was an industry. Almost all, or at least the majority, of the production of *P. indicus*, *P. merguensis*, *P. japonicus*, *P. monodon*, and much of *P. chinensis*, is based on wild-sourced hatchery production.

Although the use of hatcheries greatly increases the available supply of post-larvae, they are still subject to the unpredictability of the occurrence of, and access to, the natural resource (Kongkeo 1997, 2001). Although many hatcheries screen their broodstock for disease, the use of wild broodstock has proved a major pathway for the introduction of disease agents into production populations. For example, the Taura Syndrome Virus was introduced to Taiwan, Indonesia and other Asian locations through the introduction of *P. vannamei* (Briggs *et al.* 2005). Disease has played a major role in the evolution of the industry and the pressure to develop domesticated strains initially stemmed from a desire for more reliable supplies of disease-free stock.

Many operators have taken shrimp from production ponds, grown these to maturity and then used them for broodstock on an *ad hoc* basis. Some companies with the skill and scale to do so have developed a domesticated stock for their own use. This has occurred, to the author's knowledge, for all of the seven principal farmed species. There have been a number of attempts by individual companies, public institutions and private-public partnerships to develop domesticated stocks, many of which have ultimately failed (Benzie 1998). A few have succeeded and have developed soundly managed genetic improvement programmes for *P. chinensis*, *P. indicus*, *P. stylirostris*, *P. vannamei*, *P. japonicus* and *P. monodon*.

The utilization of these improved stocks is variable, with some restricted to the group that developed the stocks, either individual companies or a national network (Table 1). Only genetically improved strains of *P. stylirostris*, *P. vannamei*, *P. monodon* and possibly *P. chinensis* have been traded internationally. Almost all of the larval supply for the industrial production of *P. vannamei* and *P. stylirostris* is now from domesticated stocks.

Five of the seven species producing 99% of the supply of farmed shrimp rely wholly or largely on wild-sourced genetic resources. However, the fact that almost all of the seed supply for *P. vannamei* is from domesticated stock means that 62% of the world marine shrimp production now uses domesticated genetic resources. The recent commercial availability of domesticated *P. monodon* stocks suggests that this figure will rise even more in the near future. Farmed shrimp have shown a dramatic rise to more than 50% of the world supply for human consumption in the past 40 years. Farmed shrimp are now providing a dramatic shift from the almost exclusive use of wild-sourced stocks for the first 30 years of that growth to the predominant use of domesticated strains.

### Wild genetic resources

Despite the limited morphological divergence of penaeids, this group displays considerable genetic divergence among species as a result of their evolutionary separation of up to 8 million years or more (Tam & Chu 1993; Baldwin *et al.* 1998; Maggioni *et al.* 2001; Hualkasin *et al.* 2003; Lavery *et al.* 2004; Voloch *et al.* 2005).

The existence of genetic variation in wild populations and of regional variation in many species has been documented (reviewed in Benzie 2000). Early work on shrimp populations using allozymes emphasized a lack of genetic variation and a lack of geographical structure in shrimp populations. Subsequent studies, extending the geographical range sampled and using markers with greater resolution, have revealed considerable genetic variation within populations (e.g. Baldwin *et al.* 1998; De la Rosa-Vélez *et al.* 1999; You *et al.* 2008). Some species have shown no significant genetic differentiation across their range, including *P. aztecus* (McMillen-Jackson & Bert 2003), *P. brasiliensis* (Gusmao *et al.* 2005), *P. duorarum* (McMillen-Jackson & Bert 2004) and *P. chinensis* (Cui *et al.* 2007). However, *P. schmitti*, originally thought to have little structure (Espinosa *et al.* 2003; Maggioni *et al.* 2003; Gusmao *et al.* 2005), has subsequently been demonstrated to have some structure in the Cuban region (Borrell *et al.* 2007).

Other species show some significant structure, such as *P. setiferus* (Ball & Chapman 2003; McMillen-Jackson & Bert 2003), *P. paulensis* and a cryptic *Penaeus* (*Farfantepe-naeus*) sp. (Gusmao *et al.* 2005), *P. californiensis* and *P. stylirostris* (De la Rosa-Vélez *et al.* 2000), and *P. vannamei* (Valles-Jimenez *et al.* 2005, 2006). Others showed considerable gene flow over large distances punctuated with regions of sharp genetic differentiation, such as *P. monodon* (Klingbunga *et al.* 1998, 1999, 2001; Benzie *et al.* 2002; Sugama *et al.* 2002; Kumar *et al.* 2007; You *et al.* 2008) and *P. esculentus* (Ward *et al.* 2006). These disjunctions are associated with biogeographic boundaries



and are considered to reflect past divergence in conjunction with a continued lack of strong gene flow. Other, smaller significant differences in gene frequency observed in *P. vannamei* could be related to present day barriers to dispersal (Valles-Jimenez *et al.* 2005). In contrast, significant variation detected on relatively small geographical scales (García-Machado *et al.* 2001) was variable in time (Robainas-Barcia *et al.* 2005, 2008) in *P. notialis* and in *P. schmitti* (Borrell *et al.* 2007), and was considered to reflect differences in exchange and recruitment depending on shifts in local current patterns.

Particularly marked genetic differentiation between regions of the western Pacific have been interpreted recently by some researchers to indicate the presence of cryptic species within some of the principal farmed shrimp such as *P. japonicus* (Tsoi *et al.* 2005; Tsoi 2006). It is instructive that another cryptic species, identified usually as *P. subtilis*, has been identified in the west Atlantic from DNA sequence data (Gusmao *et al.* 2000, 2005).

Of the principal farmed species then (see Table 2), *P. monodon* and *P. japonicus* display considerable structure over their extensive geographical range, and the latter includes two cryptic taxa, one of which is more common in the north near Japan and the other more common in the south near Hong Kong. The greatest level of genetic variation in *P. monodon* occurs in the south-east Asian region, but there are marked differences between the Western Indian Ocean and Indo-west Pacific populations, and lesser differences between the south-east Asian and

Australian populations (Benzie *et al.* 2002; You *et al.* 2008). There is limited population genetic data on *P. merguiensis*, but a sequence from the *COI* gene is markedly different in samples of this species from the two sides of the Malaysian Peninsula, suggesting major population structuring like *P. monodon*, or perhaps the existence of cryptic species (Hualkasin *et al.* 2003). Significant structure has been reported for *P. vannamei* (Valles-Jimenez *et al.* 2005) and *P. stylirostris* (Aubert & Lightner 2000; De la Rosa-Vélez *et al.* 2000) over parts of their natural range, but much less than in *P. monodon* and *P. japonicus*. The structure in *P. vannamei* and *P. stylirostris* is considered to be related largely to present-day effects of ocean currents and environmental differences between water masses (Aubert & Lightner 2000; De la Rosa-Vélez *et al.* 2000) and different temperature effects, perhaps leading to a degree of reproductive isolation as a result of different spawning times (Valles-Jimenez *et al.* 2005). No significant spatial variation has been recorded for *P. chinensis* throughout its range (Wang *et al.* 2001; Liu *et al.* 2006; Cui *et al.* 2007). Data for only one population of *P. indicus* have been reported, providing no basis for comment on geographical variation (Benzie 2000).

Capture of alien species in the wild in the USA, West Africa and Asia suggests that there have been escapees and possibly feral populations established (Rosenberry 2007; Senanan *et al.* 2007). These data that suggest a considerable exchange of material within species ranges is

**Table 2** Wild genetic resources of the principal farmed shrimp species

Species name	Natural range	Genetic structure	Source
<i>Penaeus vannamei</i>	Western coast of Central and South America from Mexico to Peru	Significant genetic structure (Mexico to Peru): thought to be related to water mass and differences in spawning times	1, 4
<i>Penaeus monodon</i>	Indian Ocean coast from South Africa north to Arabia, India, South-East Asia, Indonesia, northern Australia, and western Pacific from Japan to Australia	Marked differences between south-west Indian Ocean and South-East Asian and Australian populations; significant, but smaller differences between Australian and South-East Asia	1–3, 11–13, 15
<i>Penaeus merguiensis</i>	Indian Ocean coast from Arabia to South-East Asia, Indonesia, western Australia and west Pacific from Philippines to eastern Australia	Limited data, evidence for major differentiation between Indian Ocean and Indo-west Pacific populations, possibly sibling species	1, 14
<i>Penaeus chinensis</i>	Chinese and western Korean coasts	Little genetic differentiation over range sampled	1, 9, 16
<i>Penaeus japonicus</i>	Indian Ocean and western Pacific coasts from Japan to Australia	Two sibling species in China Sea and perhaps others	1, 5–7
<i>Penaeus stylirostris</i>	Western coast of Central and South America from Mexico to Peru	Significant genetic differentiation in Gulf of California	1, 8, 10
<i>Penaeus indicus</i>	Indian Ocean coast from South Africa north to Arabia, India, South-East Asia, Indonesia, and northern Australia	Data from only one population	1

Data sources are: 1. Benzie (2000), 2. Sugama *et al.* (2002), 3. Benzie *et al.* (2002), 4. Valles-Jimenez *et al.* (2005), 5. Tzeng and Yeh (2004), 6. Tsoi *et al.* (2005), 7. Tsoi (2006), 8. Aubert and Lightner (2000), 9. Liu *et al.* (2006), 10. De la Rosa-Vélez *et al.* (2000), 11. Klingbunga *et al.* (1998), 12. Klingbunga *et al.* (1999), 13. Klingbunga *et al.* (2001), 14. Hualkasin *et al.* (2003), 15. You *et al.* (2008), 16. Cui *et al.* (2007).



also likely to have resulted in mixing of stocks. Data are relatively few, and the limited genetic differentiation among populations from most of a species range means that effects would be difficult to detect. However, where marked differences exist between populations, such as those of *P. monodon* in the Andaman Sea compared to the Gulf of Thailand, the ability to detect transfers exists. Evidence of genes derived from non-local populations has been demonstrated in wild populations of *P. monodon* exposed to considerable influx of material from non-local populations as a result of aquaculture operations in Thailand (e.g. Supungul *et al.* 2000; You *et al.* 2008). Other cases showing reduced genetic variation in populations near aquaculture operations (Xu *et al.* 2001) have been interpreted to demonstrate a genetic impact of culture of wild *P. monodon* stocks. Despite the deliberate release of large numbers of *P. japonicus* for restocking in Japan there is limited evidence for the presence of restocked animals only in some populations, and no evidence in others (Sugaya *et al.* 2002), indicating that natural population variation can be maintained in the face of large introductions. In general, the natural population genetic structure of shrimp aquaculture species appears to be unaffected by aquaculture activities (Benzie 2000).

### Domesticated stocks and genetically improved strains

Early development of domesticated populations involved the use of pond-reared broodstock, often in response to the variable and unpredictable supply of wild-caught broodstock, and to reduce the costs associated with buying wild broodstock. There was little consideration given to determining effective population sizes or the levels of genetic diversity required to sustain performance and avoid the deleterious effects of inbreeding (Benzie 1998). Many domesticated populations were started at a time when shrimp populations were thought to have little genetic variation or geographical structure, if that was even a consideration when the breeding populations were first set up. None involved testing a series of wild stock and selecting the best performing for inclusion in a breeding programme.

Not surprisingly, many stocks used for closed culture showed marked reductions in genetic diversity in 14 out of 15 cases in early tests using available genetic markers (Benzie 2000). The classic study in this regard was the marked decline in genetic variation, clearly associated with a reduction in spawning success, in pond-reared populations of *P. japonicus* (Sbordoni *et al.* 1986, 1987). In contrast, a reduction in genetic variation in cultured stocks of *P. vannamei* in the USA (Sunden & Davis 1991)

was not associated with the deleterious effects of inbreeding. Subsequent studies using a range of genetic markers have shown either a lack of significant reduction in molecular genetic variation in cultured stocks relative to wild ones in *P. japonicus* (Zhuang *et al.* 2000, 2001; Luan *et al.* 2006), *P. chinensis* (Wang *et al.* 2001) and *P. stylirostris* (Ramos-Paredes & Grijalva-Chon 2003) or a reduction in genetic variation in cultured stocks relative to wild populations of *P. japonicus* (Song *et al.* 1999), *P. stylirostris* (Bierne *et al.* 2000), *P. monodon* (Xu *et al.* 2001) and *P. vannamei* (Cruz *et al.* 2004).

Reductions in genetic variation as time under culture have increased have been reported in *P. japonicus* (Sbordoni *et al.* 1986, 1987), *P. chinensis* (He *et al.* 2004; Li *et al.* 2006b), *P. stylirostris* (Bierne *et al.* 2000; Goyard *et al.* 2003) and *P. vannamei* (Freitas *et al.* 2007), but the decrease over time is highly variable, with many populations held for more generations showing less loss than populations held for less time (Freitas *et al.* 2007). No decline over time was observed for stocks of *P. chinensis* (Zhang *et al.* 2004) or *P. vannamei* (Cruz *et al.* 2004; Soto-Hernandez & Grijalva-Chon 2004; Luvesto *et al.* 2007).

It is clear that the levels of molecular variation differ in domesticated stocks depending on the original variation in the founder stocks and the extent to which the nature of the management regime operated to maintain levels of variation. Few studies have examined production or reproductive performance in addition to assessing molecular diversity. Where data are available, not all declines in the levels of molecular variation have been associated with declines in production performance.

In the case of *P. stylirostris*, reduced performance emerged in the New Caledonia populations in the 21st century and was thought to be the result of inbreeding after some 25 generations in culture (Goyard *et al.* 2003), in part from evidence that better performance was seen in stocks that were more heterozygous at microsatellite loci (Bierne *et al.* 2000). The problem was addressed by introducing new, domesticated stock from Hawaii, and improved performance was clearly demonstrated in the hybrid offspring (Goyard *et al.* 2008). Other programmes that were set up using stocks with insufficient variation in the first instance have sought to include new stocks to increase the genetic diversity available to them, such as the US Shrimp Consortium Programme (Alcivar-Warren *et al.* 2009). Larger programmes have implemented improved stock handling techniques to prevent breeding of close relatives. More recently developed improvement programmes have deliberately included a wide range of genetic diversity for the species concerned as a result of those experiences (Argue *et al.* 2008).

Detailed data on genetic diversity and data used to make breeding decisions are not usually made public by



**Table 3** Existing principal domesticated genetic resources of the principal farmed shrimp species

Species name	Geographical location of the core breeding population	Generations established to 2009	Source of stock	Ownership	Marketed	Source
<i>Penaeus vannamei</i>	Hawaii, USA	20	Mexico and Ecuador	Private	International sales	4
	Florida USA	15+	Mexico and Ecuador	Private	International sales	
	Colombia	12+	Columbia, Costa Rica, Ecuador, Hawaii, Panama, Peru, Salvador, and Venezuela	Private/ Government	Local industry	5
	Mexico (several)	Various up to 11+	Mexico, Ecuador, Venezuela, Colombia, Florida	Private	Local industry	6, 8
	Venezuela	19 years	Mexico, Panama and Colombia	Private	Private use	2
	Brazil (several)	Various up to 7	Costa Rica, Ecuador, Mexico, Panama, and Venezuela	Private	Local industry	13
	China (several)	Unknown	USA, South America	Private	Local industry	9
	Thailand (several)	Unknown	USA, South America	Private	Local industry	9
	Hawaii USA	5	Indo-Pacific	Private	Open sales	12
	Madagascar	17+	South-west Indian Ocean	Private	No	
<i>Penaeus monodon</i>	Australia	8+	East and north coast of Australia	Private/ Government	Local industry	11
	Thailand	5+	Thailand waters	Government	Local industry	10
	Thailand	3+	Thailand waters	Private	Local industry	10
					domestication	
<i>Penaeus merguensis</i>	Thailand	14	Andaman Sea	Government	Experimental, local industry	10
<i>Penaeus chinensis</i>	China	12	China	Government	Local industry	1
<i>Penaeus japonicus</i>	Australia	10+	Australia	Private	Local industry	3
<i>Penaeus stylirostris</i>	New Caledonia	35	Mexico and Panama	Private	Local industry	7
	Hawaii, USA	14+	Ecuador	Private	International sales	7
<i>Penaeus indicus</i>	Saudi Arabia	Not known	Saudi waters	Private	No	9
	Iran	Not known	Persian Gulf	Cooperative	Local industry	

Data sources are: 1. Li *et al.* (2005), 2. De Donato *et al.* (2005), 3. Preston *et al.* (1999a), 4. Argue *et al.* (2002), 5. Gitterle *et al.* (2005a), 6. Castillo-Juarez *et al.* (2007), 7. Goyard *et al.* (2008), 8. Ibarra *et al.* (2007a), 9. Briggs *et al.* (2005), 10. Supattra Uraivan, Trang Coastal Fisheries Research and Development Center, Thailand (pers. comm., 2009), 11. Macbeth *et al.* (2007), 12. Argue *et al.* (2008), 13. Freitas *et al.* (2007). Generations established refer to those under domestication and not necessarily under targeted selection. See additional sources in Briggs *et al.* (2005).

the breeding groups, which makes certain assessments of their process difficult or impossible. That said, some groups have published significant information over the years. The general history of the major domesticated strains has been documented in a range of scientific papers, and in more general articles written for the aquaculture community. The principal domesticated resources are given in Table 3.

The French domestication programmes that worked on several species of shrimp, but ultimately focused on *P. stylirostris* are documented by Bedier *et al.* (1998), Goyard *et al.* (2001, 2002a,b, 2004), Lucien-Brun (2001), Cuzon *et al.* (2004), with specific comment on 'super-shrimp' by Clifford (1996). Of the several programmes for *P. vannamei*, a history of the Colombian improvement programme is given by CENIACUA (1999) and Suárez *et al.* (2002) and that for Mexico by Ibarra (1999). De Donato *et al.* (2005) detail the history of an individual

farm-based population of *P. vannamei*. The history of the US Shrimp Consortium programme on *P. vannamei* is documented in Carr *et al.* (1997), Moss (1999, 2002), Moss *et al.* (1998, 1999, 2002, 2007), Moss and Arce (2003, 2004), Doyle *et al.* (2006), Wyban and Sweeney (1991), Wyban (1992), Wyban *et al.* (1992, 1993), Wyban and Swingle (1999) and Fjalestad *et al.* (1997). The history of the Australian programme on *P. japonicus* is given by Preston *et al.* (1999a,b, 2001, 2004) and Preston and Clifford (2002). A number of the programmes for *P. monodon* in Thailand are reported by Withyachumnarnkul *et al.* (1998) and for Australia by Kenway *et al.* (2006) and Macbeth *et al.* (2007). In addition to the papers listed above, molecular variation within and between cultured stocks and some assessment of the relationship and breeding history of stocks has been assessed in *P. vannamei* in Mexico (Cruz *et al.* 2004; Soto-Hernandez & Grijalva-Chon 2004) and Brazil (Freitas



*et al.* 2007). The latter reports have demonstrated the divergence between stocks and the great variability in levels of inbreeding depending on the history and management of the stocks at individual hatcheries, even when many were derived from the same founding stocks from major domesticated broodstock suppliers.

The existence of established breeding programmes has provided the means of assessing a wider range of traits to guide breeding and to avoid the deleterious consequences of uncontrolled inbreeding. Estimates for heritability in growth are now published for *P. vannamei* (Carr *et al.* 1997; Argue *et al.* 2002; Pérez-Rostro & Ibarra 2003a,b; Gitterle *et al.* 2005a,b; Castillo-Juarez *et al.* 2007; Ibarra & Famula 2008), *P. monodon* (Benzie *et al.* 1997; Kenway *et al.* 2006) and *P. japonicus* (Hetzel *et al.* 2000); for heritability in reproductive traits in *P. vannamei* (Arcos *et al.* 2004; Ibarra *et al.* 2007a) and *P. monodon* (Macbeth *et al.* 2007), for heritability in hypoxia in *P. vannamei* (Ibarra *et al.* 2007a) and for heritability in disease in *P. vannamei* (Argue *et al.* 2002; Gitterle *et al.* 2005b). The relationship between growth measures and measures of disease resistance has been estimated in *P. vannamei* by Argue *et al.* (2002) and Gitterle *et al.* (2005b). This work has demonstrated suitable levels of heritability (approximately 0.4–0.5) to sustain selection programmes for survival, growth and some reproductive characters in *P. vannamei*, *P. stylirostris* and *P. monodon*. With the exception of TSV, where heritabilities of 0.2–0.6 have been measured and there have been sound responses to selection, measurements for resistance or tolerance to other diseases, such as WSSV, have been very low (<0.1–0), suggesting that genetic selection is not possible, or extremely costly for that trait, and in any case will require clearly planned special strategies for breeding (Argue *et al.* 2002; Gitterle *et al.* 2005b; Cock *et al.* 2009). In addition, the genetic correlations measured indicate that selecting for disease resistance would select for slow growth and *vice versa*, suggesting further that other management processes need to be developed for many shrimp diseases. This information is of great strategic importance in determining the approach used to produce the most effectively selected shrimp, and the most appropriate infrastructure and management processes for their production.

Domesticated stocks available to the industry have been developed for their general production characteristics and have not been designed to capture a particular subset of natural variation. Most of the few existing major programmes appear to have robust genetic and biosecurity management regimes (Lotz *et al.* 1995; Lotz 1997; Moss & Argue 2001; Le Moullac *et al.* 2003). In general, programmes with a focused genetic selection strategy have achieved gains in growth of approximately 4–5% per generation for growth in *P. stylirostris* (Goyard *et al.* 2001)

before inbreeding became an issue, in *P. vannamei* (Goyard *et al.* 2001; Argue *et al.* 2002; De Donato *et al.* 2005), *P. chinensis* (Li *et al.* 2005) and *P. monodon* (Argue *et al.* 2008). Comparisons of selected stock with wild, unimproved stock have generally shown that the selected stock perform significantly better, 9–14% better in the case of *P. japonicus* (Preston *et al.* 2004).

Data on genetic and environmental interactions are still limited for shrimp and it is too early to say whether regional strains will need to be developed. It is clear that domesticated strains of *P. vannamei* perform sufficiently well in a wide range of geographical locations. Most domesticated strains are under private sector ownership, with a few under joint government/private sector arrangements. Only a few are open to international sales. In most cases adult broodstock are sold, although in some cases only post-larvae are sold.

### Molecular and genomic shrimp resources

Genomic work is still limited in shrimp, but there is an increasing amount of research investigating differential gene expression in animals in different physiological states, and in the isolation and characterisation of individual genes of interest. To date most of this work has focused on genes related to disease response or with immunological function (e.g. De Lorigeril *et al.* 2005; He *et al.* 2005; Pan *et al.* 2005). Other work has focused on genes related to reproductive isolation. The reports are scattered through the literature for the most part, although relevant DNA and/or protein sequences have been deposited in major public databases such as Genbank. A significant international effort on anti-microbial genes now has a dedicated website to that work (Guegin *et al.* 2006).

First-order genetic maps exist for *P. chinensis*, *P. vannamei*, *P. japonicus* and *P. monodon* (Table 4). These maps are largely based on amplified fragment length polymorphism (AFLP) markers and the spacing of markers simply reflects the number of markers mapped, with more recent studies mapping a greater number than earlier studies for a given species, and the number of linkage groups observed is now approaching that expected from the chromosome counts (Chow *et al.* 1990) for most species. Few characters of economic importance have been mapped to date, although a quantitative trait locus associated with growth has been reported for *P. japonicus* (Li *et al.* 2006a). Sex-linked associations have been reported for *P. vannamei* (Li *et al.* 2006b; Alcivar-Warren *et al.* 2007) and *P. monodon* (Staelens *et al.* 2008), but a substantive molecular marker has been patented only for *P. monodon* (Staelens *et al.* 2008).

Most maps have resulted from specific research projects and the status of the samples used to produce them is



**Table 4** Genomic resources available for the principal farmed shrimp species

Species name	DNA sequences (including expressed sequence tags)	Large insert DNA libraries	Genetic maps					
			Marker type (number mapped)	Marker separation (cM)	Genome cover (%)	No. linkage groups	Expected linkage group no.	Source
<i>Penaeus vannamei</i>	Over 160 000	BAC library?	AFLP (267–319) SSR (30);	15–17	59–62	45	43	1
		FOSMID library						5
<i>Penaeus monodon</i>	10 000s	FOSMID library	AFLP (400–547)	4–5	92–100	42–45	44	2
<i>Penaeus merguensis</i>	None	None	None	N/A	N/A	N/A	N/A	N/A
<i>Penaeus chinensis</i>	10 000s	BAC (small insert size)	AFLP (194–197)	11–14	73–74	35–36	44	3
<i>Penaeus japonicus</i>	1000s	BAC (small insert size)	AFLP (139–245)	8	48–88	33–43	43	4
<i>Penaeus stylirostris</i>	1000s	None	None	N/A	N/A	N/A	N/A	N/A
<i>Penaeus indicus</i>	None	None	None	N/A	N/A	N/A	N/A	N/A

Sources are given for the genetic map information and are for the latest published maps for that species: 1. Zhang *et al.* (2007), 2. Staelens *et al.* (2008), 3. Li *et al.* (2006b), 4. Li *et al.* (2006a), 5. Alcivar-Warren *et al.* (2007).

unclear (i.e. whether the samples still exist, and if so whether they are available to other workers to add more markers). Samples used by two groups to produce maps for *P. monodon* are available to others (Wilson *et al.* 2002; Staelens *et al.* 2008) and those of Wilson *et al.* (2002) have been provided to other groups to improve the first map that those authors produced for *P. monodon* (Li *et al.* 2000; Glenn *et al.* 2005; Wuthisuthimethavee *et al.* 2005; Maneeruttanarungroj *et al.* 2006), and see Li *et al.* (2006a).

Thousands of EST sequences are on public databases for *P. chinensis*, *P. japonicus* and *P. monodon* and hundreds of thousands for *P. vannamei*, but few or none for the other farmed species. Public access large insert libraries are available for *P. vannamei* and *P. monodon* with work in progress towards developing physical maps and genome sequences for these species (Saski *et al.* 2009). Molecular markers have been developed for use in breeding programmes, to assess genetic diversity, track parentage and facilitate traceability in *P. chinensis* (Dong *et al.* 2006), *P. japonicus* (Sugaya *et al.* 2002; Jerry *et al.* 2004, 2006a), *P. monodon* (Jerry *et al.* 2006b) and *P. vannamei* (Alcivar-Warren *et al.* 2003).

### Global exchange of shrimp genetic resources

Early industrial developments accessed wild broodstock for seed production and there was considerable exchange of broodstock and larvae within and between countries within the natural ranges of the species, at least for the principal species farmed, such as *P. japonicus*, *P. monodon*, *P. vannamei* and *P. stylirostris*. Movement of the latter two species has been reported in detail by Briggs *et al.* (2005), and movement of *P. japonicus* has been reported by Liao and Chien (1994). The extent of the

translocations is illustrated by the fact that *P. japonicus* was introduced to several Mediterranean countries, the Atlantic coast of France, Hawaii, Tahiti, Brazil and Mauritius as well as some exchange within Asia, reflecting the ability of this species to be cultured over a broad environmental range (Liao & Chien 1994). *Penaeus stylirostris* was introduced to Tahiti from Central and South America and stocks from Tahiti were reintroduced to Central and South America in the 1970s and to Asia from there and via Mexico and the USA approximately 30 years later (Briggs *et al.* 2005). *Penaeus vannamei* was introduced from Central and South America to Tahiti in the 1970s and to mainland USA and Hawaii in the early 1980s. From the USA there have been extensive introductions of SPF stock to Asia, but rapid development of the industry in China has led to the import of wild broodstock from the natural range of the species in Central and South America (Briggs *et al.* 2005). *Penaeus monodon* was exchanged broadly within Asia and introduced to West Africa and the USA, where it appears to have established in the wild. Shrimp from Australia were provided as broodstock throughout Asia, and Asian animals were introduced to South Africa, the Seychelles and other Indian Ocean locations, Central and South America (unsuccessfully) (Briggs *et al.* 2005) and to Europe for small-scale experimentation. The pattern of dissemination has followed the timing of successful cultivation of a given species (e.g. first *P. japonicus*, then *P. stylirostris* and *P. vannamei*), the absence of alternative species or difficulties in production of established local species.

The early exchange of post-larvae and broodstock prior to the development of techniques to detect a number of shrimp viral diseases (and prior to the discovery of many of those diseases) resulted in the spread of shrimp



diseases that have had a significant effect on the development of the industry. Loss of production to diseases was a key factor in driving domestication, but, perversely, the demand for alien species also offered maintenance of production in the face of disease. Domesticated populations were established by the mid 1980s for some species, and focused genetic improvement programmes were established by the 1990s. The successful production of domesticated SPF stocks was generally outside the natural range of the species and outside the main producing regions. The usually careful initial transfer of these stocks (SEAFDEC 2005) was followed by the maintenance of stocks in variable management conditions within the receiving countries. The continuing demand for domesticated stocks has meant that many third party transfers have been undertaken, and wild stocks have continued to be imported (Briggs *et al.* 2005) with variable quality control with respect to biosecurity, SPF status and genetic constitution. Illegal movement, of unknown biosecurity status, has also been reported (SEAFDEC 2005).

The development of disease-resistant or disease-tolerant strains for both *P. vannamei* and *P. stylirostris* saw the widespread introduction of domesticated stocks of these species from breeding centres in the USA and French Polynesia, respectively, into Central and South America. The failure of the *P. stylirostris* strain to survive well in the areas into which it was introduced led to a strong retraction in the volume and geographical extent of cultivation of that species. Its production is now restricted mainly to New Caledonia, which is free of the diseases to which the species is susceptible. Sale of *P. vannamei* domesticated stocks, which included a strain that was tolerant to TSV, increased throughout Central and South America.

Difficulties of production with *P. monodon*, caused largely by disease being introduced from wild-caught broodstock, led to lobbying by Asian industries for the introduction of SPF *P. vannamei*. This species was formally allowed into China in the late 1990s and into Thailand and Indonesia in the early 2000s, and Vietnam a few years later (SEAFDEC 2005). The availability of disease-free larvae in strains suited to high-density rearing led to a surge in *P. vannamei* production, which largely replaced *P. monodon* production in Thailand within 5 years of its introduction. Purchase of one of the principal breeding companies by corporate interests in Asia assisted the rapid spread of that strain in the region. Breeding programmes for *P. monodon* have had limited success in Asia, and although significant technical advances were made in Australia, the programme remains small and supplies are limited to the local industry. The *P. monodon* programme in Madagascar was successful, but was designed to supply a local company. A domesticated strain of *P. monodon* developed in the USA has recently

become available to farmers through multiplication centres in Asia where improved SPF post-larvae can be bought (Argue *et al.* 2008).

The extent of transfer of wild broodstock for *P. chinensis*, *P. merguensis* and *P. indicus* is not clear, although it is likely to have been extensive within the range of *P. chinensis*. In each of these cases where domesticated stocks exist they are either privately held and do not appear to be traded or are jointly owned by a private/government entity and traded within national boundaries.

### Benefits of the use and exchange of shrimp genetic resources

The market dominance of *P. vannamei* (60%) demonstrates the advantages of stock selectively bred for growth and that is disease free or disease tolerant. The production of *P. stylirostris* (1%) is limited by its sensitivity to viral diseases, but it does play an important role in a regional Pacific island economy where these diseases do not occur. Viral diseases of shrimp were spread by the considerable exchange of broodstock and post-larvae in the early years of the industry and have played an important role in shaping its development.

The principal benefit of the exchange of domesticated SPF and disease-tolerant material has been continued production in the face of negative factors, such as disease, and therefore the continued existence of employment and economy for the producing countries. Penaeid shrimp is one of the highest valued aquaculture commodities and more than half of the shrimp sold on world markets is now a farmed product. Key roles in the development of genetically improved strains now distributed worldwide have been played by research groups and companies in France (Tahiti and New Caledonia), Central and South America (Mexico, Colombia, Venezuela and Ecuador) and the USA (Hawaii, Florida). Quantitative genetics and genomics expertise from the USA and Europe are applied in improvement programmes in producing regions. Although there has been some variety in the sources of stock (from the wild), the vast majority of exchange for established domesticated species comes from the restricted sources developed by the main breeding groups via intermediate breeding companies and subsets of genetic material from the core population. Genetic improvement programmes are largely in the private sector, although they may have public sector interactions.

The additional benefits of domestication are yet to be realized and depend on investment in more sophisticated approaches to genetic improvement using molecular data. An International Consortium for Shrimp Genome Sequencing has met for several years, although this concerted action is yet to be achieved, although this may



be more likely now that some effective tools are available (Saski *et al.* 2009). This approach will also provide the data on which to develop an understanding of shrimp responses to disease that will be required to develop effective disease management methods. Sections of the private sector have contributed to this, but public sector investment will be required to provide the scope and scale needed to develop the appropriate genomic platforms.

### Current practices of exchange of genetic resources and stakeholder views

A number of discussions concerning the factors that need to be considered in managing breeding programmes in aquaculture have been published over the past two decades and manuals have been published to guide both rearing protocols in shrimp (e.g. Kungvankij 1986; Chanratchakool 1993; Browdy *et al.* 2003; FAO 2007) and the genetic management of cultured populations (e.g. Tave 1995, 1999). Similarly, discussion of the factors important in the safe transfer of genetic material including the introduction of alien species and codes of practice for this have also been published (FAO 1995, 2008; Pullin *et al.* 1998, 1999; Greer & Harvey 2004; Bartley *et al.* 2005, 2007; Bartley 2006). The relevant authorities in most countries have a clear understanding of the need for quarantine processes and have regulations in place to deal with disease control and the introduction of alien species. Initiatives on access and benefit sharing arising from the Convention of Biological Diversity (see CBD 1994, 2002; Greer & Harvey 2004, CGRFA 2007a,b,c) are familiar to the relevant policymakers in many countries, particularly those that have ratified the treaty, but are not as widely known, or necessarily accepted, as those concerning, for example, quarantine. There has also been discussion of strategies for benefit sharing and the protection of intellectual property (Seiler & Dufield 2001; Rosendal *et al.* 2006; Olesen *et al.* 2007). General appreciation of these issues is less well known in the industry, although it is understood by key elements, such as specialist breeding companies and corporate entities. Limited diversity provided at any one time is used by some shrimp suppliers as a means of protecting their stock (Moss *et al.* 2007).

The dramatic negative effects of disease have meant that the industry has a strong appreciation of the need for quarantine processes (Briggs *et al.* 2005), but there is still a need for more robust tools and a more robust application of the available tools to provide for more effective practical results. This comment refers to the general transfer of material between fishermen, hatcheries and farms. The specific introduction of a new strain into a country is usually accompanied with a more stringent process, and the need for care here is generally accepted.

The application of sound genetic management practices is undertaken by specialist breeding companies and access to strongly performing disease-free stock is valued by farmers. Many farmers using spawners from their own stock to provide post-larvae do not understand or apply sound genetic management practices. Increasing demand by retailers and the public for better certification, full traceability (Maldini *et al.* 2006) and environmental impact will increase the use of domesticated stocks and may change the balance of the species used (e.g. the CO<sub>2</sub> production is greater at present for *P. vannamei* than *P. monodon*). A growing proportion of genetic resources are being distributed through commercial interactions with improved stocks being purchased from private sector owners. This is likely to become more dominant in the near future as domesticated stocks are now available for the species responsible for the second largest production in the world, *P. monodon*. The exchange is usually of adult broodstock or of post-larvae for farm stocking directly.

The development of domesticated strains of shrimp has been a response to critical issues affecting production, rather than a strategy built proactively. As a result, it is the commercial pressures to maintain production and profitability of the existing industry that have driven the process, rather than any other considerations. As the benefits of a more strategic approach are seen this is likely to encourage investment with a broader view, including technologies to limit reproduction of introduced stocks whether alien or not, and the development and implementation of best farm practice, which will benefit from the availability of improved performance SPF stocks. Hopefully this will also translate into providing resources for developing appropriate repositories to maintain both wild and domesticated resources.

### Conclusions

Despite the scale and importance of the shrimp industry there is still a remarkable reliance of large sections of the industry on wild-caught broodstock and considerable exchange of wild material, but this is changing rapidly. Most effective breeding programmes are in the private sector or largely under private sector control. There are limited genomic resources of public access for penaeid shrimp, but no preserved or live gene banks other than the strains, usually privately owned, that have been developed over the past 20–30 years.

### References

- Alcivar-Warren A, Xu Z, Meehan D, Zuniga G, Bell K (2003) *Over 150 Polymorphic Microsatellite Markers Available For Parentage Testing, Pedigree Tracing, Genetic Diversity And Genome*



- Mapping Of The Pacific White Shrimp, Penaeus (Litopenaeus) vannamei*. Aquaculture America, Louisville, Kentucky, USA.
- Alcivar-Warren A, Meehan-Meola D, Park SE, Xu Z, Delaney M, Zuniga G (2007) SHRIMPMAP: a low density, microsatellite-based linkage map of the Pacific whiteleg shrimp, *Litopenaeus vannamei*: identification of sex-linked markers in linkage group 4. *Journal of Shellfish Research* **26**: 1259–1277.
- Alcivar-Warren A, Meehan-Meola D, Das P, Booth B (2009) *Allele Diversity of a New Mexican Stock of SPF Litopenaeus vannamei Acquired to Increase Germplasm Diversity in the USMSFP Breeding Program*. World Aquaculture Society, Seattle, USA.
- Arcos FG, Racotta IS, Ibarra AM (2004) Genetic parameter estimates for reproductive traits and egg composition in Pacific white shrimp *Penaeus (Litopenaeus) vannamei*. *Aquaculture* **236**: 151–165.
- Argue BJ, Arce SM, Lotz JM, Moss SM (2002) Selective breeding of Pacific white shrimp (*Litopenaeus vannamei*) for growth and resistance to Taura Syndrome Virus. *Aquaculture* **204**: 447–460.
- Argue BJ, Benzie JAH, Brock J (2008) *Field Testing For Family Performance in the MOANA P. monodon Genetic Improvement Program*. World Aquaculture Society, Busan, Korea.
- Aubert H, Lightner DV (2000) Identification of genetic populations of the Pacific blue shrimp *Penaeus stylirostris* of the Gulf of California, Mexico. *Marine Biology* **137**: 875–885.
- Baldwin JD, Bass AL, Bowen BW, Clark JWH (1998) Molecular phylogeny and biogeography of the marine shrimp *Penaeus*. *Molecular Phylogenetics and Evolution* **10**: 399–407.
- Ball AO, Chapman RW (2003) Population genetic analysis of white shrimp, *Litopenaeus setiferus*, using microsatellite genetic markers. *Molecular Ecology* **12**: 2319–2330.
- Bart AN, Choosuk S, Thakur DP (2006) Spermatophore cryopreservation and artificial insemination of black tiger shrimp, *Penaeus monodon* (Fabricius). *Aquaculture Research* **37**: 523–528.
- Bartley DM (ed.) (2006) *Introduced Species in Fisheries and Aquaculture: Information for Responsible Use and Control*. CD-ROM. FAO, Rome.
- Bartley DM, Bhujel RC, Funge-Smith S, Olin PG, Phillips MJ (2005) *International Mechanisms for the Control and Responsible Use of Alien Species in Aquatic Ecosystems*. Report of an Ad Hoc Expert Consultation, 27–30 August 2003, Xishuangbanna, China. FAO, Rome.
- Bartley DM, Harvey BJ, Pullin RSV (eds) (2007) *Workshop on Status and Trends in Aquatic Genetic Resources: A Basis for International Policy*. FAO Fisheries Proceedings 5. FAO, Rome.
- Bedier E, Cochard JC, Le Moullac G, Patrois J, AQUACOP (1998) Selective breeding and pathology in penaeid shrimp culture: the genetic approach to pathogen resistance. *World Aquaculture* **29**: 46–51.
- Benzie JAH (1998) Penaeid genetics and biotechnology. *Aquaculture* **184**: 23–47.
- Benzie JAH (2000) Population structure in penaeid prawns. *Aquaculture Research* **31**: 95–119.
- Benzie JAH (2005) Marine shrimp genomics. Proceedings of the 1st International Symposium of the 21st Century Centre of Excellence Program Marine Bio-manipulation frontier for food production—toward advanced and safe use of aquatic organisms, pp. 53–61; 26–27 February, Sapporo, Hokkaido, Japan.
- Benzie JAH, Kenway M, Trott L (1997) Estimates for the heritability of size in juvenile *Penaeus monodon* prawns from half-sib matings. *Aquaculture* **152**: 49–53.
- Benzie JAH, Kenway M, Ballment E (2001) Growth of *Penaeus monodon* × *Penaeus esculentus* tiger prawn hybrids relative to the parental species. *Aquaculture* **193**: 227–237.
- Benzie JAH, Ballment E, Forbes AT, Demetriades NT, Sugama K, Haryanti *et al.* (2002) Mitochondrial DNA variation in Indo-Pacific populations of the giant tiger prawn, *Penaeus monodon*. *Molecular Ecology* **11**: 2553–2569.
- Benzie JAH, Argue BJ, Brock J (2008) *Disease in Shrimp: Strategies for Genetic Improvement Programs*. World Aquaculture Society, Busan, Korea.
- Bierne N, Beuzart I, Vonau V, Bonhomme F, Bedier E, AQUACOP (2000) Microsatellite-associated heterosis in hatchery propagated stocks of the shrimp *Penaeus stylirostris*. *Aquaculture* **184**: 203–219.
- Borrell YJ, Arenal F, Mbemba ZM, Santana O, Diaz-Fernandez R, Vazquez E *et al.* (2007) Spatial and temporal analysis of the Cuban white shrimp *Penaeus (Litopenaeus) schmitti*. *Aquaculture* **272** (Suppl 1): S125–S138.
- Briggs M, Funge-Smith S, Subasinghe R, Phillips MJ (2005) *Introductions and Movement of Penaeus vannamei and Penaeus stylirostris in Asia and the Pacific*. FAO Fisheries Technical Paper 476. FAO, Rome.
- Browdy CL, Moss SM, Lotz JM, Weirich CR, Otoshi CA, Ogle JT *et al.* (2003) *Recent USMSFP Advances in the Development of Biosecure Environmentally Sound Superintensive Shrimp Production Systems*. Abstracts of Aquaculture America 2003, Louisville, KY, USA. World Aquaculture Society, Baton Rouge, Louisiana, USA, p. 35.
- Carr WH, Fjalestad KT, Godin D, Swingle J, Sweeney JN, Gjedrem T (1997) Genetic variation in weight and survival in a population of specific pathogen-free shrimp, *Penaeus vannamei*. In: Flegel TW, MacRae IH (eds) *Diseases in Asian Aquaculture III. Fish Health Section*, pp. 265–271. Asian Fisheries Society, Manila.
- Castillo-Juarez H, Casares JCQ, Campos-Montes G, Villela CC, Ortega AM, Montaldo HH (2007) Heritability for body weight at harvest size in the Pacific white shrimp, *Penaeus (Litopenaeus) vannamei*, from a multi-environment experiment using univariate and multivariate animal models. *Aquaculture* **273**: 42–49.
- CBD (Convention on Biological Diversity) (1994). *Article 15 on Access to Genetic Resources*. UN, Geneva. Available from URL: <http://www.cbd.int/convention/convention.shtml>
- CBD (Convention on Biological Diversity) (2002) *Bonn Guidelines on Access to Genetic Resources and Fair and Equitable Sharing of the Benefits Arising Out of their*



- Utilization*. Secretariat of the Convention on Biological Diversity, Montreal, Canada.
- CENIACUA (Centro de Investigación de la Acuicultura en Colombia) (1999) Colombia's closed-cycle program for penaeid shrimp genetic selection and improvement. *Global Aquaculture Advocate* **2**: 71, 83–84.
- CGRFA (Commission on Genetic Resources for Food and Agriculture) (2007a) *Multi-Year Programme of Work of the Commission on Genetic Resources for Food and Agriculture*. CGRFA-11/07/21. FAO, Rome. Available from URL: <http://www.fao.org/AG/CGRFA/cgrfa11.htm>
- CGRFA (Commission on Genetic Resources for Food and Agriculture) (2007b) Report of the Commission on Genetic Resources for Food and Agriculture. 11th Session. CGRFA-11/07/Report. FAO, Rome. Available from URL: <http://www.fao.org/AG/CGRFA/cgrfa11.htm>
- CGRFA (Commission on Genetic Resources for Food and Agriculture) (2007c) *The World's Aquatic Genetic Resources: Status and Needs*. CGRFA-11/07/15.2. FAO, Rome. Available from URL: <http://www.fao.org/AG/CGRFA/cgrfa11.htm>
- Chanratchakool P (1993) *Health Management in Shrimp Ponds*. Aquatic Animal Health Research Institute, Bangkok.
- Chow S, Dougherty WJ, Sandifer PA (1990) Meiotic chromosome complements and nuclear DNA contents of four species of shrimps of the genus *Penaeus*. *Journal of Crustacean Biology* **10**: 29–36.
- Clifford HC (1996) Supershrimp: A domesticated line of *P. stylirostris* and viable alternative to *P. vannamei* culture in TSV-positive regions. World Aquaculture Society Conference Aquaculture '96, 29 Jan–2 Feb 1996, Bangkok, Thailand. Abstract 116.
- Cock J, Gitterle T, Salazar M, Rye M (2009) Breeding for disease resistance in penaeid shrimps. *Aquaculture* **286**: 1–11.
- Crane MSJ, Benzie JAH (1999) The Aquaculture CRC International Workshop on Invertebrate Cell Culture. In: *The Aquaculture CRC International Workshop on Invertebrate Cell Culture*, 2–4 November 1997, University of Technology, Sydney, Australia. *Methods in Cell Science* **21**: 171–172.
- Crane MSJ, Williams LM (2002) *Development of Continuous Prawn Cell Lines for Virus Isolation and Cultivation*. FRDC 1997/222. Fisheries Research and Development Corporation, Canberra, Australia.
- Cruz P, Ibarra AM, Mejia-Ruiz H, Gaffney PM, Perez-Enriquez R (2004) Genetic variability assessed by microsatellites in a breeding program of Pacific white shrimp (*Litopenaeus vannamei*). *Marine Biotechnology (New York)* **6**: 157–164.
- Cui Z, Li CP, Jang IK, Chu KH (2007) Lack of genetic differentiation in the shrimp *Penaeus chinensis* in the Northwestern Pacific. *Biochemical Genetics* **45**: 579–588.
- Cuzon G, Arena L, Goguenheim J, Goyard E, AQUACOP (2004) Is it possible to raise offspring of the 25th generation of *Litopenaeus vannamei* (Boone) and 18th generation of *Litopenaeus stylirostris* (Stimpson) in clear water to 40 g? *Aquaculture Research* **35**: 1244–1252.
- De Donato MD, Manrique R, Ramirez R, Mayer L, Howell C (2005) Mass selection and inbreeding effects on a cultivated strain of *Penaeus (Litopenaeus) vannamei* in Venezuela. *Aquaculture* **247**: 159–167.
- De la Rosa-Vélez J, Escobar R, Correa F, Felix E (1999) High allozyme variation and genetic similarity of two populations of commercial penaeids, *Penaeus brevivirostris* (Kingsley) and *P. vannamei* (Boone), from the Gulf of California. *Aquaculture Research* **30**: 459–463.
- De la Rosa-Vélez J, Escobar-Fernández FC, Maqueda-Cornejo M (2000) Genetic structure of two commercial penaeids (*Penaeus californiensis* and *P. stylirostris*) from the Gulf of California, as revealed by allozyme variation. *Fisheries Bulletin* **98**: 674–683.
- De Lorgeril J, Saulnier D, Janech MG, Guegin Y, Bachère E (2005) Identification of genes that are differentially expressed in hemocytes of the Pacific blue shrimp (*Litopenaeus stylirostris*) surviving an infection with *Vibrio penaeicida*. *Physiological Genomics* **21**: 174–183.
- Dong S, Kong J, Zhang T, Meng X, Wang R (2006) Parentage determination of Chinese shrimp (*Fenneropenaeus chinensis*) based on microsatellite DNA markers. *Aquaculture* **258**: 283–288.
- Doyle RW, Moss DR, Moss SM (2006) Geographical variation in the breeding value of TSV resistance among founders of a composite *Penaeus vannamei* broodstock in Hawaii. International Symposium of Genetics in Aquaculture IX, 26–30 June 2006, Montpellier, France, p. 96.
- Espinosa G, Diá R, Matos J, Becquer U, Romo J, Borrell Y (2003) Variación aloenzimática en poblaciones cubanas del camarón blanco *Litopenaeus schmitti*. *Revista Investigaciones Marinas* **24**: 11–19.
- FAO (Food and Agriculture Organization of the United Nations) (1995) *Code of Conduct for Responsible Fisheries*. FAO, Rome.
- FAO (Food and Agriculture Organization of the United Nations) (2007) *Improving Penaeus Monodon Hatchery Practices. Manual Based on Experience in India*. FAO Fisheries Technical Papers T446. FAO, Rome.
- FAO (Food and Agriculture Organization of the United Nations) (2008) *Technical Guidelines for Responsible Fisheries 5: Aquaculture. Genetic Resource Management. Supplement 5*. FAO, Rome.
- FAO (Food and Agriculture Organization of the United Nations) (2009) *The State of World Fisheries and Aquaculture 2008*. FAO, Rome.
- Fast AW, Lester LJ (eds) (1992) *Marine Shrimp Culture: Principles and Practices. Developments in Aquaculture and Fisheries Science*, Vol. 23. Elsevier, Amsterdam.
- Fjalestad KT, Gjerdem T, Carr WH, Sweeney JN (1997) Final report: the shrimp breeding program, selective breeding of *Penaeus vannamei*, vol. 17/97. AKVAFORSK Report, Ås Norway.
- Freitas PD, Calgaro MR, Galetti PM (2007) Genetic diversity within and between broodstocks of the white shrimp *Litopenaeus vannamei* (Boone, 1931) (Decapoda, Penaeidae) and



- its implication for the gene pool conservation. *Brazil Journal of Biology* **67**: 939–943.
- García-Machado E, Robainas AN, Espinosa G, Olivam M, Paez J, Verdecia N *et al.* (2001) Allozyme and mitochondrial DNA variation in Cuban populations of the shrimp *Farfantepenaeus notialis* (Crustacea, Decapoda). *Marine Biology* **138**: 701–707.
- Gitterle T, Rye M, Salte R, Cock J, Johansen H, Lozano C *et al.* (2005a) Genetic (co)variation in harvest body weight and survival in *Penaeus (Litopenaeus) vannamei* under standard commercial conditions. *Aquaculture* **243**: 83–92.
- Gitterle T, Salte R, Gjerde B, Cock J, Johansen H, Salazar M *et al.* (2005b) Genetic (co)variation in resistance to White Spot Syndrome Virus (WSSV) and harvest weight in *Penaeus (Litopenaeus) vannamei*. *Aquaculture* **246**: 139–149.
- Glenn KL, Grapes L, Suwanasopee T, Harris DL, Li Y, Wilson K *et al.* (2005) SNP analysis of AMY2 and CTSL genes in *Litopenaeus vannamei* and *Penaeus monodon* shrimp. *Animal Genetics* **36**: 235–236.
- Goyard E, Penet L, Chim L, Cuzon G, Bédier E (2001) Performance of *Penaeus stylirostris* after six generations of selection for growth. *Global Aquaculture Advocate* **4**: 31–32.
- Goyard E, Patrois J, Peignon JM, Vanaa V, Dufour R, Viallon J *et al.* (2002a) Selection for better growth of *Penaeus stylirostris* in Tahiti and New Caledonia. *Aquaculture* **204**: 461–468.
- Goyard E, Penet L, Chim L, Cuzon G, Bureau D, Bedier E (2002b) Selective breeding of the Tahitian domesticated population of Pacific blue shrimp (*Litopenaeus stylirostris*): perspectives for the New Caledonian shrimp industry. *World Aquaculture* **33**: 28–30.
- Goyard E, Arnaud S, Vonau V, Bishoff V, Mouchel O, Pham D *et al.* (2003) Residual genetic variability in domesticated populations of the Pacific blue shrimp (*Litopenaeus stylirostris*) of New Caledonia, French Polynesia and Hawaii and some management recommendations. *Aquatic Living Resources* **16**: 501–508.
- Goyard E, Peignon J-M, Vonau V, Goarant C, Imbert F, Pham D *et al.* (2004) Genetic improvement of pacific blue shrimp addresses syndrome 93 in New Caledonia. *Global Aquaculture Advocate* **7**: 86–87.
- Goyard E, Goarant C, Ansquer D, Pierre Brun P, de Decker S, Dufour R *et al.* (2008) Cross breeding of different domesticated lines as a simple way for genetic improvement in small aquaculture industries: Heterosis and inbreeding effects on growth and survival rates of the Pacific blue shrimp *Penaeus (Litopenaeus) stylirostris*. *Aquaculture* **278**: 43–50.
- Greer D, Harvey B (2004) *Blue-genes: Sharing and Conserving the World's Aquatic Biodiversity*. Earthscan and the International Development Research Center, London.
- Guegin Y, Garnier J, Robert L, Lefranc MP, Mougenot I, de Lorgetil J *et al.* (2006) PenBase, the shrimp antimicrobial peptide penaeidin database: sequence-base classification and recommended nomenclature. *Developmental and Comparative Immunology* **30**: 283–288.
- Gusmao J, Lazoski C, Sole-Cava AM (2000) A new species of *Penaeus* (Crustacea: Penaeidae) revealed by allozyme and cytochrome oxidase I analysis. *Marine Biology* **137**: 435–446.
- Gusmao J, Lazoski C, Sole-Cava AM (2005) Population genetic structure of Brazilian shrimp species (*Farfantepenaeus* sp., *F. brasiliensis*, *F. paulensis*, and *Litopenaeus schmitti*: Decapoda: Penaeidae). *Genetics and Molecular Biology* **28**: 165–171.
- He YY, Liu P, Li J, Kong J, Wang QY (2004) Analysis of genetic structure in the first cultured stock and the sixth cultured stock of *Fenneropenaeus chinensis*. *Journal of Fisheries Sciences of China* **11**: 572–575.
- He N, Qin Q, Xu X (2005) Differential profile of genes expressed in hemocytes of white spot syndrome virus-resistant shrimp (*Penaeus japonicus*) by combining suppression subtractive hybridization and differential hybridization. *Antiviral Research* **66**: 39–45.
- Hetzel DJS, Crocos PJ, Davis GP, Moore SS, Preston NC (2000) Response to selection and heritability for growth in the Kuruma prawn, *Penaeus japonicus*. *Aquaculture* **181**: 215–223.
- Hualkasin W, Sirimontaporn P, Chotigeat W, Querci J, Phongdara A (2003) Molecular phylogenetic analysis of white prawn species and the existence of two clades in *Penaeus merguensis*. *Journal of Experimental Marine Biology and Ecology* **296**: 1–11.
- Ibarra AM (1999) Steps towards the implementation of a genetic improvement program for Pacific white shrimp (*Litopenaeus vannamei* Boone 1931) in Mexico. In: Cabrera TD, Silva M (eds) *Memorias del congreso de Acuicultura '99, Acuicultura en Armonia con el Ambiente*, pp. 279–286, 17–20 Noviembre, Puerto La Cruz, Venezuela, Tomo II.
- Ibarra AM, Famula TR (2008) Genotype by environment interaction for adult body weights of shrimp *Penaeus vannamei* when grown at low and high densities. *Genetics Selection Evolution* **40**: 541–551.
- Ibarra AM, Perez-Rostro CI, Ramirez JL, Ortega-Estrada E (2007a) Genetics of the resistance to hypoxia in postlarvae and juveniles of the Pacific white shrimp *Penaeus (Litopenaeus) vannamei* (Boone 1931). *Aquaculture Research* **38**: 838–846.
- Jerry DR, Preston NP, Crocos PJ, Keys S, Meadows JRS, Li Y (2004) Parentage determination of Kuruma shrimp *Penaeus (Marsupenaeus) japonicus* (Bate) using microsatellite markers. *Aquaculture* **235**: 237–247.
- Jerry DR, Evans BS, Kenway M, Wilson K (2006a) Development of a microsatellite DNA parentage marker suite for black tiger shrimp *Penaeus monodon*. *Aquaculture* **255**: 542–547.
- Jerry DR, Preston NP, Crocos PJ, Keys S, Meadows JRS, Li Y (2006b) Application of DNA parentage analyses for determining relative growth rates of *Penaeus japonicus* families reared in commercial ponds. *Aquaculture* **254**: 171–181.



- Kenway M, Macbeth M, Salmon M, McPhee C, Benzie J, Wilson K *et al.* (2006) Heritability and genetic correlations of growth and survival in black tiger prawn *Penaeus monodon* reared in tanks. *Aquaculture* **259**: 138–145.
- Klingbunga S, Penman DJ, McAndrew BJ (1998) Genetic variation, population differentiation, and gene flow of the giant tiger shrimp (*Penaeus monodon*) inferred from mtDNA-RFLP data. In: Flegel T (ed.) *Advances in Shrimp Biotechnology*, pp. 51–59. National Center for Genetic Engineering and Biotechnology, Bangkok.
- Klingbunga S, Penman DJ, McAndrew BJ, Tassanakajorn A (1999) Mitochondrial DNA diversity in three populations of the giant tiger shrimp *Penaeus monodon*. *Journal of Marine Biotechnology* **1**: 113–121.
- Klingbunga S, Siludjai D, Wuthijinda W, Tassanakajon A, Jarayabhand P, Menasveta P (2001) Genetic heterogeneity of the giant tiger shrimp (*Penaeus monodon*) in Thailand revealed by RAPD and mtDNA-RFLP analyses. *Marine Biotechnology* **3**: 428–438.
- Kongkeo H (1997) Comparison of intensive shrimp farming systems in Indonesia, Philippines, Taiwan and Thailand. *Aquaculture Research* **28**: 789–796.
- Kongkeo H (2001) Current status and development trends of aquaculture in Asian Region. In: Subasinghe RP, Bueno P, Phillips MJ, Hough C, McGladdery SE, Arthur JR (eds) *Aquaculture in the Third Millennium*. Technical Proceedings of the Conference on Aquaculture in the Third Millennium, pp. 267–293; 20–25 February 2000, NACA, Bangkok, Thailand and FAO, Rome, Italy.
- Kumar N, Lakra WS, Majumdar KC, Goswami M, Ravinder K (2007) Genetic diversity in the Indian population of *Penaeus monodon* (Fabricius, 1798) as revealed by mtDNA sequence analysis. *Aquaculture Research* **38**: 862–869.
- Kungvankij P (1986) *Shrimp Hatchery Design, Operation And Management*. NACA Training Manual Series No.1. NACA, Bangkok.
- Lavery S, Chan TY, Tam YK, Chu KH (2004) Phylogenetic relationships and evolutionary history of the shrimp genus *Penaeus* s. l. derived from mitochondrial DNA. *Molecular Phylogenetics and Evolution* **31**: 39–49.
- Le Moullac G, Goyard E, Saulnier D, Haffner P, Thouard E, Nedelec G *et al.* (2003) Recent improvements in broodstock management and larviculture in marine species in Polynesia and New Caledonia: genetic and health approaches. *Aquaculture* **227**: 89–106.
- Li Y, Wilson KJ, Byrne K, Whan V, Iglesias V, Lehnert SA *et al.* (2000) International collaboration on genetic mapping of the black tiger shrimp, *Penaeus monodon*: progress update. Plant and Animal Genome VIII Conference, Jan 2000, San Diego, CA, USA.
- Li J, Liu P, He Y, Song Q, Mu N, Wang Y (2005) Artificial selection in the new breed of *Fenneropenaeus chinensis* named “Yellow Sea 1” based on fast growth trait. *Journal of Fisheries of China* **29**: 1–5. (in Chinese).
- Li Y, Dierens L, Byrne K, Miggiano E, Lehnert S, Preston P *et al.* (2006a) QTL detection of production traits for the Kuruma prawn *Penaeus japonicus* (Bate) using AFLP markers. *Aquaculture* **258**: 198–210.
- Li Z, Li J, Wang Q, He Y, Liu P (2006b) The effects of selective breeding on the genetic structure of shrimp *Fenneropenaeus chinensis* populations. *Aquaculture* **258**: 278–282.
- Liao IC, Chien Y-H (1994) Culture of kuruma prawn (*Penaeus japonicus* Bate) in Asia. *World Aquaculture* **25**: 18–33.
- Limsuwan C, Chanratchakool P (2004) *Shrimp Farming Industry in Thailand*. National Research Council of Thailand, Bangkok.
- Liu P, Meng XH, Kong J, He YY, Wang QY (2006) Polymorphic analysis of microsatellite DNA in wild populations of Chinese shrimp (*Fenneropenaeus chinensis*). *Aquaculture Research* **37**: 556–562.
- Lotz JM (1997) Special topic review: viruses, biosecurity and specific pathogen-free stocks in shrimp aquaculture. *World Journal of Microbiology and Biotechnology* **13**: 405–413.
- Lotz JM, Browdy CL, Carr WH, Frelier PP, Lightner DV (1995) USMSFP suggested procedures and guidelines for assuring the specific pathogen status of shrimp broodstock and seed. In: Browdy CL, Hopkins JS (eds) *Swimming Through Troubled Waters*. Proceedings of the Special Session on Shrimp Farming, Aquaculture Conference, pp. 66–75, Feb 1995, San Diego, CA, USA. World Aquaculture Society, Baton Rouge, LA, USA.
- Luan S, Kong J, Wang QY (2006) Genetic variation in wild and cultured populations of the Kuruma prawn *Marsupenaeus japonicus* (Bate 1888) using microsatellites. *Aquaculture Research* **37**: 785–792.
- Lucien-Brun H (2001) Shrimp farming in New Caledonia. *Global Aquaculture Advocate* **4**: 63–64.
- Luveto E, Freitas PD, de Galetti PM (2007) Genetic variation in a closed line of the white shrimp *Litopenaeus vannamei* (Penaeidae). *Genetics and Molecular Biology* **30**: 1156–1160.
- Macbeth M, Kenway M, Salmon M, Benzie J, Knibb W, Wilson K (2007) Heritability of reproductive traits and genetic correlations with growth in the black tiger prawn *Penaeus monodon* reared in tanks. *Aquaculture* **270**: 51–56.
- Maggioni R, Rogers AD, Maclean N, D’Incao F (2001) Molecular phylogeny of Western Atlantic *Farfantepenaeus* and *Litopenaeus* shrimp based on mitochondrial 16S partial sequences. *Molecular Phylogenetics and Evolution* **18**: 66–73.
- Maggioni R, Rogers AD, Maclean N (2003) Population structure of *Litopenaeus schmitti* (Decapoda: Penaeidae) from the Brazilian coast identified using six polymorphic microsatellite loci. *Molecular Ecology* **12**: 3213–3217.
- Maldini M, Marzano FN, Fortes GG, Papa R, Gandolfi G (2006) Fish and seafood traceability based on AFLP markers: elaboration of a species database. *Aquaculture* **261**: 487–494.



- Maneeruttanarungroj C, Pongsomboon S, Wuthisuthimethavee S, Klingbunga S, Wilson KJ, Swan J *et al.* (2006) Development of polymorphic expressed sequence tag-derived microsatellites for the extension of the genetic linkage map of black tiger shrimp (*Penaeus monodon*). *Animal Genetics* **37**: 363–368.
- McMillen-Jackson AL, Bert TM (2003) Disparate patterns of population genetic structure and population history in two sympatric penaeid shrimp species (*Farfantepenaeus aztecus* and *Litopenaeus setiferus*) in the eastern United States. *Molecular Ecology* **12**: 2895–2905.
- McMillen-Jackson AL, Bert TM (2004) Genetic diversity in the mtDNA control region and population structure in the pink shrimp *Farfantepenaeus duorarum*. *Journal of Crustacean Biology* **24**: 101–109.
- Moss SM (1999) Biosecure shrimp production: emerging technologies for a maturing industry. *Global Aquaculture Advocate* **3**: 50–52.
- Moss SM (2002) Marine shrimp farming in the western hemisphere: past problems, present solutions, and future visions. *Reviews in Fisheries Sciences* **10**: 601–620.
- Moss SM, Arce SM (2003) SPF defined, pathogen-free status of shrimp limited. *Global Aquaculture Advocate* **6**: 86–87.
- Moss DR, Arce SM (2004) OI research reveals inbreeding depression in pacific white shrimp. *Global Aquaculture Advocate* **7**: 50–51.
- Moss SM, Argue BJ (2001) Biosecurity and genetic improvement of penaeid shrimp: Applications to the marine ornamental industry. *Aquarium Sciences and Conservation* **3**: 231–240.
- Moss S, Arce S, Calderon F, Otoshi C, Moss D, Lotz J *et al.* (1998) Cultivo de camarones peneidos con resistencia a enfermedades experiencias del programa de cultivo de camarones marinos de los EEUU (Breeding for disease resistance in penaeid shrimp: experiences from the US Marine Shrimp Farming Program). In: Jory DE (ed.) *Memorias del primer congreso latinoamericano de camaricultura, Acuicultura en Armonia con el Ambiente*, pp. 1–8, 6–10 Octubre 1998, Republica de Panama, Panama.
- Moss SM, Argue BJ, Arce SM (1999) Genetic improvement of the Pacific white shrimp *Litopenaeus vannamei*, at the Oceanic Institute. *Global Aquaculture Advocate* **3**: 41–43.
- Moss DR, Hennig OL, Moss SM (2002) Sexual growth dimorphism in penaeid shrimp. Potential for all female culture? *Global Aquaculture Advocate* **5**: 60–61.
- Moss DR, Arce SM, Otoshi CA, Doyle RW, Moss SM (2007) Effects of inbreeding on survival of the pacific white shrimp, *Litopenaeus vannamei*. *Aquaculture* **272** (Suppl 1): S30–S37.
- Olesen I, Rosendal GK, Tvedt W, Bryde M, Bensen HB (2007) Access to and protection of aquaculture genetic resources—Structures and strategies in Norwegian aquaculture. *Aquaculture* **272**: S47–S61.
- Pan D, He N, Yang Z, Liu H, Xu X (2005) Differential gene expression profile in hepatopancreas of WSSV-resistant shrimp (*Penaeus japonicus*) by suppression subtractive hybridization. *Developmental and Comparative Immunology* **29**: 103–112.
- Pérez-Farfante I, Kensley B (1997) *Penaeoid and Sergestoid Shrimps and Prawns of the World. Keys and Diagnoses for the Families and Genera*. Memoires du Museum National d'Histoire Naturelle, Paris.
- Pérez-Rostro CI, Ibarra AM (2003a) Heritabilities and genetic correlations of size traits at harvest size in sexually dimorphic Pacific white shrimp (*Litopenaeus vannamei*) grown in two environments. *Aquaculture Research* **34**: 1079–1085.
- Pérez-Rostro CI, Ibarra AM (2003b) Quantitative genetic parameter estimates for size and growth rate traits in Pacific white shrimp *Penaeus vannamei* (Boone 1931) when reared indoors. *Aquaculture Research* **34**: 543–553.
- Preston NP, Clifford HC (2002) Genetic improvement of farmed shrimp. *Global Aquaculture Advocate* **5**: 48–50.
- Preston NP, Brennan DC, Crocos PJ (1999a) Comparative costs of postlarval production from wild or domesticated *Penaeus japonicus* (Bate) broodstock. *Aquaculture Research* **30**: 191–197.
- Preston NP, Crocos P, Moore SS (1999b) *Comparative Growth of Wild and Domesticated Penaeus japonicus in Commercial Production Ponds*. World Aquaculture, Sydney, Australia, p. 612.
- Preston NP, Baule VJ, Leopold R, Henderling J, Atkinson PW, Whyard S (2000) Delivery of DNA to early embryos of the Kuruma prawn, *Penaeus japonicus*. *Aquaculture* **181**: 225–234.
- Preston NP, Crocos PJ, Jackson C, Duncan P, Zipf M, Koenig R (2001) Farming the Kuruma shrimp (*Marsupenaeus japonicus*) in Australia – a case history. In: Browdy CL, Jory DE (eds) *The New Wave*. Proceedings of a Special Session on Sustainable Shrimp Culture, Aquaculture 2001, pp. 57–63. The World Aquaculture Society, Baton Rouge, LA, USA.
- Preston NP, Crocos PJ, Keys SJ, Coman GJ, Koenig R (2004) Comparative growth of selected and non-selected Kuruma shrimp *Penaeus (Marsupenaeus) japonicus* in commercial farm ponds; implications for broodstock production. *Aquaculture* **231**: 73–82.
- Primavera JH (1998) Tropical shrimp farming and its sustainability. In: De Silva SS (ed.) *Tropical Mariculture*, pp. 257–289. Academic Press, London.
- Pullin RSV, Williams MJ, Preston NC (1998) Domestication of crustaceans. *Asian Fisheries Science* **11**: 71–80.
- Pullin RSV, Bartley DM, Koojman J (eds) (1999) *Towards Policies for Conservation and Sustainable Use of Aquatic Genetic Resources*. ICLARM Conference Proceedings 59. ICLARM, Manila.
- Ramos-Paredes J, Grijalva-Chon JM (2003) Allozyme genetic analysis in hatchery strains and wild blue shrimp, *Penaeus (Litopenaeus) stylirostris* (Stimpson), from the Gulf of California. *Aquaculture Research* **34**: 221–234.
- Rinkevich B (2005) Marine invertebrate cell cultures: new millennium trends. *Marine Biotechnology* **7**: 429–439.
- Robainas-Barcia A, Espinosa Lopez G, Hernandez D, Garcia-Machado E (2005) Temporal variation of the population structure and genetic diversity of *Farfantepenaeus notialis* assessed by allozyme loci. *Molecular Ecology* **14**: 2933–2942.



- Robainas-Barcia A, Espinosa Lopez G, Hernandez D, Garcia-Machado E (2008) Spatiotemporal genetic differentiation of Cuban natural populations of the pink shrimp *Farfantepenaeus notialis*. *Genetica* **133**: 283–294.
- Rosenberry B (2002) *World Shrimp Farming 2001*. Shrimp News International, San Diego.
- Rosenberry B (2007) *Shrimp News International*. Shrimp News International, San Diego.
- Rosendal GK, Olesen I, Bensen HB, Tvedt W, Bryde M (2006) Access and legal protection of aquaculture genetic resources—Norwegian perspectives. *Journal of World Intellectual Property* **9**: 392–412.
- Saski CA, Hlederman R, Chapman RW, Benzie JAH (2009) Advancing shrimp genomics. Plant and Animal Genome XVII Conference, January 2009, San Diego, USA.
- Sbordoni V, De Matthaeis E, Cobolli-Sbordoni M, La Rosa G, Mattoccia M (1986) Bottleneck effects and the depression of genetic variability in hatchery stocks of *Penaeus japonicus* (Crustacea, Decapoda). *Aquaculture* **57**: 239–251.
- Sbordoni V, La Rosa G, Mattoccia M, Cobolli-Sbordoni M, De Matthaeis E (1987) Genetic changes in seven generations of hatchery stocks of the Kuruma prawn, *Penaeus japonicus* (Crustacea, Decapoda). In: Tiews K (ed.) *Selection, Hybridization and Genetic Engineering in Aquaculture*, pp. 143–155. Heenemann-Verlag, Berlin.
- SEAFDEC (Southeast Asian Fisheries Development Center) (2005) *Regional Technical Consultation on the Aquaculture of Penaeus vannamei and Other Exotic Shrimps in Southeast Asia*. SEAFDEC, Manila.
- Seiler A, Dutfield G (2001) *Regulating Access and Benefit Sharing: Basic Issues, Legal Instruments, Policy Proposals*. Skripten-46. German Federal Agency for Nature Conservation, Bonn.
- Senanan W, Tangkrock-Olan N, Panutrakul S, Barnette P, Wongwiwatanawute C, Niphonkit N *et al.* (2007) The presence of the Pacific whiteleg shrimp (*Litopenaeus vannamei*, Boone, 1931) in the wild in Thailand. *Journal of Shellfish Research* **26**: 1187–1192.
- Song LS, Xiang JH, Li CX, Zhou LH, Liu BZ, Liu RY (1999) Study of population genetic structure in *Penaeus japonicus* with RAPD markers. *Oceanologica et Limnologia Sinica* **30**: 261–266.
- Soto-Hernandez J, Grijalva-Chon JM (2004) Genetic differentiation in hatchery strains and wild shrimp *Penaeus (Litopenaeus) vannamei* (Boone, 1931) from northwest Mexico. *Aquaculture International* **12**: 593–601.
- Staelens J, Rombaut D, Vercauteren I, Argue B, Benzie JAH, Vuylsteke M (2008) High density linkage maps and sex related markers for the black tiger shrimp *Penaeus monodon*. *Genetics and Molecular Biology* **179**: 917–925.
- Suárez JA, Gitterle T, de la Vega E, Angarita MR, Faillace J (2002) Genetic improvement of *Litopenaeus vannamei* in Colombia. *Aquaculture* **204**: 242–248.
- Sugama K, Haryanti, Benzie JAH, Ballment E (2002) Genetic variation and population structure of the giant tiger prawn, *Penaeus monodon*, in Indonesia. *Aquaculture* **205**: 37–48.
- Sugaya T, Ikeda M, Taniguchi N (2002) Relatedness structure estimated by microsatellites DNA and mitochondrial DNA polymerase chain reaction-restriction fragment length polymorphisms analyses in the wild population of Kuruma prawn *Penaeus japonicus*. *Fisheries Science* **68**: 299–305.
- Sun PS, Venzon JNC, Calderon FRO, Esaki DM (2005) Evaluation of methods for DNA delivery into shrimp zygotes of *Penaeus (Litopenaeus) vannamei*. *Aquaculture* **243**: 19–26.
- Sunden SLF, Davis S (1991) Evaluation of genetic variation in a domestic population of *Penaeus vannamei* (Boone): a comparison with three natural populations. *Aquaculture* **97**: 131–142.
- Supungul P, Sootanan P, Klinbunga S, Kamonrat W, Jarayabhand P, Tassanakajon A (2000) Microsatellite polymorphism and the population structure of the black tiger shrimp (*Penaeus monodon*) in Thailand. *Marine Biotechnology* **2**: 339–347.
- Tam KT, Chu KH (1993) Electrophoretic study on the phylogenetic relationships of some species of *Penaeus* and *Metapenaeus* (Decapoda: Penaeidae) from the South China Sea. *Journal of Crustacean Biology* **13**: 697–705.
- Tave D (1995) *Selective Breeding Programmes for Medium-sized Fish Farms*. FAO Fisheries Technical Paper 352. FAO, Rome.
- Tave D (1999) *Inbreeding and Broodstock Management*. FAO Fisheries Technical Paper 392. FAO, Rome.
- Tsoi KH (2006) Molecular population structure of the kuruma shrimp *Penaeus japonicus* species complex in the western Pacific. *Marine Biotechnology* **150**: 1345–1364.
- Tsoi KH, Wang ZY, Chu KH (2005) Genetic divergence between two morphologically similar varieties of the kuruma shrimp *Penaeus japonicus*. *Marine Biotechnology* **147**: 367–379.
- Tzeng TD, Yeh SY (2004) Population structure of the kuruma prawn (*Penaeus japonicus*) in East Asia inferred from mitochondrial DNA sequences. *ICES Journal of Marine Science* **61**: 913–920.
- Valles-Jimenez R, Cruz P, Perez-Enriquez R (2005) Population genetic structure of Pacific white shrimp (*Litopenaeus vannamei*) from Mexico to Panama: microsatellite DNA variation. *Marine Biotechnology* **6**: 475–484.
- Valles-Jimenez R, Gaffney PM, Perez-Enriquez R (2006) RFLP analysis of the mtDNA control region in white shrimp (*Litopenaeus vannamei*) populations from the eastern Pacific. *Marine Biotechnology* **148**: 867–873.
- Voloch CM, Friere PR, Russo CAM (2005) Molecular phylogeny of penaeid shrimps inferred from two mitochondrial markers. *Genetics and Molecular Research* **4**: 668–674.
- Wang W-J, Kong J, Bao Z-M, Deng J-Y, Zhuang Z-M (2001) Isozyme variation in four populations of *Penaeus chinensis* shrimp. *Biodiversity Science* **9**: 241–246.
- Ward RD, Ovenden JR, Meadows JRS, Grewe PM, Lehnert SA (2006) Population genetic structure of the brown tiger prawn, *Penaeus esculentus*, in tropical northern Australia. *Marine Biology* **148**: 599–607.



- Wilson KJ, Li Y, Whan V, Lehnert SA, Byrne K, Moore S *et al.* (2002) Genetic mapping of the black tiger shrimp, *Penaeus monodon*, with amplified fragment length polymorphism. *Aquaculture* **204**: 297–309.
- Withyachumnarnkul B, Boonsaeng W, Flegel TW, Panyim S, Wongteerasupaya C (1998) Domestication and selective breeding of *Penaeus monodon* in Thailand. In: Flegel T (ed.) *Proceedings of the Special Session on Advances in Shrimp Biotechnology*, Fifth Asian Fisheries Forum: International Conference on Fisheries and Food Security Beyond the Year 2000, pp. 67–70; 11–14 November 1998, Changmai, Thailand.
- Wuthisuthimethavee S, Lumubol P, Toojinda T, Tragoonrung S, Vanavichit A (2005) SSLP-based linkage map construction in black tiger prawn (*Penaeus monodon* Fabricius). *Science Asia* **31**: 91–97.
- Wyban JA (1992) Selective breeding of specific pathogen free (SPF) shrimp for high health and increased growth. In: Fulks W, Main KL (eds) *Diseases of Cultured Penaeid Shrimp in Asia and the United States*. Workshop Proceedings, pp. 257–268; 27–30 April 1992, Oceanic Institute, Honolulu, Hawaii, USA.
- Wyban JA, Sweeney JN (1991) *Intensive Shrimp Production Technology*. High Health Aquaculture, Hawaii.
- Wyban J, Swingle J (1999) *Selective Breeding for Fast Growth and Taura Syndrome Resistance in High Health P. vannamei*. In: *Abstract Book*, World Aquaculture Conference, p. 819; Feb 1999, Sydney, Australia. World Aquaculture Society, Baton Rouge, LA, USA.
- Wyban JA, Swingle JS, Sweeney JN, Pruder GD (1992) Development and commercial performance of high health shrimp using specific pathogen free (SPF) broodstock *Penaeus vannamei*. In: Wyban J (ed.) *Proceedings of the Special Session on Shrimp Farming, Aquaculture Conference*, pp. 254–260; Feb 1992, Orlando, FL, USA. World Aquaculture Society, Baton Rouge, LA, USA.
- Wyban JA, Swingle JS, Sweeney JN, Pruder GD (1993) Specific pathogen free *Penaeus vannamei*: commercial trials indicate the progeny of SPF shrimp can dramatically outperform the progeny of wild shrimp in cultured systems. *World Aquaculture* **24**: 39–45.
- Xiang J, Li F, Zhang C, Zhang X, Yu K, Zhou L *et al.* (2006) Evaluation of induced triploid shrimp *Penaeus (Fenneropenaeus) chinensis* cultured under laboratory conditions. *Aquaculture* **259**: 108–115.
- Xu Z, Primavera JH, de la Pena LD, Pettit P, Belak J, Alcivar-Warren A (2001) Genetic diversity of wild and cultured Black Tiger Shrimp (*Penaeus monodon*) in the Philippines using microsatellites. *Aquaculture* **199**: 13–40.
- You E-M, Chiu T-S, Liu K-F, Tassanakajon A, Klinbunga S, Triwitayakorn K *et al.* (2008) Microsatellite and mitochondrial haplotype diversity reveals population differentiation in the tiger shrimp (*Penaeus monodon*) in the Indo-Pacific region. *Animal Genetics* **39**: 267–277.
- Zhang L, Kong X, Yu Z, Kon J, Chen L (2004) A survey of genetic changes and search for sex-specific markers by AFLP and SAMPL in a breeding program of Chinese shrimp (*Penaeus chinensis*). *Journal of Shellfish Research* **23**: 897–901.
- Zhang L, Yang C, Zhang Y, Li L, Zhang X, Zhang Q *et al.* (2007) A genetic linkage map of Pacific white shrimp (*Litopenaeus vannamei*): sex-linked microsatellite markers and high recombination rates. *Genetica* **131**: 37–49.
- Zhuang ZM, Meng XH, Quan JX, Dai JX, Deng JY (2000) Genetic diversity in the wild population and hatchery stock of *Penaeus japonicus* shrimp by isoenzyme analysis. *Zoological Research* **21**: 323–326.
- Zhuang ZM, Kong J, Shi T, Liu P, Deng JR, Dai JX (2001) Genetic diversity in the wild population and hatchery stock of *Penaeus japonicus* shrimp by RAPD analysis. *Progress in Natural Science* **11**: 250–255.