Promoting responsible use and conservation of aquatic biodiversity for sustainable aquaculture development

Expert Panel Review 3.1

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Benzie, J.A.H., Nguyen, T.T.T., Hulata, G., Bartley, D.M., Brummett, R., Davy, B., Halwart, M., Na-Nakorn, U., & Pullin, R. 2012. Promoting responsible use and conservation of aquatic biodiversity for sustainable aquaculture development. *In* R.P. Subasinghe, J.R. Arthur, D.M. Bartley, S.S. De Silva, M. Halwart, N. Hishamunda, C.V. Mohan & P. Sorgeloos, eds. *Farming the Waters for People and Food*. Proceedings of the Global Conference on Aquaculture 2010, Phuket, Thailand. 22–25 September 2010. pp. 337–383. FAO, Rome and NACA, Bangkok.

Abstract

The world's wealth of aquatic biodiversity at the gene, species and ecosystem levels provides great potential for the aquaculture sector to enhance its contribution to food security and meet future challenges in feeding a growing human population. To realize and explore this potential, issues of access and use of aquatic genetic resources for aquaculture need to be considered. A global approach to responsible use and conservation, effective policies and plans, better information including characterization of aquatic genetic resources at different levels, and wider use of genetic applications in aquaculture are

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identified as some of the important elements needed towards an improved management of aquatic genetic resources for aquaculture, and all of these issues are dealt with in this review.

KEY WORDS: *Biodiversity, Conservation, Genetics, Sustainable aquaculture.*

Introduction

Aquaculture, the farming of fish, molluscs, crustaceans and aquatic plants (FAO, 1995) now provides more than half the total world production, traditionally supplied by wild fisheries (FAO, 2009a). It provides 15 percent of the animal protein eaten by humans, sources of key micronutrients and oils needed for healthy development, and is particularly important for human nutrition in poorer, subsistence communities (FAO, 2008). The projected increase in the world's human population is thought to require an increase in food production of 1.5–2.0 times the current production by 2050 (FAO, 2009b). Given the static or declining return from wild fisheries, the increasing demand for seafood can only be met by increasing aquaculture output (FAO, 2009a).

A doubling of aquaculture production will need to replicate agriculture development in far less time than it took to domesticate terrestrial species, in circumstances where the sites for food production are limited and which demand approaches that take account of the risk to natural biodiversity. Rapid growth of aquaculture over the last 20 years, and optimism that rapid domestication can and is being achieved in aquatic species (Duarte, Marbá and Holmer, 2007) is countered by evidence of slow penetration of genetic improvement programmes in aquaculture production (Hulata, 2001; Gjedrem, 2010). Understanding the constraints to domestication will be critical for planning effective strategies to increase sustainable production of aquatic species. This paper summarizes the history and current use of aquaculture genetic resources, identifies similarities and differences with agriculture development, and discusses the issues that will need to be addressed in promoting the responsible use and conservation of aquatic biodiversity for sustainable aquaculture development.

Biological constraints to domestication of terrestrial and aquatic species

The domestication of most aquaculture species occurred in the last 100 years (Duarte, Marbá & Holmer, 2007). In contrast, about 90 percent of land animals and plants currently farmed were domesticated more than 5 000 years ago. Duarte, Marbá and Holmer (2007) suggested that species are rapidly domesticated in aquaculture because of the ease with which they can be reproduced and that, on average, about a decade of research was required in order to domesticate an aquatic species. The recency of domestication of most aquatic species is not disputed, but Bilio (2007a) has argued that Duarte,

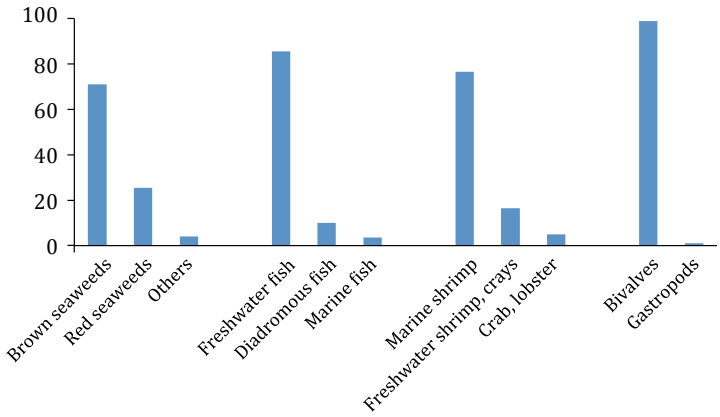
Marbá and Holmer (2007) and others (e.g. Liao and Huang, 2000) overestimate the number of domesticated aquatic species by including those reproduced in culture from only wild-derived parents. Bilio (2007a) suggested that a criterion for domestication should be reproduction from parents raised entirely under culture for at least three consecutive generations. The issue is not one of dry definition. It is important for realistically assessing the speed with which farmed species can be improved by selective breeding. Other reviews have suggested that production from domesticated and selectively bred stocks has been limited (Hulata, 2001; Dunham *et al.,* 2001; Gjedrem, 2010). It is important to recognize that Bilio's (2007a) definition is also arbitrary, and that in any case, the few years of reproduction under culture in aquatic species is not comparable to the thousands of years experienced by terrestrial domesticated species.

Patterns of production and number of species farmed

Few species have the characteristics that make them exceptional organisms for food production (Diamond, 1997, 2002). In agriculture, those species were chosen not just because they were useful, but because they could be domesticated easily. In total, of the 200 000 wild species of higher plants known worldwide, only about 100 have become major domesticated crops, and only five account for more than 90 percent of crop production (Diamond, 2002). Similarly, only 14 out of the 148 species of large herbivores have been domesticated worldwide and five animal species are responsible for more than 90 percent of agricultural production – cattle, sheep, pigs, goats and chickens (FAO, 2007). This is despite many more species within these groups, and thousands of species in total, being accessed regularly by hunters and gatherers (Diamond, 2002). Similar constraints appear to apply to aquaculture, with only 29 species (16 finfish, 7 molluscs, 4 crustaceans and 2 seaweeds) responsible for 90 percent of production (Tables 1–5 – see end of this manuscript) although there are 31 000 finfish, 47 000 crustacean, 85 000 molluscan and 13 000 seaweed species described worldwide (World Conservation Union, 2010).

The pattern of aquaculture production for the last 20 years has been remarkably consistent and is dominated by finfish (around 50 percent) followed by plants and molluscs (each around 20–25 percent) and crustaceans (2–9 percent) (FAO, 2009a). Only 15 species have contributed to the top ten producers in that time (see Garibaldi, 1996; De Silva, 2001). Freshwater species dominate finfish production, brown and red algae, bivalves and marine shrimp dominate plant, mollusc and crustacean production, respectively (Figure 1). Bivalves filter feed naturally produced plankton from the medium and require relatively simple husbandry. Although there are some gastropods, the need for these to access considerable surface areas to graze has restricted farming to high-value species (e.g. abalone). Coastal macroalgae (seaweeds) with rapid growth are the principal plant species farmed for human consumption (McHugh, 2003). Species with long larval lives (>2–3 weeks) are not economic to farm even if their life cycles can be closed, and so shrimp and crab larvae are produced

FIGURE 1
Mean proportion of aquaculture production, by weight, of major taxonomic groups over the last 20 years (1988–2008), given to the nearest whole percent, using only data from production assigned to specific classes



Source: after FAO (2009a).

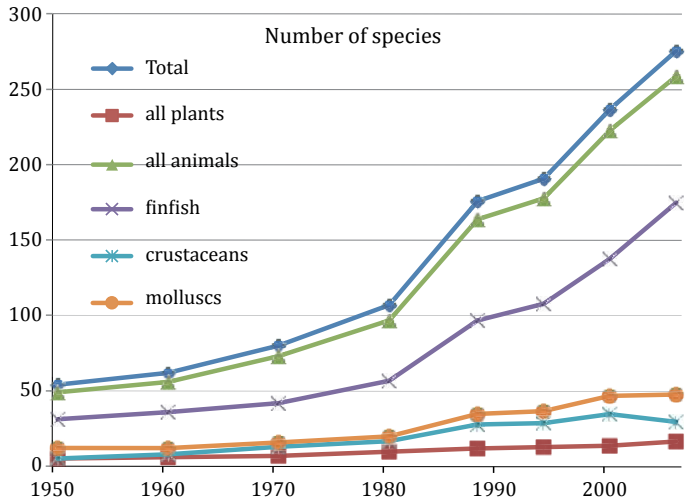
in hatcheries, but spiny lobsters are not. Species with larval stages that are difficult to feed or where aggression or cannibalism is high (e.g. in larvae or juvenile growout) are also not farmed, and these aspects of biology explain why few crabs, crayfish, lobsters and marine finfish are farmed.

Estimates of the total number of aquatic species now farmed range from 336 (Bartley *et al.,* 2009) to more than 430 (Duarte, Marbá & Holmer, 2007). Although records vary in quality (see Garibaldi, 1996), it is clear that the number of species in culture has increased at least five or six-fold from the 1950s to 339 in 2008 (Figure 2). Ninety nine percent of production in each of the major groups over the last ten years is achieved by 20–30 percent of the species farmed, but 80 percent is achieved by only 6–10 percent of farmed species, that is by 44 out of 227 finfish, 19 out of 77 molluscs, 11 out of 35 crustaceans and 2 out of 20 seaweeds (Tables 1–5).

The application of genetic improvement technologies

Humans had no planned foresight for developing agriculture and would simply have interacted with the species in their environment. Stocks were modified over several thousand years by farmers retaining only those individuals that displayed preferred features such as greater docility, milk yield or grain size, and that survived in culture conditions (Ladizinsky, 1998; Zohary and Hopf, 2000). Later, understanding of the nature of inheritance and the interaction among characters allowed the targeted and rapid improvement of many agriculture species in the last 50–100 years. Equivalent or greater gains than those attained by thousands of years of general domestication were achieved in decades.

FIGURE 2
Number of aquatic species cultured in each of the major taxonomic groupings for selected years between 1950 and 2006, where production was recorded for FAO statistics in that year



Source: Fishstat Plus (FAO, 2010b).

Given this experience with terrestrial agriculture, the advantage of utilizing genetic approaches to speed the domestication and improvement of aquaculture species was considered from the beginning of the industrial development of aquaculture. The status has been reviewed by several authors in the intervening period (e.g. Benzie, 1998, 2009, 2010; Dunham *et al*., 2001; Hulata, 2001; Wikfors and Ohno, 2001; Penman, 2005; Gjedrem, 2005, 2010; Mair, 2007; Bilio, 2007a, b, 2008a, b; De Santis and Jerry 2007; Canario *et al.,* 2008; Bartley *et al.,* 2009; Hulata and Ron, 2009; Lo Presti, Lisa and Di Stasio, 2009; Neira, 2010; Rye, Gjerde and Gjedrem, 2010) and indicates that the speed of application of these methods is variable among groups and has yet to impact production as widely as had been hoped.

In order to provide an up-to-date assessment of the current status of the application of genetic improvement technologies to aquaculture production, a series of searches of the scientific literature using major digital science databases subsequent to the times of publication of a number of major reviews in the last decade or so (see citations in previous paragraph) were undertaken. Attention is focussed on the species responsible for the major proportion of production for the ten years from 1999–2008, using only production that could be traced to a named taxon. All entries for unidentified classes (most designated "nei" in the FAO data) were excluded. The proportion of species in each group for which particular data or technologies exist are summarized in Table 1, and detailed results are tabulated separately for finfish (Table 2), molluscs (Table 3), crustaceans (Table 4) and seaweeds (Table 5).

TABLE 1

The proportion (percent) of finfish, molluscan, crustacean and seaweed species for which there is information on wild stock structure; domestication (D), genetic selection programmes (GI), genetic parameter estimates (GP); hybridization (C – crossbreeding of strains; H – interspecies hybridization); molecular resources including EST numbers (Est), parentage tracking (PT), quantitative trait locus markers (Qtl), large insert libraries such as BACs or FOSMIDs (LIL), and microarrays (Mar); genetic maps and other genetic methodologies such as cryopreservation (Cr), sex manipulation (SM), gynogenesis (G), androgenesis (A), clonal lines (CL), ploidy manipulation (Pl), and direct gene transfer (GMO). Tot represents the proportion of species for which any of these technologies exist for molecular and map resources or for other genetic technologies. The information is abstracted from Tables 2–5 which give information for each species of each of the major taxonomic groupings. Production data are from *Fishstat Plus* (FAO, 2010b).

	Wild stock structure	Genetic election			Hybrids		Molecular resources					Genetic maps		Other genetic technologies							
		D,	GI,	GP	C	H	Est,	PT,	Qtl,	LIL,	Mar		Tot	Cr,	SM,	G,	A,	CL,	Pl,	GMO,	Tot
Finfish																					
99 % of production (44 species)	89	66	32	39	18,	34	27,	18,	20,	23,	16	39	**50**	23,	20,	27,	9,	9,	41,	32,	**52**
Others (<1% of production) (183 species)	67	34	4	9	2,	9	10,	9,	2,	1,	5	4	**21**	9,	6,	4,	7,	1,	12,	5,	**25**
Molluscs																					
99 % of production (19 species)	100	42,	21,	26	5,	0	32,	16,	11,	0,	11	21	**42**	21,	0,	0,	0,	2,	37,	5,	**42**
Others (<1% of production) (58 species)	79	38,	24,	12	4,	8	3,	3,	5,	2,	0	7	**12**	0,	0,	0,	0,	0,	22,	0,	**22**
Crustaceans																					
99 % of production (11 species)	100	73,	36,	55	9,	0	45,	45,	18,	36,	0	36	**46**	45,	9,	0,	0,	0,	18,	36,	**64**
Others (<1% of production) (24 species)	71	4,	8,	13	0,	0	4,	4,	0,	0,	0	0	**4**	4,	4,	0,	0,	0,	4,	0,	**13**
Seaweeds																					
99 % of production (2 species)	100	100,	100,	100	100	100	0,	100,	0,	0,	0,	0	**100**	0,	0,	0,	0,	100,	0,	100,	**100**
Others (<1% of production) (20 species)	?											0									

TABLE 2

Finfish species responsible for 99 percent of aquaculture production traceable to individual species from 1999–2008, ranked in order of average production over that period (*Fishstat Plus*, FAO, 2010b). The tally for 80, 90, 95 and 99 percent of production is given in the species ID column to the right of the species name. The total number of species recorded includes those in the FAO records and others recorded from the literature as being farmed, but which are not all recorded separately in the FAO statistics. The table summarizes whether there is information on a) wild stock structure [+ yes, (+) very limited, - no]; b) domestication (D), with time in years given for the longest programme known for domestication (Dyr) [∞ from Bilio (2007a,b) refers to many generations, probably >30] and genetic improvement by selection (GIyr), and whether there are genetic parameter estimates (h – heritability, gc – genetic correlations, r – response to selection, gxe – genotype environment interactions); c) hybridization (C – crossbreeding of strains; H – interspecies hybridization); d) molecular markers EST numbers, parentage tracking (PT) quantitative trait locus markers (Qtl), large insert libraries (LIL) such as BACs or FOSMIDs, or whether a microarray (Mar) of genes exists for that species; e) genetic maps with the type of marker (A – AFLP, M – microsatellite, S – SNP, o – other: capitals for major component, lower case for small contribution) noted, and the largest number of markers mapped on any one map for that species; f) other genetic methodologies used: Cr – cryopreservation, SM – sex manipulation, G – gynogenesis, A – androgenesis, P – ploidy manipulation, CL – clonal lines, GMO – direct gene transfer. * – indicates use in industry, b – use in breeding programmes, e – experimental scale operation, t – commercial trials. The number of species for which data or a given technology exists is given in the row named TOTAL (number of taxa listed given in parentheses), and below this a summary of data for the additional finfish species with lower production values, for which space limitations prevented inclusion of their individual data in the Table. The number in bold face at the right of the column for other technologies indicates the proportion of species for which any of these technologies exist. Summary references for the sources are given in a separate list at the end of the paper.

Species	Wild stock	Genetic selection	Hybrids	Molecular markers	Genetic maps	Other genetic technologies	Source
	structure	D, Dyr,Glyr,GP	C H	Est,PT,Qtl,LIL,Mar	Type, No.	Cr, SM, G, A, CL, P, GMO	
Silver carp, *Hypophthalmichthys molitrix*	+	D*, ∞, >20, h	e	- , PT-,-,-	AM 483	Cr, SMe, Ge,	1,2,5,14,16,18,50
Grass carp, *Ctenopharyngodon idella*	+	D*, ∞, - , h	e	10^2,-,-,-	Ms 279	Cr, SMe, Ge, Pb*, GMOe	1,2,4,6,8,13,17,18
Common carp, *Cyprinus carpio*	+	D*, ∞, >40 , h,r,gxe	b* -	10^4,-,-,BAC, M	MA 719	Cr, SM*, Ge, A*,CL, Pe, GMOet	1,2,4,6,7,8,9,12,19,20, 21,22,23,26
Bighead carp, *Hypophthalmichthys nobilis*	+	D*, ∞, - , -	e	-	Am 153	Cre, Pe	1, 2,5,6,15,18
Crucian carp, *Carrassius carassius*	(+)	D*, -, -, -	e e	-	-	Cre, Gb, A, CL, Pb*, GMOe	1,7,18,27
Nile tilapia, *Oreochromis niloticus*	+	D*,∞,>20, h,r,gxe	b* *	10^5,-,<10,BAC,-	M 525	SMb*,Ge, - CL, Pe, GMOe,	1,2,4,5,6,7,11,31
Atlantic salmon, *Salmo salar*	+	D*,∞,>39, h,r,gxe	e	10^5,-,10-20,BAC, M	A,MS 527	SMb*,Gb, Pb*,GMOet	1,2,3,4,5,6,7,8,10,47, 48,51
Catla, *Catla catla*	+	D, ∞, ? , -	-	-	-	Pe, GMOe	1,2,6,18,28,29
Roho labeo, *Labeo rohita*	+	D, 6+, ? , h	e -	-	-	Cre, GMOe	1,2,6,7,8,18,30
Milkfish, *Chanos chanos* 80	+	-	-	-	-	-	1,40,41
Rainbow trout, *Oncorhynchus mykiss*	+	D*,∞,>39, h,r,gxe	b* b	10^5,-,>20,BAC, M	AMSo 1359	Cre, SMb*,Gb*,Ab,CL, Pb*,GMOe,	1,2,4,5,6,7,8,10,49,51

TABLE 2 (Continued)

Species	Wild stock	Genetic selection	Hybrids	Molecular markers	Genetic maps	Other genetic technologies	Source
	structure	D, Dyr,Glyr,GP	C H	Est,PT,Qtl,LIL,Mar	Type, No.	Cr, SM, G, A, CL, P, GMO	
Blunt snout bream, *Megalobrama amblycephala*	(+)	D*,>30,>25, r	-	-	-	Pe, GMOe	1, 6,18,32,57
Mrigal carp, *Cirrhinus cirrhosus*	+	D, ∞, ? , -	-	-	-	Cre, GMOe	1,2,18,24,25
Channel catfish, *Ictalurus punctatus*	+	D*, ∞, 19, h,r	b* b*	10^5,PT,-,BAC, M	A,Ms 331	Cre, SMb, Gb, Pe, GMOe	1,2,4,5,6,8,33,34,35, 36,37
Black carp, *Mylopharyngodon piceus*	+	-	-	-	-	-, Ge	18
Japanese eel, *Anguilla japonica* 90	+	-	-	10^2,-,-,-,-	-	-	4,38,39
Amur catfish, *Parasilurus asotus*	+	-	-	-	-	-	58
Flathead grey mullet, *Mugil cephalus*	+	-	-	-	-	-	42,43,44
Japanese amberjack, *Seriola quinqueradiata*	-	-	-	10^3,-,-,-,-	M 175	-	59,60, 61
Snakehead, *Channa argus argus*	(+)	-	-	-	-	-	62
Mandarin fish, *Siniperca chuatsi*	+	-	-	-	-	-	45,46
Coho salmon, *Oncorhynchus kisutch*	+	D*, ∞,-,h,gc,r	- e	-,-,<10,-, -	AM 281	SM*, Pe, GMOe	1,2,5,6,7,8,10,51,63, 64,65,66
Gilthead seabream, *Sparus aurata*	+	D*, >5,8,h,r,gxe,c	b* -	10^3,PT,<10,BAC,M	M 204	Pe	1,2,4,5,6,52,53,54,55, 56
Asian swamp eel, *Monopterus albus* 95	+	-	-	-,-,-,BAC,-	-	-	67,68,69
Largemouth black bass, *Micropterus salmoides*	+	D,?,6,r	-	-	-	-	70,71
Goldlined seabream, *Rhabdosargus sarba*	-	D,?,-,-	-	-	-	GMOe	1,8
Pond loach, *Misgurnus anguillicaudatus*	+	-	- e	-	M 153	Cr, Ge,Ae, NT, Pb, GMOe	1, 6,8,72,75,76
Mud carp, *Cirrhinus molitorella*	(+)	-	-	-	-	-	18,77
European seabass, *Dicentrarchus labrax*	+	D*,20,5, h,gc,gxe	-	10^4,PT,10-20,BAC,M	MAs 368	Pe	1,4,5,6,78,79,80,81,

TABLE 2 (Continued)

Species	Wild stock	Genetic selection	Hybrids	Molecular markers	Genetic maps	Other genetic technologies	Source
	structure	D, Dyr,Glyr,GP	C H	Est,PT,Qtl,LIL,Mar	Type, No.	Cr, SM, G, A, CL, P, GMO	
Pacu, *Piaractus mesopotamicus*	-	D, ∞,-,-	- *	-,PT,-	-	-	2,82
Japanese seabass, *Laterolabrax japonicus*	+	D*, ∞, -,-	-	-	-	-	3,83
Asian redtail catfish, *Hemibagrus nemurus*	+	-	-	-	-	-	84,85
Mozambique tilapia, *Oreochromis mossambicus*	+	D,?,?,-	- *	-, - , <10,-,-	-	-	86,87,88
Bastard halibut, *Paralichthys olivaceus*	+	D*, >5,-,h,gc	-	10^3,PT,1,BAC,M	AM 463	SM*, G*, P* MAS	1,3, 4, 5,6,89,95,96
Large yellow croaker, *Larimichthys crocea*	+	D*, ∞, -, -	-	-	Am 188	Ge, Pe	3,90,91,92,93
Snakeskin gourami, *Trichogaster pectoralis*	+	-	-	-	-	-	94
Chachama, *Colossoma macropomum*	+	D, >30,-,-	- *	-	-	-	2,100,101
Barramundi, *Lates calcarifer*	+	D, >3,-, h,gc	-	10^3,PT,10-20,BAC,-	Mo 240	Pe	2,3,4,97,98,99,102
Red drum, *Sciaenops ocellatus*	+	D, ∞,-,- h,gc,	-	-,PT,-	M 237	-	2,3,103,104,105,106, 107
Giant gourami, *Osphronemus goramy*	-	-	-	-	-	-	-
North African catfish, *Clarias gariepinus*	+	D, ∞, >4,-	e b*	-,PT,-	-	Pe	1,2,6,7,73,74
Blackhead seabream, Korean/ Schlegel's black rockfish, *Acanthopagrus schlegelii schlegelii*	+	D*, ∞,-,-	-	-	-	-	3,108,109
Striped catfish, *Pangasianodon hypophthalmus*	+	D, >30,>10, h,gc,r	- *	-	-	-	2,110,111
Bonylip barb, *Osteochilus vittatus* 99	-	-	-	-	-	-	18
TOTAL (44 species)	39	D 29 Gl 14 GP 17	8, 15	12, 8, 9, 10, 7	17	10, 9, 12, 4, 4, 18, 14 **23**	
Others (<1% of production) (183 species)	123	D 62 Gl 8 GP 16	3, 17	19, 17, 3, 2, 9	7	17, 10, 8, 12, 2, 22 9 **45**	

A higher proportion of species contributing to the top 99 percent of production were domesticated according to Bilio's (2007a) criteria (42–73 percent) compared with those contributing less than 1 percent of production (4–38 percent) in each taxonomic group (Table 1). This pattern is repeated more strongly for all other classes of technology. A higher proportion of top producing species have molecular resources or other genetic technologies developed compared with low-production species. There is also a trend for greater development of sophisticated technologies in species produced in developed rather than developing countries; for example – silver carp (*Hypophthalmichthys molitrix*) (1st ranking), grass carp (*Ctenopharyngodon idella*) (2nd) and bighead carp (*H. nobilis*) (4th) have much fewer molecular resources and other genetic technologies applied to them compared to common carp (*Cyprinus carpio*) (3rd), Nile tilapia (*Oreochromis niloticus*) (6th), Atlantic salmon (*Salmo salar*) (7th), rainbow trout (*Oncorhynchus mykiss*) (11th), channel catfish (*Ictalurus punctatus*) (14th), gilthead seabream (*Sparus aurata*) (23rd) or European seabass (*Dicentrarchus labrax*) (29th) (Table 1). A greater proportion of high-production finfish and crustacean species have been subjected to genetic improvement and/or genetic parameter estimation (32–55 percent), molecular resource (46–50 percent) or other genetic technology development (52–64 percent) than molluscs, which have respectively 21–26 percent, 42 percent and 42 percent of species in each of these categories. Each of the technologies is now considered in more detail.

Quantitative genetics and selective breeding

Selective breeding can only be achieved in populations in which the life cycle has been closed and the species reliably and routinely reproduced each generation from parents reared in culture (i.e. domesticated). Only about half of the high-production species in each of finfish, molluscan and crustacean groups recorded as domesticated is subject to targeted genetic improvement today (Table 1). Genetic parameters, which provide information needed to design efficient selection programmes, have been estimated for slightly more because these can be estimated using measures over one generation, and are often done to assess the potential utility of applying selection to a species.

Genetic parameter estimation

The genetic parameter estimates available for seaweeds (Chapman, 1974; Patwary and van der Meer, 1992), finfish (Dunham *et al.,* 2001; Carlson and Seamons, 2008) molluscs (Boudry, 2009) and crustaceans (Jerry, Purvis and Piper, 2002; Wong and McAndrew, 1994; Thanh *et al.,* 2009; Benzie, 2010) have been summarized by those authors. In general, heritabilities show values of around 0.3–0.5 for characters related to growth, suggesting they would respond well to selection, as have a range of other characters related to reproduction and resistance to some diseases. Low heritabilities (<0.1 to 0) for responses to other disease agents suggest that attempts to breed resistant

strains for these are unlikely to be economic. Genetic correlations show a variety of relationships but indicate strong correlation of various measures of growth, and often divergent correlations between these and reproductive or disease tolerance traits, and between larval and postlarval growth in molluscs (Boudry, 2009). These results indicate care is required in the design of breeding programmes so that selection for one advantageous character does not result in selection against another economically important one.

Aquatic species tend to have higher genetic variance (20–35 percent) than agricultural ones (10 percent or less), and higher fecundity which, in general, allows for potentially higher selection intensity (Dunham *et al.,* 2001). Good response to selection has been observed with improvements in growth of 10–20 percent per generation recorded for several finfish (including salmon, carp and tilapia) and shrimp, although longer-term responses in many programmes average around 5 percent per year for most finfish, shrimp and molluscs. The number of cases in which the results of selection have been estimated to be similar in different environments (GxE or genotype by environment interaction) are few. However, lack of GxE effects for Atlantic salmon, Nile tilapia or Sydney rock oyster (*Saccostrea glomerata*) allowed the development of single improved strains that provided better production in a variety of environments.

Genetic improvement through selective breeding

Despite the generally positive results from estimation of genetic parameters, there are still relatively few breeding programmes of significant production scale. In seaweeds, there has been genetic improvement and successful novel strain development only in *Laminaria* (Wu and Lin, 1987), *Porphyra* (Miura, 1976; Ohme, Kunifuji and Miura, 1986; Shin and Miura, 1990) and *Undaria* (Chaoyuan and Guangheng, 1987). Significant improvement of plant quality and yield, disease resistance and stress tolerance of *Laminaria* varieties has been achieved, with more than ten varieties used in cultivation (Zhang *et al.,* 2007). Improvements in some strains include 8–40 percent more biomass and/or some 20–50 percent more iodine than original stocks (Wu and Lin, 1987).

Despite some of the largest production by individual species being from molluscs, few have been domesticated. Boudry (2009) lists only three subject to significant genetic improvement programmes: Giant cupped oyster (*Crassostrea gigas*), Sidney rock oyster and New Zealand green mussel (*Perna canaliculus*), and only the smaller programme for American cupped oyster (*C. virginica*) is recorded in addition in Table 3 for high-production species. Programmes have been started for the greenlip abalone (*Haliotis laevigata*) and the Peruvian calico scallop (*Argopecten pupuratus*). Among crustaceans, large-scale genetic improvement programmes exist only for marine prawns (Benzie, 2009), although some small-scale programmes exist for freshwater crayfish (Wickens and Lee, 2002) and recently for two freshwater prawn (*Macrobrachium*) species (New, 2005; Thanh *et al.,* 2009, 2010). There are two or three major programmes

TABLE 3

Molluscan species responsible for 99 percent of aquaculture production traceable to individual species from 1999–2008, ranked in order of average production over that period (*Fishstat Plus*, FAO, 2010b). The tally for 80, 90, 95 and 99 percent of production is given in the species ID column to the right of the species name. The total number of species recorded includes those in the FAO records and others recorded from the literature as being farmed, but which are not all recorded separately in the FAO statistics. Details of the technologies and column headings are given in the legend to Table 2 for finfish. Summary references for the sources are given in a separate list at the end of the paper

Species	Wild stock	Genetic selection	Hybrids	Molecular markers	Genetic maps	Other genetic technologies	Source
	structure	D, Dyr,Glyr,GP	C H	Est,PT,Qtl,LIL,Mar	Type, No.	Cr,SM,G,A,CL,P,GMO	
Manila clam, *Ruditapes philippinarum*	+	D, ∞, -, -	-	-, PTe, -, -, -	-	Cre, Pe	1,3,5,7,18,19
Giant cupped oyster, *Crassostrea gigas*	+	D*, ∞,>30, h,gc,r,gxe	b* -	10^4, PT, <10, - , M	A,M 119	Cr, Pb*	1,2,3,4,5,6,7,9,10,11, 12,23,24
Constricted tagelus, *Sinonovacuta constricta*	+	D, ∞, -, -	-	10^3, -, -, -, -	-	-	3,15,29
Granular ark, *Tegillarca granosa*	+	D, ∞, -, -	-	-	-	-	3,30,31
Asian brown mussel, *Perna viridis*	+	-	-	-	-	-	13,14
Large weathervane scallop, *Patinopecten yessoensis* 80	+	-	-	10^3, PTe, -, -, -	Am 166	Pe	1,3,5,16,17,20,21,22, 27,28
Blue mussel, *Mytilus edulis*	+	D, ∞, 2e, -	-	10^4, -, -, -, -	A 198	Pe	1,2,3,4,5,7,11,25,26
Bay mussel, *Mytilus galloprovincialis*	+	-, 3, -, -	-	10^4,-,-	-	Pe	2,32,33,38,39
New Zealand green mussel, *Perna canaliculus* 90	+	D*, 8, 8, -	-	-PT,-, -, -	-	Cre	4,50,56
Chilean mussel, *Mytilus chilensis*	+	-, -, -, h,gxe	-	-	-	-	4, 48,49
American cupped oyster, *Crassostrea virginica*	+	D*,>10,>10, h,gc,r,gxe	-	10^3,-,10-20, - , M	Am 114	Pe, GMOe	2, 4, 7, 8, 23,36,37,41, 55
Swan mussel, *Anodonta cygnea*	+	-	-	-	-	-	51
Chinese mystery snail, *Cipangopaludina chinensis* 95	+	-	-	-	-	-	47
Far eastern mussel, *Mytilus coruscus*	+	-	-	-	-	-	4,46
Japanese hard clam, *Mercenaria meretrix*	+	-	-	-	-	-	45
Northern quahog hard clam, *Mercenaria mercenaria*	+	D*, >10, -, h,gc,gxe	-	-	-	Pe	2, 7, 34, 44, 52,53,54
Peruvian calico scallop, *Argopecten purpuratus*	+	-, -, -, h	-	-	-	-	35,43
Asian clam, *Corbicula fluminea*	+	-	-	-	-	-	42
Philippine cupped oyster, *Crassostrea iredalei* 99	(+)	-	-	-	-	-	40
TOTAL (19 species)	19	D 8, GI 4, GP 5	1, 0	6, 3, 2, 0, 2	4	4, 71 **8**	
Others (<1% of production) (58 species)	46	D 22, GI 14, GP 7	1, 2	2, 2, 3, 1, 0	4	0, (CL 1), 13 0 **13**	

established for whiteleg shrimp (*Litopenaeus vannamei*) and a smaller number for giant tiger prawn (*Penaus monodon*), but many regional programmes have utilized stock from the major programmes (Benzie, 2009). They have achieved strains improved for growth and for resistance to Taura syndrome virus (TSV).

Only 22 species of finfish out of 91 recorded as domesticated, and only 14 of the high-production species are subject to selective improvement (Table 2). These programmes have focused on carps, salmonids, tilapia, channel catfish, striped catfish (*Pangasianodon hypophthalmus),* gilthead seabream and European seabass. The ancient and separate domestication of regional varieties of common carp (European, Asian and Far Eastern), and their extensive regional trade has produced more than 60 recognized breeds in China, including 20 alien varieties or hybrid lines, and 80 strains (60 national and 25 foreign) in central and eastern Europe (Flajšhans and Hulata, 2007; Jeney and Jian, 2009). Many of these arose from long-term domestication, but a number of programmes have now been developed for targeted genetic improvement through hybridization and selection. The other major carp producing species (labeo roho (*Labeo rohita*), silver carp, grass carp, bighead carp and Crucian carp (*Carassius carassius*)) were also domesticated in the distant past, but targeted genetic improvement established only in the last 10–20 years (Bilio, 2007a, b). Bilio does not mention commercial genetic improvement programmes but does mention establishment of pedigrees for some of these species in Europe. There are a few references for heritability (h^2) estimation and/or selective breeding from China (Li, Peng and Zhao, 1987; Gheyas *et al.,* 2009) and Viet Nam (Penman, 2005) for silver carp.

There are captive breeding programs for several stocks of each of rainbow trout, chinook (*Oncorhynchus tshawytscha*) and sockeye salmon (*O. nerka*), and for some 32 natural stocks of Atlantic salmon (*Salmo salar*) aimed at restocking and conservation. Genetic improvement programmes aimed at aquaculture production of Atlantic salmon began in Norway in 1971, and there are now 14 different selective breeding programmes for this species, the latest started in Australia in 2004. There are four for rainbow trout, the first started in Norway in 1971 and the latest in Chile in 2000, two for arctic char (*Salvelinus alpinus alpinus*) begun in 1986 and 1992, and one for chinook salmon (Solar, 2009). In general, these have demonstrated considerable response to selection for increased growth rates of five percent per generation in rainbow trout, Atlantic salmon, channel catfish, tilapia and other species summarized in Dunham *et al.* (2001) and Gjedrem (2005); and to resistance to some diseases, such as furunculosis in brook trout (*Salvelinus fontinalis*) (by 67 percent), infectious pancreatic necrosis virus (IPNV) in rainbow trout (by 92 percent), and for other key production traits.

Irrespective of the time for which a species has been domesticated, the breeding programmes designed for food production from aquaculture are all less than 40

years old: five of the 14 high-production finfish and one of the three molluscs are less than 10 years old, 7 finfish, 1 mollusc and 3 shrimp are 10–20 years old, and 4 finfish, 1 mollusc and 1 shrimp more than 20 years old.

Crossbreeding and hybridization

Hybrids whose growth rate is greater than either of the parent strains (i.e. they display heterosis), which have useful combinations of characters not found in the parents, which are sterile or are composed largely of only one sex are valuable for production. Different breeding regimes to those designed to increase performance by selecting each generation within a line are needed for these. Bartley, Rana and Immink (2001) review the use of hybrids in aquaculture and some detail of both intra- and inter-specific crosses is summarized in Dunham *et al.* (2001).

Crossbreeding strains of the same species is rarely used in molluscs, with records of its use only for *C. gigas* and one low-production species (Table 3), and not at all in crustaceans (Table 4), although some strain testing has been carried out for *Macrobrachium* (Thahn *et al.,* 2010). It is reported for eight of the high-production finfish species (Table 2). Most interspecific crosses result in few or no offspring, which are often inviable or poorly performing. This is the case in all crustacean (Benzie, 2009) and nearly all molluscan (Boudry, 2009) hybrids which have been tested. Although most finfish crosses fail, more have proved successful (Dunham *et al.,* 2001). Therefore, no use of interspecies hybrids is reported for the high-production molluscs and crustaceans, while hybridization at an experimental level at least is reported for 34 percent of high-production finfish (Table 2).

Large increases in growth rate of crossbreeds of channel catfish (55 percent improvement), rainbow trout (22 percent) and a few common carp strains (3 of 140 tested) have been reported (Dunham *et al.,* 2001). Only five-high production species crossbreeds contribute significantly to production (i.e. common carp, Nile tilapia, rainbow trout, channel catfish and gilthead seabream), but it is impossible to determine their relative contribution to production. High-production species whose interspecies hybrids have faster growth than their parental species include hybrids of channel and blue catfish (*Ictalurus furcatus*) and *Clarias* catfish hybrids. Those which are preferred for better combinations of growth rate and ratio of head to body size include crosses of common carp with labeo rohu, mrigal carp (*Cirrhinus cirrhosus*), catla (*Catla catla*) and fringed-lipped peninsula carp (*Labeo fimbriatus*) in Asia, and of chachama (*Colossoma macropomum*) and pacu (*Piaractus mesopotamicus*) in South America. Other finfish hybrids have been used to produce single-sex populations (several tilapia species for largely male progeny, and striped bass (*Morone saxatilis*)/yellow bass (*M. mississippiensis)* crosses for all-female offspring). The advantage of these crosses is the greater production of the faster-growing sex, giving better size distribution in the production populations. Sterile hybrids can have improved

TABLE 4

Crustacean species responsible for 99 percent of aquaculture production traceable to individual species from 1999–2008, ranked in order of average production over that period (*Fishstat Plus*, FAO, 2010b). The tally for 80, 90, 95 and 99 percent of production is given in the species ID column to the right of the species name. The total number of species recorded includes those in the FAO records and others recorded from the literature as being farmed, but which are not all recorded separately in the FAO statistics. Details of the technologies and column headings are given in the legend to Table 2 for finfish. Summary references for the sources are given in a separate list at the end of the paper

Species	Wild stock	Genetic Selection	Hybrids	Molecular markers	Genetic maps	Other genetic technologies	Source
	structure	D, Dyr,Glyr,GP	C H	Est, PT, Qtl, LIL, Mar	Type, No.	Cr, SM, G, A,CL,P, GMO	
Whiteleg shrimp, *Litopenaeus vannamei*	+	D*, ∞,>20, h,gc,r,gxe	-	10^5, PT, <10, BAC FOS, -	A,M,S 418	Cr, GMOe	1,2,3,4,9
Giant tiger prawn, *Penaeus monodon*	+	D*, ∞,>10, h,gc,r,gxe	-	10^4, PT, -, FOS, , -	AMo 547	Cr, GMOe	1,2,3,4,9
Chinese mitten crab, *Eriocheir sinensis*	+	-	-	10^4 PT, -, -, , -	-	Cr,	2,5,6,7,8,13,14
Giant river prawn, *Macrobrachium rosenbergii* 80	+	D, >30,-, h,gc	-	-	-	-, SM	2,15,17
Oriental river prawn, *Macrobrachium nipponense*	+	-	-	-	-	-	15,16,18,19
Red swamp crawfish, *Procambarus clarkii*	+	-,-,-, h	-	-	-	GMOe	9,10,11,12,21
Fleshy prawn, *Fenneropenaeus chinensis* 90	+	D*,∞,12/30,h,gc,r	-	10^4, PT, -, BAC, -	A,M 197	Cr, Pe	2,3,4
Giant mud crab, *Scylla serrata*	+	D, ∞, -	-	-	-	-	3,20
Banana prawn, *Fenneropenaeus mergiuensis* 95	+	D*, 14,?,-,-	-	-	-	-	1,2,4
Kuruma prawn, *Marsupenaeus japonicus*	+	D*,∞, >10, h,gc,r,gxe	-	10^3, PT, <10, -BAC, -	A 245	Cr, Pe, GMOe	1,2,3,4
Indian white shrimp, *Fenneropenaeus indicus* 99	(+)	D, 6, ?, -	-	-	-	-	2,4
Number with data/technology							
TOTAL (11 species)	11	D 8, GI 4, GP 6	0, 0	5, 5, 2, 4, 0	4	5, 1, 2, 4 **7**	
Others (<1% of production) (24 species)	17	D 1, GI 2, GP 3	0, 0	1, 1, 0, 0, 0	0	1, 1, 1, 0 **3**	

growth rates by saving the energy used in gamete production, but a significant advantage in the absence of improved growth is the lack of inter-breeding with wild populations. That is one of the principal reasons for the use of hybrids of salmonid species. Inter-species hybridization of gametophytes in seaweeds has successfully provided exploited heterosis in the progeny and an elite *Laminaria* variety, 90-1, introduced to production in 1997, spread rapidly to occupy about one-third of the cultivation area in China by 2004 (Zhang *et al.,* 2007).

Case studies of structured breeding programmes

The first structured breeding programme with a goal to selectively improve fish for aquaculture production was begun on Atlantic salmon in the early 1970s, and its history is recorded by Gjedrem (2010). It is the closest to a process using agriculture experience as a guide, and it is no accident that those involved had a background in livestock breeding. Several salmonid species were considered and their performance in freshwater and seawater culture assessed, with Atlantic salmon and rainbow trout proving to have the best characteristics desired for farming. Inter-species crosses were tested for heterosis but proved difficult to produce and to have poor performance, so excluding crossbreeding as an effective approach to improvement in salmon. An extensive comparison of 100 or more strains of Atlantic salmon from different rivers showed up to a 20 percent difference in performance in culture. The inclusion of only the best-performing strains in constructing the base breeding population meant large immediate gains. Testing more than 200 families per year allowed the estimation of the heritability and genetic correlations for a number of traits of interest, and testing in different locations and different environments showed genotype by environment interaction were low, suggesting only one line would be required to provide a selectively improved fish useful in the full range of farming environments used. The programme achieved 10 percent improvement in fish growth per year, and by 1992 had provided a specific benefit to the Norwegian industry of NOK194 million, a return on investment of 15:1, and a substantial industry producing more than 130 000 tonnes per year from a start only 20 years before. Extensive transfer of these stocks worldwide, in particular to Chile, allowed the development of new industries in the southern hemisphere. From no genetically improved stocks being available in 1970, 97 percent of Atlantic salmon production in 2003 was estimated to be from genetically improved stocks.

The other successful large-scale domestication and breeding programme, for tilapia, used a similar approach most recently summarized in Eknath and Hulata (2009), Ponzoni, Nguyen and Kaw (2007), Ponzoni, Kaw and Yee (2010) and Ponzoni *et al.* (2010). International funding provided to a non-governmental organization (NGO), the International Center for Living Aquatic Resources Management (ICLARM) in 1988, allowed testing several tilapia strains in a number of different environments in the Philippines, the estimation of a number of genetic parameters and the subsequent construction of a substantial

TABLE 5

Plant species responsible for 99 percent of aquaculture production traceable to individual species from 1999–2008, ranked in order of average production over that period (*Fishstat Plus*, 2010b). The tally for 76 and 99 percent of production is given in the species ID column to the right of the species name. The total number of species recorded includes those in the FAO records and others recorded from the literature as being farmed, but which are not all recorded separately in the FAO statistics. Details of the technologies and column headings are given in the legend to Table 2 for finfish. All seaweed species listed have additionally techniques for somatic hybridization applied to them. Sources are to original work only if the basic information is not provided in major reviews, which are otherwise referenced. Summary references for the sources are given in a separate list at the end of the paper

Species	Wild stock	Genetic Selection	Hybrids	Molecular markers	Genetic maps	Other genetic technologies	Source
	structure	D, Dyr,Glyr,GP	C H	Est,PT,Qtl,LIL,Mar	Type, No.	Cr,SM, G, A, CL,P, GMO	
Japanese kelp, *Laminaria japonica* 76	+	D*, ∞,>40, h	b* b*	-, PT, -, -, -	-	CL, GMOe	1,2,3,
Wakame, *Undaria pinnatifida* 99	+	D*, ∞,>30, h	b* b*	-, PT, -, -, -	-	CL, GMOe	1,3,4
Number with data/technology							
TOTAL (2 species)	2	D 2, GI 2, GP 2	2, 2	0, 2, 0, 0, 0	0	2 2 2	
Others (<1% of production) (18 species)	?	?	?	?	?	?	

pedigree-based selection programme. Low GxE suggested only one line would provide for production in a range of environments. The programme achieved growth improvements of 12 percent per generation, an ultimate return on investment of more than 70 percent, and a resource supporting new aquaculture developments in much of Asia, including the development of several regional selective breeding programmes. Key components of the programme included the development of distribution networks for the improved fry so that farmers could access the material. The Genetic Improvement of Farmed Tilapia (GIFT) programme demonstrated the feasibility and cost-effectiveness of genetic improvement for tropical fish by its completion in 1997. At that stage, the breeding operations were transferred to a non-profit body. However, this was ultimately uneconomic and was taken over by a private company that now supplies tilapia seed to the aquaculture industry worldwide. In addition, several independent breeding programmes starting from GIFT material are also carried out in several countries in Southeast Asia.

In contrast, many other programmes developed from the immediate need to provide more reliable supplies of seed for production systems and closed breeding populations were produced as a result. Begun with little thought for quality and genetic diversity, many of these failed through lack of sufficient capital and the deleterious consequences of unintended inbreeding. Others were able to introduce new stocks, develop sound breeding approaches and ultimately become successful. Examples are provided by several shrimp species, including *L. vannamei,* summarized in Benzie (2009). This species' development was greatly advantaged by research over two decades on several aspects of shrimp biology by the US Marine Shrimp Consortium, and led to strains improved for growth and TSV resistance. Improved broodstock were supplied internationally by the research agency involved and by United States producers, and nearly all production of *L. vannamei* worldwide now uses selectively improved stock.

Key to the continued success of all these programmes, and the molluscan ones as described by Boudry (2009), was the collaboration between government and industry, and access to adequate investment and key skills over the time needed to develop the improved stocks. Whether planned from the outset or developed as a response to challenges emerging from changing circumstances, these collaborations and interactions between various sectors, often from different countries, were required for the successful transformation of a good technical programme into an effective supply of improved stock to farmers. However, even where technical success is achieved, improved strains may have little impact if rejected by industry, as Boudry (2009) describes for oyster programmes in Europe. Even where significant investment and strong genetic skills are applied for significant periods (more than ten years as in the cod improvement programme), effective industrial production may not be achieved if aspects of husbandry technology are not efficient or market conditions not suitable.

Molecular and genomic tools

Molecular genetic, genomic and biotechnological applications for a wide range of cultured fish are reviewed in Dunham (2004), Canario *et al.* (2008), Gjedrem and Baranski (2009) and Cerdà, Douglas and Reith (2010); reviews of genomics in molluscs are given by Saavedra and Brachère (2006), and Gestal *et al.* (2008) and for aquaculture generally by Kocher and Kole (2008) and Clark *et al.* (2010). A range of molecular tools, including allozymes (protein-based markers), and a number based on detecting variation in DNA, such as restriction fragment length polymorphisms (RFLPs), amplified fragment length polymorphisms (AFLPs), microsatellites, and most recently, single nucleotide polymorphisms (SNPs) have been developed to determine the amount of genetic variation present in populations, the relationships between populations and interactions with wild stocks; track parentage; enable traceability; and provide markers for important economic traits (Liu and Cordes, 2004; Liu, 2007). Cheaper and more effective DNA-based markers have generally replaced allozymes and older DNA-based markers. Today, microsatellites and, increasingly, SNPs are the variants of choice for collecting genetic information. Nearly all the high-production species have some number of molecular variants available for such use. Usually this is a handful of polymorphisms (<10–20) most often used for population genetic work and assessing the level of variation within cultured populations. The number of species for which there is no information on wild stocks provides a useful proxy for those for which it is unlikely there are any markers available. Among the high-production species there are only five such finfish (11 percent) and none of the molluscan, crustacean or seaweed species lack these resources. However, 20–30 percent of low-production species appear to do so.

The information that even small numbers of polymorphisms have provided is that cultured populations frequently have reduced variation relative to wild ones. They often differ considerably in the frequency of genetic variants from the wild stocks from which they were derived, even after only one or two generations. Both effects can result from taking only a sample of the wild variation in stocking a culture system (a founder effect), breeding occurring from only a small number of individuals in the captured populations (low effective population size) and/or the effects of unintended or deliberate selection of breeders within the culture system. Each of these effects has been reported for finfish (Dunham, 2004) molluscs (Boudry, 2009) and crustaceans (Benzie, 2009). Suites of markers used to identify parents and their young (PT in the Tables) have been reported for far fewer species though – 26 finfish (Table 2), 6 molluscs (Table 3) and 5 crustaceans (Table 4) in total, and 9, 4 and 4 species, respectively, for the high-production species. So the tools exist for some species to be able to assess effective population sizes of cultured populations and to establish pedigree data from molecular markers and so potentially better manage inbreeding and mating schedules. They are used for cultivar identification, parentage assessment and to provide species identification and study geographical patterns of genetic

variation in the seaweeds *Laminaria* (Wang *et al.,* 2004; Bartsch *et al.,* 2008), *Porphyra* (Weng *et al.,* 2004) and *Undaria pinnatifida* (Wang *et al.,* 2006; Endo *et al.,* 2009). Recently, an assessment of tools for identifying the genetic origin of fish and monitoring their occurrence in the wild has been undertaken as part of GENIMPACT – a European network (Blohm *et al.,* 2007).

Resources for marking and mapping

The ability to use markers to assist the efficiency of breeding programmes by identifying molecular variants associated with traits of economic importance demands access to significant numbers of markers, and assessments of their relationships with each other and those traits. Sequence data can be used to identify variable sites that can be used as markers and to detect particular candidate genes known in other organisms to be important for key processes such as growth or disease resistance. The number of Expressed Sequence Taga (ESTs) or sequences of gene fragments that are major sources for marker discovery is a good proxy to indicate where such resources may exist. There are EST libraries with more than 100 ESTs for 27–34 percent of high-production species in all taxonomic groups (Table 1). However, the level of such resources needed for sound genomic work is on the order of 10^4 or greater, and only ten high-production finfish, six molluscs and five crustaceans have these. No aquaculture species has published values of 10^6 or greater. Large EST libraries are associated with additional resources such as large insert libraries (BACs or bacterial artificial chromosome and FOSMIDS or cloning vectors), and microarrays, although relatively fewer molluscs have these resources developed compared with finfish or crustaceans.

Genetic maps

Genetic maps exist for 24 finfish, 8 molluscan and 4 crustacean species in total, and 17, 4 and 4 species, respectively, of the high-production species. Only a handful use significant numbers of SNPs as markers (two finfish and one shrimp). Microsatellites were used as major markers in 88 percent of finfish species maps and 50 percent have AFLPs, while 100 percent of molluscan and crustacean species maps used AFLPs and 75 percent some microsatellites. The importance of marker type is that AFLPs do not mark the same position in a map based on a different set of samples, whereas microsatellites, SNPs and other markers do. AFLP markers themselves therefore do not have general applicability, and such maps are of limited use. Another key observation is that relatively small numbers of markers have been positioned on any one map. The highest number of markers is for rainbow trout at 1 359; only Atlantic salmon, Nile tilapia, common carp and giant tiger prawn are greater than 500, and no mollusc map exceeds 200. For comparison, the maps used to great effect in major agricultural crop and livestock species have several to tens of thousands of markers. Although work on channel catfish linkage mapping began in the 1980s and several maps were produced in the 1990s, the majority of finfish maps, and all molluscan and crustacean ones have been produced in the last decade, and all clearly improved in quality over time.

Markers for specific traits and quantitative trait loci

Among the high-production species, quantitative trait loci (QTLs) are reported for only nine finfish, two molluscan and two crustacean species. Most have fewer than ten QTLs and more than 20 are reported only for rainbow trout. Most are associated with growth, some disease resistance, feed conversion efficiency, tolerance of bacterial disease, spawning time, embryonic developmental rates and cold tolerance. A candidate DNA marker linked to infectious haematopoietic necrosis (IHN) disease resistance has also been identified in salmon. The reason for small numbers of QTLs being identified is that few studies measure the characters of interest in the same individuals in which the markers are assayed, fewer still corroborate the validity of the linkage observed in the initial mapping families in wider population studies, and the ability to finely map candidate genes is limited by the low marker density in most aquaculture species. Sex markers have been reported for shrimp, molluscs and several finfish and growth QTLs are most frequently reported, but few are used to date in marker assisted selection programmes (see below).

Marker assisted selection

Marker assisted selection (MAS) refers to selective breeding in which selection is based on the genotypes (Liu and Cordes, 2004) or on a combination of value estimates based on marker genotype and phenotypic trait data (Gjedrem and Baranski, 2009). MAS is particularly important for traits with low heritability, limited, late in life or after slaughter recording. Sonesson (2007) demonstrated that MAS could generate up to twice the total genetic gain of the corresponding non-MAS scheme in within-family selection. The large QTL for IPN resistance identified in Atlantic salmon was incorporated in MAS in Norway, increasing the rate of genetic improvement of this trait by up to 50 percent (Gjedrem and Baranski, 2009). A successful marker-assisted breeding for disease-resistance in an aquacultured species was the case of lymphocystis in Japanese flounder (*Paralichthys olivaceus*) (Fuji *et al.,* 2007). Genomic selection (Meuwissen, Hayes and Goddard*,* 2001) could be immensely beneficial for multitrait selection, but requires a relatively large number of markers, now practical in aquatic species, with the development of new sequencing technologies and whole genome and transcriptome sequencing.

Gene expression

The last decade has seen an explosion of activity in the isolation and characterization of individual genes. It is beyond the scope of this review to cover this literature, as genes are often isolated because of the interest of an individual researcher in a particular gene or gene group, often with no particular interest in any aquaculture application. So isolation, characterization and expression of single genes in one or more tissues for many of the species being cultured, irrespective of their production volume, have been reported. However, there are few programmes of significant scale designed to detect candidate genes of interest for genetic improvement programmes. For example significant

microarray resources have been developed for only 16 finfish, only 7 of which are high-production species (Table 2), 2 molluscs, *C. virginica* and *C. gigas,* but no crustaceans (Tables 3 and 4).

Other technologies

Sex manipulation

Sex manipulation is not used in molluscs (Tables 1 and 3), but sex reversal has been achieved in freshwater shrimp (Sagi and Aflalo, 2005) and crayfish (De Bock and López Greco, 2010) through surgery and/or by mating strategies using feminized males which produce all-male offspring when mated to normal males (Table 4). Similarly, mating strategies using physiologically or surgically sex-reversed finfish are used to produce single-sex populations which have the advantage of reduced variability at harvest and/or the use of only the faster growing sex for production (Dunham, 2004). Sex reversal is often achieved using gynogenesis or androgenesis, hence the co-occurrence of these technologies in the list in Table 2.

Gynogensis and androgenesis

Mechanisms to manipulate sex, but which also aid discovery of new genes and understanding of the genetic control of key characters include gynogenesis (the production of young through excluding the male contribution and doubling the female one) or androgenesis (the production of young through excluding the female contribution and doubling the male one) (Dunham, 2004). Similar mechanisms for doubling chromosome complements are used to change the number of chromosome set copies (ploidy manipulation) to produce polyploid individuals (usually triploids), either because these grow faster than the usual diploids, or because they do not breed. Mitotic gynogens (produced during mitosis) and androgens are totally homozygous, and are therefore less likely to complete development because of the uninhibited expression of deleterious genotypes, and hence more difficult to obtain. They can be used to produce clonal lines. Meiotic gynogens are not homozygous because recombination during oogenesis mixes genes from the female and male parent before exclusion of the second polar body.

Application of these methods is not reported for crustaceans or molluscs, although clonal lines are reported for two molluscs, northern quahog hard clam (*Mercenaria mercenaria*) and Farrer's scallop (*Chlamys farreri*) (Tables 1, 3 and 4). Androgenesis is more rarely applied in high-production finfish species than gynogenesis, although this pattern is reversed in low-production species. Coupled with sperm cryopreservation, androgenesis may serve a major role in conservation of endangered species or stocks. One or another technique has been applied to 16 high-production finfish, but inbred clonal lines have been produced for only four: common carp, grass carp, Nile tilapia and rainbow trout (Table 2). Despite being genetically identical, individual performance within

these clones is highly variable. These do not play a major role in production, but the use of gynogenetic female lines and gynogenetic sex-reversed inbred male lines was critical in the Hungarian common carp crossbreeding programme.

Ploidy manipulation

Application of stress to early (single-cell) stages of fertilized eggs through pressure, temperature or chemical manipulation can increase the number of chromosome set copies and is used normally to make triploids (with three rather than two chromosome set copies) and rarely tetraploids. The latter are constructed so that triploids can be made by crossing tetraploid with diploid parents. At least experimental activity has been undertaken on about 40 percent of finfish and molluscs, but only 18 percent of crustaceans (Table 1). Practical application to industry has not been achieved for crustaceans, but has for a number of fish species (Dunham, 2004) and molluscs (Boudry, 2009) for both increased growth and use of sterile production stocks (Piferrer *et al.,* 2009). Large-scale application is made for oysters, particularly *C. gigas* in the United States industry.

Cryogenics

Cryogenics, the frozen storage of gametes (usually sperm), a technology that allows storage of genetic material and enables mating between parents that is otherwise difficult (e.g. when one sex is rare, or individuals come into reproductive condition at different times) or impossible (e.g. between generations of an annual species). Methods have been established experimentally for 20 percent of high-production finfish and molluscs and 45 percent of crustaceans (Table 1), but the level of its routine use in breeding programmes is hard to establish. Although the technology exists, the only cryobanks designed to store aquaculture genetic resources established so far are in the Institute of Fishery and Hydrobiology, Vodňany, Czech Republic, and recently for aquaculture in Brazil.

Genetic engineering

Direct insertion of specific genes to create a genetically modified organism (GMO) has been attempted in each of the four taxonomic groups (Table 1), although only experimentally for one high-production mollusc (*C. virginica*), three penaeid shrimp and the red swamp crawfish (*Procambarus clarkii*) (Tables 3 and 4). Introduction of DNA into crustaceans and molluscs is technically demanding and though achieved, the results have not been rewarding to date. By far more work has been done with finfish, including at least experimental work with 23 of the 44 high-production species (Table 2). This work has been reviewed by Kocher and Kole (2008) and despite the level of experimental work, particularly in the developmental fish models (zebra danio (or zebrafish, *Danio rerio*) and Japanese rice fish (or medaka, *Oryzias latipes*)) and in the salmonids, only two aquaculture species are the subject of larger trials, and none has achieved regulatory approval for commercial production.

Although genetic engineering is in an early phase with searches for algal promoters and effective means of gene transfer, the existence of haploid (gametophyte) and diploid (sporophyte) phases and clonal propagation of seaweeds suggests considerable scope for transgenic approaches (Minocha, 2003). Work on seaweeds as novel bioreactors is being addressed experimentally, with expression of targeted genes achieved in transformed explants in a number of cultured species, *Kappaphycus*, *Laminaria*, *Porphyra* and *Undaria* (Hallmann, 2007; Li *et al.,* 2009a). Additional biotechnological applications include the use of native and recombinant enzymes to assist the preparation of protoplasts, the use of which could allow genetic improvement through somatic hybridization (Inoue, Kagaya and Ojima, 2007; Reddy *et al.,* 2007). Genomic information is becoming available through sequence information held on international databases and will become increasingly useful with the completion of seaweed genome sequencing projects, including a *Porphyra* species.

Dispersal of farmed stocks

Terrestrial animals and plants were first domesticated about 12 000 years ago in about nine geographically restricted regions (Diamond, 1997, 2002). Archaeological and population genetic data show a rapid spread of these species from their regions of origin several thousand years ago to regions suited for major production (these data are summarized for both plants (FAO, 1997) and animals (FAO, 2007)). The first strains spread regionally and may have prevented independent attempts to domesticate that species. Therefore, those with restricted distributions (e.g. wheat, barley and peas) were subject to one domestication event, those with wider distributions to multiple domestication origins (e.g. pigs, horses, cattle and chickens), and independent domestication of the same or closely related species occurred where there were significant barriers to migration (e.g. potatoes, maize, peppers, beans and squash).

Several publications (Bartley *et al.,* 2009) have summarized how many aquaculture species have been distributed within, and far beyond their natural range. A number of finfish species were widely stocked for sport fishing (e.g. brown trout (*Salmo truttae*) and other salmonids, and centrarchids), often well beyond their natural range, and for more than a 100 years. Since then, many species have been introduced to new areas with a view to developing aquaculture industries. All of the high-production species listed in Tables 2–5 have been subject to exchange between local and regional populations for the purposes of aquaculture, and many distributed intercontinentally or worldwide. The role of alien species in Asian aquaculture and its links to food production were highlighted by De Silva *et al.* (2006) and De Silva *et al.* (2009), respectively. Extensive exchange of common carp has occurred for hundreds of years. Some 259 separate introductions of *Cyprinus carpio* strains have been recorded, and some strains recognized as local have originated from alien introductions with hybridization to local stocks in the distant past (Jeney and Jian, 2009). In many

cases, large-scale production takes place in regions far from the natural range of the species, and relatively little, if any, in its native range (e.g. redclaw crayfish found naturally in tropical Australia is produced mainly in China; the east Pacific endemic whiteleg shrimp *Litopenaeus vannamei* is produced in North and South America and throughout Asia; Atlantic bay scallop (*Argopecten irradians*) found in North America is produced mainly in China; Atlantic salmon are produced in Chile and Australia as well as in their natural range in Norway and Canada; Nile tilapia, an African endemic, is mainly produced in Asia). Extensive movements of wild-caught marine finfish seed have been documented for Asia by Nguyen *et al.* (2009).

Crayfish species have been spread across several continents, in many cases for restocking or to provide alternative wild fisheries in circumstances where the naturally occurring species had previously declined. Other species used in aquaculture have spread because of their natural invasive capabilities, such as the Chinese mitten crab, *Eriocheir sinensis*, thought to have spread in ship ballast waters. All the major cultivated seaweed species have been moved extensively. The primary development of *Laminaria japonicus* and *Porphyra* culture was in Japan, but the export of key varieties to China led to greatly increased production there. Cultivated varieties of *Kappaphycus alvarezii* have been introduced to many parts of the world for the development of seaweed farming and are now produced in the Philippines, Indonesia, Malaysia (Sabah), Fiji and Tanzania (Munõz, Freile-Pelegrín and Robledo, 2004).

The movements parallel the history for terrestrial species, but the rapidity is greater for aquaculture species, reflecting the ease of egg and larval transfer, the globalization of trade and the speed of present day travel. The extensive movement of terrestrial and aquatic species has given rise to concern about the impacts of alien species through the establishment of feral populations, their interactions in the ecosystems to which they have been introduced and the transfer of diseases, or associated commensals, to endemic biota. Negative impacts have been described in all these regards, with feral populations of some penaeid shrimp, molluscan and finfish species established outside their natural ranges (Bartley *et al.,* 2009). Hybridization with related species (e.g. in crayfish species (Perry, Lodge and Feder, 2002) and catfish (Senanan *et al.,* 2004)) resulting in the loss of regional endemics; loss of regional variation or introgression of genetic material from genetically differentiated populations from different parts of a species' range resulting in modification of local wild stocks have also been documented (Cross, 2003; McGinnity *et al.,* 2003). However, other studies on tilapia and carps have shown no impacts or impacts that are judged acceptable by local communities in view of the social and economic benefits arising from culture (Arthur *et al.,* 2010). There is particular concern about genetic exchange between wild stocks and GMOs.

Wild genetic resources

Molecular tools revolutionized understanding of the genetic diversity in wild populations from the late 1960s, revealing large amounts of variation, and often considerable differences in gene frequencies within species over their geographical range. The relevant tools have recently been assessed by Blohm *et al.* (2007). The development had important consequences for the conservation and exploitation of natural resources (Thorpe, Sole-Cava and Watts, 2000). In fisheries, cryptic species or spatial and temporal genetic structure were detected, indicating that what was thought to be one fishery was exploiting several stocks that should be more appropriately managed separately. Rapid life history changes in fish and shellfish stocks under intense selection pressure from fisheries, resulting in, for example, early maturation and smaller adult sizes in fished populations, were demonstrated. Many species with high dispersal capability appear not to move as much as expected, and therefore may not recolonize depleted regions, and regional genetic differentiation is likely. Strong evidence has been obtained that the molecular differentiation of local stocks of fish, and salmonids in particular, reflects adaptation to local environments. These findings have important implications for the effective management and exploitation of natural fisheries resources and are discussed in more detail in several reviews (see papers in Hauser, Waples and Carvalho, 2008).

Molecular work has shown cryptic taxa exist in what are considered to be single aquaculture species (e.g. the recent discovery of a cryptic species of *Marsupenaeus japonicus* in Asia (Benzie, 2009); of cryptic tuna species by COI DNA barcoding (Yancy *et al.,* 2008), and confirmed species complexes in several groups including the crab *E. sinensis* (Li *et al.,* 2009b)). Difficulty in assessing the numbers of species farmed because of poor taxonomic distinction applied to farmed stocks is particularly important for molluscs and aquatic plants, but can be significant in finfish, where cultured stocks can be unrecognized interspecies derivatives. Oysters comprise species complexes in Asia that are poorly understood, and the catch-all title of Pacific oyster probably includes several species (Klinbunga *et al*., 2005). Algae are often referred to by genus name alone, and there are significant difficulties in determining cryptic taxa in species where there is known to be substantial, environmentally induced, morphological variation (Wikfors and Ohno, 2001).

However, molecular tools to provide accurate molecular diagnosis of species provide tools for traceability of products, forensic assessments of products and introductions to the wild, and interactions between wild and cultured stocks (Teletchea, 2009). They have been used to identify and analyse the pathways used by invasive species (e.g. *E. sinensis* (Dittel and Epifanio, 2009)), and the nature of genetic interactions between wild and cultured stocks of salmon (e.g. McGinnity *et al.,* 2003). Naylor *et al.* (2005) presented a thorough analysis of the risks posed by escaped salmon from net-pen aquaculture: risk of feral

stock establishment; competition with wild fish for mates, space and prey; pathogen transmission; and most relevant to this review – risks associated with genetic interactions with wild stocks. Atlantic salmon has been shown to genetically affect wild populations of other salmonids as well (e.g. sea trout (*Salmo trutta*) (Coughlan *et al.,* 2006)). The effects of cultured species on their respective wild populations are visible in the last two or three decades also with the Mediterranean gilthead seabream and European seabass (Dimitriou *et al.,* 2007). Escaped hybrid catfish (female bighead catfish, *Clarias macrocephalus* × male North African catfish, *C. gariepinus*) from farms in central Thailand may interbreed with *C. macrocephalus* individuals in the wild (Na-Nakorn, Kamonrat and Namsiri, 2004; Senanan *et al*., 2004). In contrast, no effects of cultured catfish were observed on wild stocks by Simmons *et al.* (2006). Considerable shifts in gene frequencies in some wild populations subject to high levels of introductions have been reported (e.g. Hindar, Ryman and Utter, 1991; Waples and Do, 1994). These often occur where populations are subjected to sustained restocking from hatcheries, and there is evidence of short-term advantage for hatchery-produced stocks relative to wild ones, but poorer performance under stress, and presumably over longer time periods, than wild individuals. However, the burgeoning research on both terrestrial and aquatic alien introductions shows large variation in the extent and timing of their effects, and much research needs to be done to understand these. Recent work has shown how wild populations change in gene frequency over short times, and that they are selected by a changing environment (e.g. Clutton-Brock and Pemberton, 2004). The ability of fish to track their environment through changing genetic constitution will bring into question how to interpret genetic difference detected spatially at one time point and requires greater application of evolutionary science to these issues.

To avoid the risks of alien species, it has been suggested it is better to use local species for aquaculture. In a region such as the lower Mekong, there is a trend to encourage the use of indigenous species for aquaculture and stock enhancement purposes (e.g. Sverdrup-Jensen, 2002; Ingthamjitr, 2009), driven by the need to mitigate purported negative impacts from exotic species. Significant downsides to this approach that are not usually discussed include the fact that cultured indigenous populations are more likely to be able to interbreed with local wild stocks. Managing the cultured stock as one would a hatchery stock designed for wild population enhancement, and so reduce genetic impact would prevent the development of a line that was efficient for food production (De Silva *et al.,* 2009). In addition, the need to develop effective understanding of the biology of a given species, including husbandry, feeds and reproductive control prior to being able to undertake practical genetic improvement on an industrial scale means that there will be a lead time of a decade or likely far longer to bring such species into effective production.

A technical solution to this would be for the development of sterile production stocks, and highly secure facilities for the core breeding population of cultured

species (Cotter *et al.,* 2002; Mair, Nam and Solar*,* 2008). However, for some, the use of sterile production animals gives rise to concerns about ownership of the breeding stock. These examples illustrate the complex interaction of technical capability, production needs, environmental concerns, and issues of ownership and benefit sharing.

Strategic consequences of biological constraints

In aquaculture today, a small number of now widely spread species that are particularly easy to farm dominate production, as in agriculture. While production of some new species has increased and replaced previously higher-ranking species, examples are few (an exception is pangasiid catfish), and usually involve changes in ranking of species that have been cultured for some time. It is possible that new major production species will emerge in aquaculture, as many species are still being tested. The market and ecological concern also drives choice of species/strain to be farmed, but while these issues may attract investment or drive additional work to overcome technical challenges, the available data suggest that those species that are easy to farm are those most likely to become widely farmed. Just as some new top performers may be found, some species that are recorded as domesticated now may be discarded in the future, or support only small regional production. Already, in shrimp, of more than 20 species for which aquaculture technologies were successfully developed, only seven now provide 99 percent of shrimp production. Two species for which there are specific pathogen free (SPF), genetically improved stocks supply 86 percent, one of which, *Litopenaeus vannamei*, now dominates world supply. With production systems, supply chains and retailers tailored to this product, competition from other species is made more difficult.

The rapid gains of modern genetics that were achieved with terrestrial species during the last century were obtained using a resource which had already undergone thousands of years of domestication. A wealth of information on physiology, disease, behaviour, reproduction, biochemistry and routine husbandry was available for these species by then. This information is often lacking for aquaculture species, and it takes time to obtain as experience is gained in the husbandry of a new species in different environments. Basic research can change practical applications in ways never imagined by researchers. However, many incremental findings are needed to assimilate new knowledge, and the contributions of commercial producers and users are critical to the practical application of scientific knowledge and the creation of demand for products (Wikfors and Ohno, 2001). The need to have an integrated application of a variety of technologies to sustain selective breeding programmes has slowed, and will continue to slow, the pace of genetic improvement over a broad front. Important production species which are not domesticated, and for which the only source of seed supply are wild stocks include the Japanese eel (*Anguilla japonica*), flathead grey mullet (*Mugil cephalus*), milkfish (*Chanos*

chanos) and mandarin fish (*Siniperca chuatsi*), and for many other species the principal source of seed is still from the wild (Mair, 2007).

The application of molecular genetics and biotechnological tools on an industry-wide scale requires the stable platforms of fully domesticated (probably more than the three generations in culture arbitrarily chosen in this paper as a definition for domestication of aquaculture species), if not genetically improved stocks. The increasing simplicity and decreasing cost of molecular and genomic work means that the initial research undertaken to find markers or candidate genes is relatively easy to undertake. The longer-term work to assess their effects in whole organisms is dependent on having knowledge of biochemistry, physiology, etc. and the means to undertake expensive experiments to determine their effect and construct practical applications. Genomic work for most aquatic species is at an early stage with maps based on relatively few markers, few QTLs and only one or two used to date in marker assisted selection. Technical difficulties and consumer resistance means there is little practical application of GMO technology so far.

Conclusions

The analysis of the current state of the art is important for considering pathways for future development. No one pathway would sensibly be followed to the exclusion of others. However, these results suggest that with respect to the aims of increasing food production and reducing risk to biodiversity, that 1) there be a greater focus on developing selective breeding programmes, and 2) that there might be greater return by focusing on easily farmed species already in production rather than a concerted search to develop new species.

Key shortcomings

Ten years ago only 1–2 percent of farmed fish and shellfish production was thought to be derived from modern genetic improvement programmes (Gjedrem, 2000). If it is assumed that all the production from the species recorded to have a genetic improvement programme, however small, is from genetically improved stocks, then, using production figures for those species from FAO data (FAO, 2009a), an upper limit of 15 percent of molluscan, 67 percent of crustacean, 76 percent of finfish, 99 percent of seaweed and 73 percent of total aquaculture production would be from improved stocks. However, more detailed information from particular industry sectors indicate these figures are too high (Bartley *et al.,* 2009). In the case of crustaceans, where better information is available, almost all production for *L. vannamei* is from improved sources, but most production for all other species is not, providing an estimate of 45 percent of crustacean production from improved sources (Benzie, 2009). In the case of the main carp species, assuming that only 10 percent of carp production is from improved sources means only 7 percent of fish production and 38 percent of all fish production is genetically improved. These calculations serve to illustrate the

dearth of reliable information on genetic resources used in aquaculture and the need to improve this. The present analysis, based on production identified to species, accounts for only 70 percent recorded by FAO for aquaculture – thus, data on almost a third of world production is absent.

In addition, plant resources were poorly represented. Although by far the major production, only seaweeds are discussed in any detail, and more than 100 species have been tested for aquaculture (Ohno and Critchley, 1993), and cultured aquatic plants comprise a range of higher plants including reeds, *Lotus,* water spinach (*Ipomea aquatica*), and water cress, but statistics on these individual groups are difficult to access. In recent years, there has also been considerable growth in the use of microalgae as feeds for aquaculture species, and there is increasing use of some microalgal species (e.g. *Spirulina*) for human food consumption, often as a nutriceutical (Wikfors and Ohno, 2001), and for a range of biotechnologies, reviewed in Hallmann (2007).

Resources available to assist best practice

A number of resources have been developed to provide guidance on best practice in breeding and genetic improvement in aquaculture to farmers, technical staff, extension and development officers and policy-makers (e.g. Tave, 1995, 1999; Gjedrem, 2005). Direct environmental effects of the aquaculture process on land use and effluents have long been recognized and have led to the development of manuals and codes of practice for aquaculture internationally and nationally for various sectors of the industry (e.g. in shrimp farming: FAO/NACA/UNEP/WB/WWF, 2006). The importance of effects of biodiversity itself took longer to appreciate (Beveridge, Ross and Kelly, 1994; Pullin, 1996). The growing recognition of the complexity of genetic variation within species, the presumed adaptive nature of this variation, and the potentially deleterious effects of breeding between aquaculture populations (whether local or introduced) and local wild stocks have led to the development of strategies to assess and monitor risk and implement improved management practices (e.g. Pullin, Bartley and Kooiman, 1999; FAO, 2008). These approaches extend the procedures developed for the introduction of alien species, the threats of disease transfer and potential ecological impacts which have been appreciated for much longer (Pullin, Bartley and Kooiman, 1999; Bartley *et al.,* 2005, 2009, FAO, 2008). However, it is difficult to assess the extent to which these voluntary codes have assisted aquaculture development and ameliorated negative impacts.

Guidelines for better-practice approaches to the development of domesticated stocks all suggest paying attention to some, or all, of the following criteria:

– knowledge of genetic resources available;
– choice of appropriate resources to include in cultured population;
– adequate genetic variation in founder stocks;
– adequate management of the stock to avoid deleterious inbreeding;
– environmental impact of cultured stocks on wild populations;

– maintenance of genetic variety in cultured populations and protection of variation in wild stock;
– introduction of alien farmed species to new locations (outside their natural range);
– issues of ownership and benefit from domesticated stock; and
– food security

The global and national legal frameworks underpinning the ownership and use of natural resources have changed in the last 20 years – biodiversity was once considered the heritage of all mankind, but sovereign nations own the biodiversity within their boundaries (CBD, 1994). However, the development of improved strains for culture demands considerable investment and the application of key knowledge. Access to biodiversity and determination of the ownership of the resulting strains or intellectual property require effective mechanisms to assess appropriate benefit sharing. This issue is all the more acute because of differences in the global distribution of producers and consumers of aquaculture products. Aquaculture growth in developing countries is double or more that of developed nations, with 60 percent of world production coming from China (FAO, 2010a).There are differences in the location of skilled technologists and investors, the source areas of natural stocks and the locations of most cost-effective production. A doubling of aquaculture production will need to replicate agriculture development in far less time than it took to domesticate terrestrial species, in circumstances where the likelihood sites will be prioritized for food production is reduced and which demand new approaches that take account of the risk to natural biodiversity. There are, then, a range of technical, social, political and commercial issues to be considered in increasing food production from aquaculture. For example, Brummett and Ponzoni (2009) note the risks to native biodiversity need to be assessed, but that the use of improved lines of tilapia could provide immediate economic benefit, and the development of new improved lines should be encouraged as opposed to using available wild stocks.

The change in ownership of biological diversity resulting from the Convention of Biological Diversity (CBD, 1994) led to the development of the Bonn Guidelines on access to genetic resources and fair and equitable sharing of the benefits arising out of their utilization (CBD, 2002). However, the fact that policy development and legislation relating to different aspects of development are often under different departments with different key goals can lead to significant conflict. This is common circumstance in government, and in the present context, much of the development of the processes related to the CBD has been undertaken by environment departments, while responsibility for food production and industry development and research and development are in different departments. The possible impact of CBD-related policies on food production has only been recently been appreciated, and while environmental organizations are aware of the developments, much of industry, and some departments of trade, commerce

and industry are not (see papers in Bartley *et al.*, 2009). There is a need to undertake formal surveys to establish the extent and depth of understanding of these policies outside the specialist groups developing them.

Despite the existence of useful publications on policies, codes of practice and best practice, their implementation is variable because of gaps in dissemination of the information, lack of effective technologies or over-riding factors of economy and/or practicality.

Summary

There is scope for increasing aquaculture production by accessing new regions for fish farming, such as the open sea, but this will require innovative approaches and high levels of investment. Coastal and inland aquaculture sites are limited and their use is subject to strong competition. More production from existing areas will be necessary to increase aquaculture output. The bulk of aquatic animal production is based on freshwater species where these constraints are greater and impacts on wild resources potentially higher. Aquaculture has shown sustained growth in production for 20 years through increasing the number of species farmed, but mainly through increasing production of a few of these. Aquaculture is subject to a more rapid application of domestication and genetic improvement than occurred in the historical development of agriculture. Selection programmes and advanced technologies are being applied in the early stages of domestication of many new species.

However, major constraints relating to the fundamental attributes of a species, the lack of accumulated knowledge concerning biology and husbandry, and the restricted levels of investment limit the effectiveness and speed of application of these techniques. Many high-production species are not subject to modern methods of genetic improvement. Even in many species where a domesticated line has been established, an unknown but large proportion of seed supply for industry production still relies on access to wild genetic resources. Contribution of genetically improved strains to total aquaculture production is still limited compared to that in terrestrial species. Continued large-scale use of wild sources for seed supply can have large impacts on the wild stocks and effectively imposes additional fishing pressure on them (Mair, 2007). It is imperative that closed breeding populations are established to reduce these effects, to obtain improved efficiencies through selection and the option to develop stocks with reduced capacity to interact with wild populations.

The risks to natural biodiversity, the source of useful genetic resources in the future, are real. Application of population genetics and evolutionary biology to aquatic species has increased understanding of genetic biodiversity in the last two decades. However, the available data vary in quality and quantity. There is a need for more high-quality studies with improved coordination and collaboration between groups with complementary skills. Continued production of scientists

that can provide the depth of analysis and interpretation is needed to better understand the nature of interactions of wild and cultured populations and advise how these can be managed.

The few successful genetic improvement programmes have all involved collaboration of several sectors of government, industry and NGOs, often internationally, to achieve technical and practical success. Sometimes these were established outside the natural range of the species and by investment from countries/companies other than the major producing regions or the place of origin of the original stocks. These circumstances indicate the mutual dependence of different sectors in achieving effective food production, and the need to appreciate their relative strengths and roles, and their rights in relation to access and benefit sharing. Systems to assist dialogue among those with responsibility for achieving varied, divergent and sometimes contradictory goals of conservation and food production will be vital.

The lack of effective means to track the contribution of various genetic resources means estimates of their contribution to world food supply range from 7–70 percent in the case of finfish and anywhere between 20 and 70 percent of total production, depending on assumptions. There is a critical need to improve knowledge of the state of the world's aquatic genetic resources. Timely information on the status of these and the technologies in use in food production systems is critical in order to assess and guide the process of sustainable aquaculture development.

There is a clear role for the FAO in conjunction with regional organizations and institutions and national governments, to assist that dialogue, to continue to better document aquatic genetic resources available in the wild and in current production systems through the Multi-Year Programme of Work of the Commission on Genetic Resources for Food and Agriculture. There is a need for FAO, the Consultative Group on International Agriculture Research (CGIAR), other regional and international organizations dedicated to aquaculture development and individual states to better disseminate information on best practice and to assist dialogue between groups focused on different aspects of development and conservation in order to develop effective sustainable use of aquatic genetic biodiversity.

Recommendations

The responsible use and conservation of aquatic biodiversity for sustainable aquaculture therefore requires the use of efficient mechanisms for production, and technologies to minimize environmental and genetic impact.

Ten years ago, a review of the status of aquaculture genetics for the Conference on Aquaculture in the Third Millennium (Dunham *et al.*, 2001) recommended a series of actions to encourage the continuing development of genetic

improvement in aquaculture and the increased characterization and protection of wild genetic resources. This was to be achieved by:

- encouraging networking of experts, CGIAR, other regional and international organizations dedicated to aquaculture development;
- improving training programmes in hatchery processes, genetic management and breeding skills;
- promoting greater investment in a range of genetic research; and
- promoting stronger national, regional and international controls on the exchange of genetic material, and
- promoting stronger enforcement of existing legislation.

In the ten years since then, it is clear that there has been increased activity in all these areas, but that continued effort is needed on all.

The analysis carried out in the present synthesis has confirmed the main patterns of technology use described ten years ago. However, consideration of the patterns of use of these technologies and the speed with which they are applied to large-scale food production has emphasized the central role of selectively bred stocks and the range of constraints to achieving stable programmes that ensure their maintenance for aquatic species. It has demonstrated that information on genetic resources is limited and often difficult to access, particularly in relation to the use of material in production systems.

There has been a considerable increase in knowledge of wild resources and of impacts of introduced species, and there are shortcomings in the data available concerning the wild resource, the nature and extent of genetic improvement and its impact in particular circumstances. Interpretations are not necessarily straightforward and improved skills for this are required.

Recommendations for expert panel theme 3.1 were to:

1. Improve information on the state of aquatic genetic resources including wild populations, cultured strains; the state of application and benefits of genetic technologies; and the status of, and impacts on, wild populations, including the effectiveness of technologies designed to mitigate such effects. This improved information should be shared through appropriate mechanisms such as regional networks, reporting mechanisms to FAO, and FAO's work towards a State of the World on Aquatic Genetic Resources with the FAO Commission on Genetic Resources for Food and Agriculture (CGRFA).
2. Better focus investment in genetic R&D on establishing sound genetic resource management programmes with clear objectives, and which provide the necessary foundation for application of a variety of other technologies and encourage their application to a) production and b) wild aquatic genetic resource protection.
4. Encourage exchange among the diverse groups needed for better understanding of aquaculture and conservation activities and improved

technology transfer by, e.g. continued dissemination of sound resource material and advice already available.

5. Strengthen the foundation for science-based risk analysis and control (through increased understanding, knowledge, technology development and regulatory capability) of interactions between wild and cultured stocks. This can be achieved by increasing the breadth and depth of case studies and encouraging the application of the precautionary approach.
6. Access to and exchange of aquatic genetic resources has played a major role in the rapid growth of aquaculture. Unlike terrestrial plant and animal genetic resources that were domesticated thousands of years ago and maintained by traditional knowledge, aquatic organisms have only been domesticated recently. A significant portion of that process has been accomplished using high levels of technological and financial input by private and public/private partnerships in areas far away from the native range of the species concerned. Access/exchange must be continued with adequate risk analysis, and benefit sharing must be considered. In formulating policies and laws, the unique character of AqGR must be incorporated.

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