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Biodiversity in aquatic systems in relation to aquaculture

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Abstract

This paper first considers the perception and dimensions of biodiversity. We suggest that biodiversity can be viewed as a biospatial, hierarchically distributed structure of variability among living organisms with five levels of complexity (and including agricultural systems). Loss of biodiversity, value of biodiversity and knowledge of aquatic biodiversity are reviewed briefly. Methods for measuring biodiversity, especially at the genetic level, are discussed and considerable emphasis is laid on effective population size as a controlling factor in biodiversity.

Finally, a range of impacts of aquaculture upon biodiversity are considered, including competitive and introgressive effects from farmed stocks. The development and use of reversibly sterile strains is seen as highly beneficial to both aquaculture and the maintenance of biodiversity.

Introduction

The consequences of aquaculture on biodiversity in aquatic systems are still imperfectly analysed. Considerable concern is expressed about the possible effects of direct competition between cultured exotic species and wild endemic species but this may be, in part, founded upon the commonly held view that biodiversity involves mainly or only a species diversity element. We draw attention to the different levels of organization of biodiversity that biodiversity as a whole must have and offer a definition which we consider to be capable of being used.

The main thrust of this paper focuses upon the genetic level of biodiversity as it is that which underpins all the others.

Definition and dimensions of biodiversity

It is surprising that, given the significance attached to biodiversity, there was until very recently little agreement as to how it should be defined and as to what elements, taken together, constituted it. Terrestrial biologists and systems have dominated the discussion, and one of the few to consider aquatic environments (Norse 1993) has said 'Although biologists have been interested in diversity for decades, the term 'Biological Diversity' (which is sometimes shortened to 'Biodiversity') appeared in conservation publications only about 1980, and its originators either did not define it (Lovejoy 1980) or defined it inadequately (Norse & McManus 1980)'. However, it should be noted that Norse himself also failed to give an adequate definition. A definition which we find useful is one which is hybrid in origin and views biodiversity as a biospatial, hierarchically distributed structure of variability among living organisms with five levels of complexity and which, unusually, includes agricultural systems (Table 1) (see also Groombridge 1992).

This definition is comprehensive, ordered and capable of being translated (albeit with some difficulties) into quasi-numerical values. It also brings out the fact that, at some levels, consideration of biological elements must go hand in hand with

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Table 1 Components of biological diversity

	Component	Order of complexity	Overall effect of agricultural systems
1.	Whole systems (ecosystems or landscapes)	Greater	–
2.	Assemblages (associations or communities of species) with their habitats		–
3.	Species		–
4.	Populations within species		+/–
5.	Genes within populations	Lesser	+/–

consideration of the non-biological factors that contribute to diversity.

The natural focus for many workers is that of level three – the species as relative species richness forms the most obvious index of biological diversity. However, while for some terrestrial habitats accurate species counts could be made, for aquatic environments considerable uncertainty exists with respect to numbers of species. For example, the number of species in the deep oceans has been variously estimated at 0.5 m to 10 m and while about 50 000 species have been described from coral reefs this figure is said to represent only about 10% of reef species diversity (Culotta 1994).

Loss of biodiversity

It is clear that, if the definition of biodiversity illustrated as above is accepted, reductions in total biodiversity in a given area may come about through change in any one of a number of the components. There is, however, a natural tendency to focus upon species loss as the most potent index of reduced biodiversity. It should be remembered, nevertheless, that the normal fate of a given species, in the long run, is to become extinct. The species now existing on earth constitute a very small fraction (possibly as low as 1×10^{-3}) of all the species that have ever existed. Concern should therefore be focused upon rate of extinction rather than extinction *per se* (Lawton & May 1995). Current rates of extinction are estimated to be 10^2–10^3 times higher than in pre-human times (Pimm, Russell, Gittleman & Brooks 1995)

While risks to terrestrial biodiversity tend to be highlighted, the risks to aquatic diversity are less well publicized. They may nevertheless be considerable. Moyle & Leidy (1992) concluded that 20% of freshwater fish species (globally) are already extinct or in serious decline. In the last 100 years North American freshwater environments have lost 21 of 297 mussel and clam species (with 120 more currently under threat), and 40 of ⊤ 950 fish species (Myers 1993). Of the 115 native Californian fish taxa, 63% are extinct or in danger of extinction (Moyle 1995). In South East Asia, Zakaria-Ismail (1994) estimates that 41% of native fish species in the Gombak river basin were lost in the last 25 years.

It is clear that fresh water environments are particularly sensitive to anthropogenically induced loss of biodiversity, both because of high levels of endemism and because of the massive global demand for water and water services (such as hydroelectric power, cooling water, irrigation and waste disposal).

Value of biodiversity

There is no generally accepted set of the values attached to biodiversity, but we identify five:

1 aesthetic;
2 ethical;
3 economic;
4 evolutionary survival of individual species;
5 maintenance and stability of systems.

Of these, numbers (1) and (2) derive from value judgements, (3) is frankly utilitarian, and (4) and (5) are concerned with perceptions of the desirability of maintenance of diversity (at species and system levels, respectively) for the biosphere as a whole. We do not intend to discuss these in detail although it should be evident that each factor is complex and that there are interactions between them. More detailed treatments of values are to be found in McNeely (1988) and Western & Pearl (1989).

We do, however, draw attention to the obvious points that 'successful' aquaculture, as for example

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in the Norwegian salmon industry, is extremely dependent on the availability of genetic capital in the form of exploitation of new strains and species and that aquaculture itself may have dramatic effects on local biodiversity.

Knowledge of aquatic biodiversity

Compared with terrestrial ecosystems, aquatic ecosystems are poorly understood, although they occupy close to three-quarters of the surface of the earth and contain the greater proportion of biological diversity, particularly in relation to the number of species. One consequence of this is that the species of marine macrofauna so far described may represent only a small proportion of extant species. Add to this that only 6% of taxonomists are estimated to be based in developing countries – the areas of highest diversity – and it is evident that values of species richness may often be significantly underestimated (Gaston & May 1992). The oceans have the highest diversity of animals and plants with 28 phyla, freshwater ecosystems contain 14 phyla whilst terrestrial systems contain only 11 phyla. In addition, the bulk of this biological diversity is concentrated in and around tropical and subtropical developing countries where it faces considerable threats through habitat destruction, degradation and fragmentation, resource overexploitation, introductions, pollution, and climatic change, with pressure towards economic development acting as the principal underlying force.

Extent and measurement of biodiversity

Measuring biodiversity

Measures of diversity have recently been discussed by inter alia May (1994) and Templeton (1994), although the centre of the discussion tends to focus upon terrestrial systems. Regardless of the system there are two general factors that should be considered: the first is the need for reliable methods of measurement; the second is the need for integration and standardization of information with reasonably accessible databases. Here computerized databases have an important role to play in coordinating and documenting data-gathering processes, making information accessible to scientists and administrators of all disciplines. An example of such a database for fish is the ICLARM FishBase project (Pauly & Froese 1991). Agustin, Froese, Eknath & Pullin (1993) described a useful function of this database for the documentation of genetic resources for aquaculture although this application is hampered to some extent by the absence of standardized nomenclature for description of domesticated strains. Similarly, Ward, Skibinski & Woodwark (1992) demonstrated how a comprehensive database on protein diversity can be used to relate levels of genetic variation of species from different ecosystems to their taxonomic differentiation. Reliable estimates of biodiversity at all of the various levels of complexity listed in Table 1 are extremely difficult to achieve. To do this effectively requires an approach in which information on habitat and species diversity gathered from community ecology is integrated with information on systematics and population genetics, with the introduction of appropriate weightings and scales. To the best of our knowledge this has not yet been attempted except on a very small scale.

We are particularly concerned in this paper with the most fundamental (and yet for many the least obvious) of the components of diversity: that of genetic variation. This variation is examined through the methods of population genetics, in which levels of genetic variation can be quantified and compared both within and between taxa. The methodology is currently undergoing rapid evolution, with the development of numerous molecular and immunogenetic techniques for characterizing genetic variation at the DNA level within individual organisms, populations, species and genera. Traditional techniques, which directly and indirectly investigated gene products such as blood groups and enzymes, and the study of morphometric and meristic characteristics are being overtaken by newer molecular techniques. It should, however, be noted that Skibinski (1994) determined that the advent of the new DNA techniques has so far had little impact on advances in population genetics and systematics in aquatic invertebrates, compared with those arising from the technique of allozyme electrophoresis (see, for example, Ward, Woodwark & Skibinski 1992). The recent advent of newer DNA techniques utilizing the polymerase chain reaction (PCR), such as random amplification of polymorphic DNA (RAPD) and microsatellites may provide greater and more useful levels of discrimination.

At the level of individual genes, the extent of genetic variation can be expressed as the percentage

Table 2 Estimates of genetic variation in a range of life forms (after Nevo, Beiles & Ben-Shlomo 1984) (*n*, no of species)

	n	Heterozygosity (H)	Polymorphism (P)
Mollusca	46	0.148	0.468
Crustacea	122	0.082	0.313
Pisces	183	0.051	0.209
Mammalia	184	0.041	0.191

Table 3 A comparison of genetic variation measured as H and as numbers of different genotypes

Population	Locus	H	No. of Alleles
1	1	0.5	2
	2	0.4	2
	3	0.3	2
	Average	0.4	2
	No. of different genotypes	27	
2	1	0.4	3
	2	0.3	3
	3	0.2	2
	Average	0.3	2.66
	No. of different genotypes	108	

of loci (P) found to be polymorphic (i.e. for which two or more alleles are present in the population studied) and the percentage of loci that are heterozygous in an average individual (H). Typical values for these parameters in a wide range of life-forms are given in Table 2.

Useful as H may be as a general index of diversity at the genetic level, it is not perfect. In particular it does not adequately describe the range of genetic variation. Table 3 gives a comparison of two populations as an example. For the loci considered (assumed to be typical of the genome as a whole), population 1 has the higher value of H. However, genetic variation, expressed as the number of different genotypes, is greater (108) in population 2 than that seen (27) in population 1. This comparison brings out the need to distinguish between quantitative and qualitative differences in diversity and this distinction is important when the maintenance, in populations, of genes present at very low frequencies is being considered.

It should also be noted that there is no necessary correlation between measures of genetic diversity at the level of DNA sequences and the phenotypic consequences implied. Thus, genetic variation at a locus with a regulatory effect is likely to be of much greater consequence for, say, adaptive potential than variation in many other non-regulatory sequences.

Table 4 Average values of H for aquatic species in different life zones (pooled data for fish, molluscs and crustaceans, after Nevo, Beiles & Ben-Shlomo 1984)

Distribution	H	species
Polar	0.049	11
Temperate	0.060	157
Tropical	0.071	56
Tropical & temperate	0.156	30
Cosmopolitan	0.132	6

Correlations of biodiversity elements

Reference to Table 2 shows that, not surprisingly, there is a positive correlation between P and H. It is also generally true that groups with smaller body size tend to have lower values of P and H than those with larger body size. The reasons for this may be a function of perceived environmental heterogeneity or grain (Levins 1968) and/or population size. It is also well known that species diversity within groups tends to increase from high latitudes to low latitudes. A good example of this is seen in a study by Rex, Stuart, Hessler, Allen, Sanders & Wilson (1993) of bivalves, gastropods and isopods in both hemispheres. Five out of the six regressions of species diversity on latitude were found to be negative and statistically significant, and in the case of the Northern Hemisphere all three regressions were statistically very highly significant.

There is also a striking correlation between the level of genetic variation as measured by H and the life zone. This is exemplified by the data in Table 4, based on more than 250 species of fish, crustaceans and molluscs. It is clear that the average heterozygosity increases both with decreasing latitude and with the extent of geographical distribution.

There is a further correlation which suggests that

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Table 5 Distribution of genome size (10^{12} base pairs) in 100 families of fish (derived from Hinegardner & Rosen 1972)

Genome size ($\times 10^{12}$ bp)	More generalized families	More specialized families
<9.1	16	33
9.2–13.6	13	16
>13.7	11	1
Total	50	50

there may be a functional relationship between the amount of genetic information in, and the extent of variation in the environments inhabited by, a species. This depends on data (Hinegardner & Rosen 1972) which show that more specialized families of fish have, on average, considerably smaller genomes than those families considered to be more generalized (Table 5). Given the considerable extent to which fish lineages have undergone gene duplication and polyploidization (White 1978), these observations suggest that larger genomes are, on average, effectively more heterozygous than smaller genomes.

Importance of population size

The maintenance of genetic diversity in any population is directly dependent upon the effective population size which is, broadly, in a gonochoristic species the number (N_e) of breeding individuals. Reductions (whether acute or chronic) in N_e to low levels have marked effects upon levels of genetic variation.

As Table 6 shows, although population 2 has a slightly higher arithmetic mean of population size than population 1, because average N_e derives from a geometric mean the N_e of population 2 is considerably less than that of population 1 following a relatively severe bottleneck event in generation three. Hence the value of H, the measure of genetic diversity, will be correspondingly reduced as compared with that of population 1. Table 7 illustrates the effect of chronically small N_e. In the absence of selection and new genetic inputs, heterozygosity diminishes by a fraction roughly equivalent to $1/_{2N}$ in each generation.

This discussion underlines the need to maintain N_e at a reasonable level in both natural and cultured populations if genetic variation is to be maintained.

Table 6 The effect of bottlenecks (in this example, in generation 3) on effective population size

Generation	N_e population 1	N_e population 2
1	1000	1000
2	1500	2000
3	500	50
4	1000	1000
5	1200	1200
$\overline{N}$	1040	1050
$\overline{N}_e$	909	214

$$\overline{N}_e = \frac{\textit{No. of estimates, } T}{\sum \frac{1}{N_1} + \frac{1}{N_2} + \ldots\ldots + \frac{1}{N_T}}$$

Table 7 Per cent loss of heterozygosity over generations as a function of effective population size

	N_e			
Generations	10	50	100	1000
10	38.6	8.5	4.9	0.5
50	87.3	39.2	22.0	2.5
100	99.2	63.0	39.2	4.9
500	⊤100	99.3	91.7	22.1

If numbers have to be made up, individuals unrelated to those already in the population should be used. Failure to recognize this is responsible for widespread poor genetic management of broodstocks in aquaculture. Frequently, broodstock are derived from a small founding number and the numbers of broodstock fish kept are frequently small. It is, then, not surprising that many of the land races of common carp, *Cyprinus carpio* L., developed over many decades in central Asia and Eastern Europe, have very low levels of genetic variation. Founder stocks for domesticated populations are often very small, and it is not unknown for entire aquaculture industries to be based on the introduction of a single family. In the Philippines, the commonly cultured 'Israel' strain of Nile tilapia (*Oreochromis niloticus* Trewavas), which is the major contributor to an annual production of over 90 000 tonnes, is derived from a single

Table 8 Examples of superiority of multiple heterozygotes

Species	Character	Reference
Artemia franciscana	Fertility (♀♀)	Gajardo & Beardmore (1989)
Artemia franciscana	Mating success (♂♂)	Zapata, Gajardo & Beardmore (1990)
Mytilus edulis	Growth	Gentili & Beaumont (1988)
Placopecten magellanicus	Growth	Zouros & Pogson (1994)
Poecilia reticulata	Survival	Beardmore & Shami (1979)
Oncorhynchus mykiss	Size	Danzmann, Ferguson & Allendorf (1988)

introduction of 100–200 fry, possibly from a single family (Pullin 1988). Other introductions of tilapia in Asia have been similarly small (Pullin 1988; Pullin & Capili 1988). Poor broodstock management commonly leads to further loss of genetic variation, especially in highly fecund species such as the carps where few broodstock are needed to provide large numbers of fry. Eknath & Doyle (1990) estimated that the N_e of hatchery populations of Indian major carp in Karnataka state, southern India ranged from as low as 3 up to a maximum of 30. Fifty is often considered to be a minimum acceptable N_e, although as Table 7 shows, the loss of H over time is far from negligible at this level of N_e. Some recent considerations suggest that calculations of minimum numbers required to protect genetic diversity should be revised sharply upwards (Lande 1995).

Why is heterozygosity important?

Heterozygosity is important to the well-being of natural and artificial populations for two reasons. Firstly, it allows, through the normal processes of recombination and segregation, the production of a range of genotypes that can exploit the available resources in subtly different ways and which are available as a spectrum of different types which can be drawn upon for adaptive response to changed conditions. Secondly, there is a large body of evidence that indicates that usually (although not invariably), more heterozygous individuals are superior to less heterozygous individuals in characteristics like growth, fertility and disease resistance. Some examples of these are given in Table 8.

The effect of inbreeding, usually as a result of low N_e, is to produce greater average homozygosity, which is generally deleterious, and this is true for both natural and artificial populations (the evidence is reviewed by Frankham 1995).

It is, thus, of paramount importance that genetic diversity should be maintained in cultured and wild populations.

The impact of aquaculture on biodiversity

Possible or actual impacts of the development of aquaculture on biodiversity may result from a variety of causes. It has been argued that these impacts are occasionally positive, sometimes neutral and usually negative. Negative impacts may be direct, e.g. by genetic introgression, or indirect (and probably more importantly) by, e.g. loss of habitat (Beveridge, Ross & Kelly 1994). Clearly therefore, on the whole, positive measures have to be taken to ensure that biodiversity is protected, so far as possible, from such impacts, which include:

1 habitat destruction to create ponds;
2 pollution of local water, by intensive production;
3 effects of antibiotics and other chemical treatmeats on local microfauna and macrofauna;
4 intensive collection of wild seed;
5 competition with endemic fauna by escaped exotics;
6 introduction of pathogens and parasites;
7 genetic introgression with local fauna by introduction of:
- 7.1 populations,
- 7.2 species,
- 7.3 transgenics.

Habitat destruction

Deforestation, agricultural development and industrial and urban development are responsible for

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the majority of aquatic habitat destruction in South East Asia, with aquaculture development in most instances possibly playing a minor role. The exception here is the destruction of mangroves for the establishment of brackish water aquaculture (principally for shrimp culture, although milkfish culture has also contributed significantly in the Philippines). It is considered by many workers that aquaculture development has been largely responsible for the loss of the majority of mangrove habitats, with consequent reduction in species diversity and genetic variation in these wetland ecosystems. It is estimated that 70% of former mangrove forest has been eliminated in the Philippines since the 1920s. Of this, half has been used for shrimp aquaculture (Primavera 1991). Similar dramatic losses are recorded for other areas of Asia.

Pollution resulting from aquaculture

No reliable systematic data on this are known to us. It is, however, unlikely that the considerable burden of organic matter resulting from intensive production, particularly of shrimp (*Penaeus*), can have other than generally negative effects on local biodiversity.

Some pertinent cases can, however, be cited. Laws & Redalje (1982) describe an example of sewage pollution on a reef in Hawaii which was followed for 30 years. The sewage stimulated algal growth; the growth of sponges, other filter feeders and green algae was favoured and the corals diminished rapidly. When the outfall was relocated, recovery of the corals and the reef became evident. This is, incidentally, an example of the considerable resilience inherent in some systems. In general, environmental stress may be expected to reduce, through directional selection, genetic diversity as shown by Nevo, Lavie & Ben-Schlomo (1983), who produced good evidence for shifts in the gene pool of several species exposed to various forms of pollution.

At a higher level of complexity, Havens (1994) reported that copper stress gave rise to decreased plankton species richness and decreased community diversity.

It is also possible that pollution may give rise to increased biodiversity in species pathogenic to humans. Jiang & Paul (1994) suggest that eutrophication (through organic pollution) and subsequent plankton blooms may provide abundant hosts for viruses. It is also noteworthy that the local incidence of cholera in Bangladesh has long been associated with the seasonality of coastal algal blooms (Epstein 1993). The cholera bacterium, *Vibrio cholerae*, has been isolated from a wide range of marine species including cyanobacteria, diatoms, phaeophytes, copepods as well as plants, and phyto- and zooplankton of fresh water (Jiang & Paul 1994).

Some contaminants of water (e.g. some hydrocarbons and insecticides) are mutagenic. As a consequence, in aquatic populations exposed to such agents, increased frequencies of mutations may be expected. This will lead to an increase in genetic diversity although, as mutations are on average deleterious, not a welcome increase (Beardmore 1980).

Effects of antibiotics and chemicals

Despite the fact that many of the diseases associated with intensive shrimp culture are viral in origin, antibiotics are used in large doses by many fish farmers. By virtue of the strong selection pressure this exerts on local bacterial populations, novel recombinant and mutant genotypes will increase in frequency and hence enhance bacterial biodiversity. However, this will not be seen as desirable by many fish farmers and by local human populations which may, as a consequence, be at increased risk of infection by antibiotic-resistant strains of bacteria. That the problems here are not trivial is shown by the finding of Hatha & Lakshmanaperumalsamy (1995) that 90% of *Salmonella* strains isolated from fish and crustaceans showed multiple antibiotic resistance. The increasing use of chemical treatments in aquaculture is also likely to lead to losses of biodiversity through destabilization of ecosystems subjected to effluents.

Intensive collection of seed

The pressure on local natural populations of shrimp species through collection of fish larvae (or berried females) may be very severe in some areas with significant shrimp-based aquaculture. Likewise, the collection of young milkfish, *Chanos chanos* (Forsskål), found in some areas of the Philippines, probably removes fractions of local populations at levels that are unsustainable. The consequences for biodiversity then depend upon the genetic structure of the species concerned. Very little knowledge of milkfish gene pools is available, but the work of Sodsuk, McAndrew & Penman (1994) shows that there is considerable

genetic differentiation between geographical populations of *Penaeus* shrimp and that severe local collection pressure will therefore reduce overall genetic diversity.

Competition from exotic species

Wherever aquaculture is practised, escapes will occur and a proper assessment should be made before new species are introduced. The Mozambique tilapia, *Oreochromis mossambicus* (Peters), introduced many years ago to a number of SE Asian countries, turned out to be not only a very poor species for use in aquaculture but an adept colonizer, to the extent that it has become, in the words of an Indonesian colleague, 'an animal weed' in many waters in the region. In this case, however, displacement of resident species does not appear to have taken place. This is not always so. Possibly the most notorious example of an alien introduction is that of the Nile perch, *Lates niloticus* (L.), into Lake Victoria in the 1950s. This was for a fishery rather than aquaculture but the lesson to be learned is exactly the same. This introduction may have contributed to the extinction of up to 260 endemic fish species (Leveque 1995). This truly dramatic example underlines the principle that, as alien introductions are of uncertain impact (because their ecological interactions in new environments are unpredictable), careful assessment prior to introduction is essential if the interests of biodiversity are to be safeguarded. It is a good principle to try to use endemic species for aquaculture if possible, even though this will often require some investment of research to determine optimal conditions for culture.

Introduction of pathogens and parasites

An effect of much intensive aquaculture is to increase the population size and density of pathogens and parasites. Sea lice (*Lepeophtheirus salmonis* and *Caligus elongatus*) on cultured Atlantic salmon, *Salmo salar* L., are thought to provide foci for infection of wild stocks. However, it is also likely that the passage of such parasites is a two-way process. The extent and consequences of such cross infection remain to be quantified (McVicar 1997).

Introgression

Populations

At first sight there seems little to be risked by using fish of the same species, albeit from different populations or stocks, in local aquaculture. However, this view is simplistic.

Hybridization of different strains and occasionally species is commonplace in tilapias, carps and catfishes – the three commonest groups of freshwater cultured fish species in the developing world – and has two consequences. Firstly, the genetic integrity of locally adapted source strains may be compromised. The American salmon industry – probably the fishery to have received most input from genetic studies – has many examples of reduced performance of introduced compared with locally adapted strains (Fleming & Gross 1993; review: Allendorf, Ryman & Utter 1987). If source populations are not protected, particular adaptations can be permanently lost, and introductions of non-adapted genotypes, for example in restocking programmes, can have detrimental effects on effective population size and adaptive flexibility (Kruegar, Gharret, Debring & Allendorf 1981; Thorpe, Koonce, Borgeson, Henderson, Lamsa, Maitland, Ross, Simon & Walters 1981). Secondly, the ecological characteristics of interstrain hybrids are usually unknown, and may have dramatic effects on local biodiversity. Indian carp hybrids, for example, are frequently reported to exhibit undesirable characteristics (Padhi & Mandal 1994).

The scale of aquacultural activity should also be borne in mind. Hard data are not readily available but it is reported (Gausen & Moen 1991) that the production of salmon in cages in Norway in 1988 was two orders of magnitude greater than the harvest from coastal and estuarine fisheries. It is, then, not surprising that a major fraction of the harvest for those fisheries is thought to consist of escapes from aquaculture. There seems to be no general agreement as to what effect such large-scale inputs of genetic material have on resident populations, although in general one might expect overall genetic diversity in wild populations to be reduced and for factors such as sea age of maturity and male parr maturity to be affected (Ferguson, McGinnity, Stone, Taggart, Cooke, Cotter, Hynes & Cross 1997). However, Hindar *et al.* (1991) conclude that where it is possible to make an assessment, performance characteristics of cultured strains in natural conditions appear to be generally inferior to those of wild populations. This would in general be expected where a process of domestication had occurred (as with carp and salmon).

While farmed salmon ♀♀ produce significant numbers offspring they do this at a lower rate than wild ♀♀ because of lower reproductive output arising

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from less successful eggs and shorter breeding periods (Einum & Fleming 1997).

There are also important behavioural differences between farmed and wild salmon which influence Darwinian fitness. Farmed males are more aggressive and risk-prone than wild ♂♂ and become wounded more often. Their courtship behaviour is less marked than that of wild ♂♂ and they have greater difficulty in acquiring mates and therefore in reproducing (Jonssen 1997).

Although these indications of lower fitness of farmed stock are helpful, it seems prudent to recommend wherever possible the development and use of reversibly sterile strains for use in aquaculture. This would also have benefits for aquaculture itself.

Species

One example of a potentially major conflict between the interests of aquaculture and those of biodiversity is posed by catfish culture in Thailand. The walking catfish, *Clarias macrocephalus* Gunther, is widely cultured in Thailand and has desirable flesh characteristics but is slow growing. The African walking catfish, *C. gariepinus* (Burchell), has a faster growth rate but less desirable flesh characteristics. The hybrid has acceptable flesh, a growth rate intermediate between the two parent species and is now widely cultured. It is not clear what the level of risk posed in local populations of *C. macrocephalus* may be, but F_1 hybrids may cross readily with the resident fish. Laboratory experiments suggest that the ability of future specific F_1 hybrids to produce reliable backcross progeny is low (McAndrew, personal communication), but nevertheless there is the possibility that the viability of populations of *C. macrocephalus* may be threatened. Similar problems may arise in Bangladesh through the use of hybrid *C. batrachus* (L.) × *C. gariepinus* in aquaculture (Rahman, Bhadra, Begum, Islam & Hussain 1995).

In each of these cases, a possible outcome is the development of local populations that consist of individuals of hybrid origin, with long-term threats to survival of one or more species. The hazard may be greater in cases such as these where geographically distant populations of two species are intercrossed than in cases like the brown trout, *Salmo trutta* L., and Atlantic salmon (*S. salar*). With these species, natural hybrids are found at low frequency, but there is no evidence of introgression probably because of considerable disturbances to meiosis and generation of triploids in backcross progeny (Johnson & Wright 1986). However, the same view of the desirability of use of sterile strains applies here, especially as species such as Nile tilapia are being spread geographically at a rapid rate.

Transgenics

Introduction of transgenics to aquaculture has not yet started, but already there is considerable interest in their use and it seems very likely that over the next two decades significant uptake of transgenic strains in aquaculture will take place. It may, in passing, be noted that successful transfer of fish genes to bacterial systems may represent a useful alternative pathway for protein production. A considerable amount of transgenic work has been done on fish, particularly with growth hormone genes (review: Maclean & Rahman 1995).

While such transgenics appear to offer useful advances in production efficiency, the experience with terrestrial species suggests that results are seldom predictable, and that undesirable side-effects are common.

No clear evidence is available as to the size and nature of the risk, if any, that attaches to interbreeding of transgenics with resident populations. The most that can be said is that it is likely that the transgenic fish in most instances are of lower Darwinian fitness than wild fish. However, it is certainly correct to take a cautious view as to long-term effects.

Conclusion

There are difficulties associated with measuring and defining biodiversity. Nevertheless, human activities, including aquaculture, have, on the whole, to be seen as producing negative effects on levels of biodiversity. Our understanding of many of the effects is still very poorly developed. Of considerable concern are effects at the genetic level, which are less obvious but no less important than those at high levels of complexity.

Factors such as the maintenance of reasonable effective population sizes in natural populations and the relative scale of population sizes of farmed and wild fish are of great importance and merit careful study. The development and use of (reversibly) sterile strains could be of considerable benefit and should be an objective.

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