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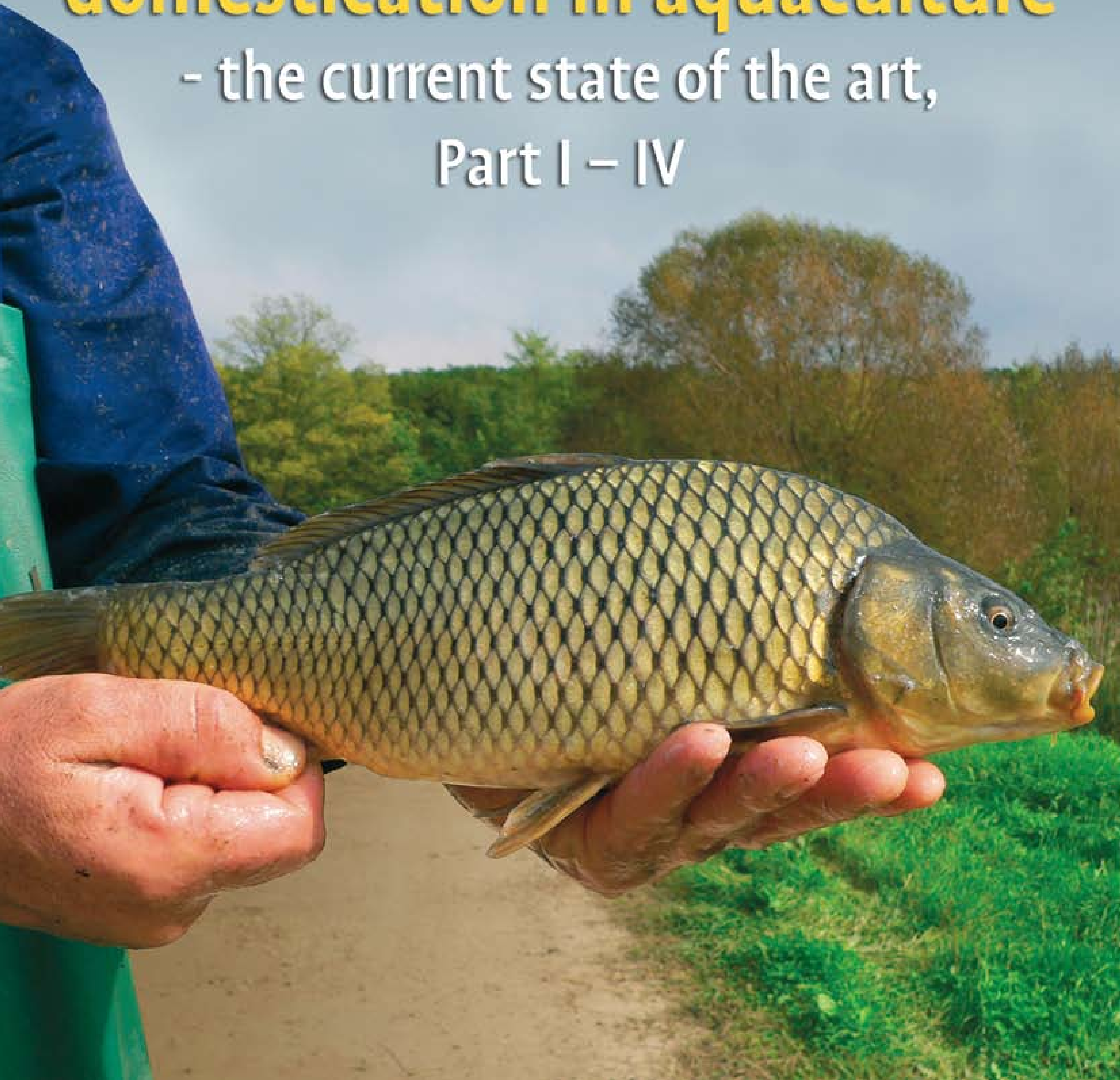
Controlled reproduction and domestication in aquaculture

- the current state of the art,
Part I – IV



Controlled reproduction and domestication in aquaculture

THE CURRENT STATE OF THE ART

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SYNOPTIC OVERVIEW

The sustainability of aquaculture will depend on **continuous controlled reproduction**, i.e. reproduction continuously achieved from generations bred and maintained in captivity, not on the permanent supply of seed or breeders from the wild. Supply from the wild will remain doubtful as long as the sustainability of the capture fisheries is not assured.

Continuous controlled reproduction is an indispensable prerequisite for **domestication**. Sustainability conditions of aquaculture other than continuous controlled reproduction are of a secondary nature. As long as the biological conditions of sustainability are not fulfilled, the future of aquaculture will continue to be uncertain.

Once continuous controlled reproduction is achieved, true domestication of a species begins. This process can be **uncontrolled or targeted**. Whereas in the remote past domestication was largely uncontrolled, nowadays growing knowledge of the rules and laws of inheritance permits precise targeting. The detailed structural knowledge of chromosomes and genes is even bringing **biotechnological genetic improvement** into the realm of practicability.

The **number of domesticated aquatic species** has been greatly overestimated compared with terrestrial species, due to the use of incompatible criteria for comparison. Currently, the number of domesticated aquatic animals probably does not exceed that of domesticated terrestrial animals.

Domestication allows production increases far beyond the maximum sustainable yields of the capture fisheries. However, such increases can seriously threaten con-specific wild populations through escapes from aquaculture installations, in particular from floating cages. Genetic intermingling of farmed and wild fish, parasite- and disease-transfer from farmed to wild fish pose great problems that must be overcome, or at least substantially reduced, before extensive production increases can unfold their benefits. Improved confinement and, possibly, the creation of genetic barriers through targeted domestication or genetic engineering would have to become effective before the wild populations are seriously affected.

Aquaculture is faced with a critical alternative regarding its future development:

(A) Proceed with unbridled inter-specific diversification, thereby running the risk of seriously compromising the integrity and sustainable utilisation of many wild stocks by exploiting them indefinitely for capture-based aquaculture.

(B) Fully domesticate a few representative species and exploit their intra-specific diversity potential, on the one hand at the risk of compromising their con-specific wild populations but on the other hand enhancing the chances of survival and sustainability for the capture fisheries of numerous others.

Full domestication can provide access to an intra-specific diversity potential similar to that of domesticated land animals. With today's practical experience and scientific knowledge it should also be possible to accelerate the domestication process in promising species hitherto difficult to breed continuously under controlled conditions. High cost would be justified by the gains offered by domestication. **Well targeted selective breeding leading to pedigree establishment, could even adapt existing species to new environmental conditions produced by climate change.** Proven stability of new races created by selective breeding or genetic engineering is, however, an indispensable prerequisite of safety.

Substantial production increases through full domestication satisfying the increasing world demand for fish, would relieve wild populations from the current fishing pressure. **Sufficient aquaculture production derived from domesticated species could allow undisturbed replenishment, conservation and saving measures through culture-based capture fisheries shielded, as much as possible, from pre-domestication and domestication effects.** Subjecting rare and particularly valuable "niche" species to aquaculture experiments would become superfluous. The niche role could be taken over by wild species with appropriate characteristics, sustainably exploited by capture fisheries.

The further the domestication of high-priced species advances and their production increases, the more prices will decline and the species will become affordable to growing segments of the middle classes. Losing their exclusive character, these species could then be replaced by rare (and delicious) alternatives caught from the wild and playing niche roles themselves. The new niche species could be brought into the focus of the super-rich by appropriate advertising. Launching adequate species (preferably detritivores and filter-feeders) as food for the poor through domestication would require strong R&D inputs and continuing support from the richer segments of society.

Aquaculture is a business conditioned by prices that determine profit. The involvement of stakeholders is needed when deciding and planning the course of future development. Fishers and fish farmers, practical people and scientists, producers and consumers, public officials and resource protectionists must communicate at their respective information levels, and have a say in planning and decision-making. **Living animals, suitable feed-stuffs, clean water and adequate space are limited resources the use of which has to be balanced among all interested parties.**

Note: since bivalve shellfish have not been the primary focus of this paper, some aspects of the discussion and recommendations might vary from those for finfish and crustaceans: (a) the unintentional selective-breeding process (e.g. increased disease resistance) potentially resulting from repeated long-term maintenance of certain populations in semi-restricted growing areas (Canzonier, pers. com.), would be a bivalve-specific example of pre-domestication in the sense of the present paper (Part I, p. 16-19). (b) Filter-feeding on particulate matter offered by the open environment makes control of tissue quality and contaminant uptake more problematic than when artificial feeds are used.

TABLE OF CONTENTS

Part I (p. 5-14)

Part II (p. 5-23)

Part III (p. 5-19)

Tables

Part I

Part II

Figures (diagrams)

Part III

Part IV

ON THE COVER OF PART ONE - next page
Wild common carp (*Cyprinus carpio*) from the Tisza River, Hungary
INSETS FROM LEFT: Domesticated Szarvas P 34 hybrid scaly common carp, Domesticated Szarvas 215 hybrid mirror common carp and Domesticated Szarvas P 33 scaly common carp.
All photos courtesy of the Research Institute for Fisheries, Aquaculture and Irrigation (HAKI), Szarvas, Hungary.

PART I

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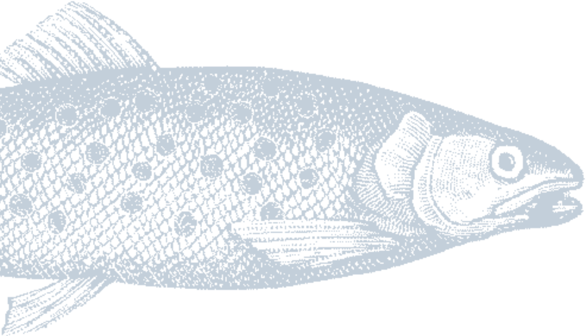

Controlled reproduction and domestication in aquaculture

THE CURRENT STATE OF THE ART PART I

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INTRODUCTION

Objectives and scope

There is considerable uncertainty about the meaning of the term "domestication" in aquaculture. While the process of domestication of the majority of *terrestrial* animals and plants has benefited from thousands of years of trial and error first and deliberate selection of promising traits later, only a very low number of *aquatic* organisms has benefited from such a vast experience. When in the second half of the last century hunger rose to worldwide concern, the unexploited potential of aquatic protein production finally began to attract public attention. Increasing efforts were made to tap this source and "aquaculture" was introduced as a twin term to agriculture.

Terrestrial animal husbandry and crop cultivation can be sustained as long as adequate living conditions can be created and controlled. Continuous control of reproduction is no concern. With many of the aquatic organisms currently subjected to culture conditions, control of reproduction is still problematic and their production dependent on supplies of seed or broodstock from the wild. Such dependence sets limits to the sustainability of culture production. Long-term sustainability can only be guaranteed when continuous controlled reproduction is achieved and, with this, the major prerequisite of domestication fulfilled (see below).

Continuous controlled reproduction – and, based upon this, domestication - thus assumes the character of an overriding indicator of the sustainability of aquaculture development. Knowing the progress of domestication can thus give valuable insight into the status and prospects of aquaculture. It is for this reason that the present attempt is being made to put the pertinent information together and interpret and evaluate the outcome. Table 1 is the central part of this paper and conceived in a way that it can easily be updated and evaluated anew.

Taxonomic and geographic range

While finfishes, crustaceans and bivalves are considered in the present paper, gastropods (with the exception of abalones), amphibians, reptiles, exclusively ornamental fishes, and aquatic plants are not. Worldwide coverage was intended since the culture of a number of species is attempted in different parts of the world. It is probable, however, that some relevant species are absent from Table 1 due to lack of available information.

Antecedents

My awareness of the importance of the prerequisites of domestication in aquaculture goes back to 1984 when, visiting Taiwan, I made a key experience of my aquaculture career: I got an immediate insight into the need for continuously controlled reproduction of a cultured organism in order to secure the long-term success of its farming.

Aquaculture in Taiwan was at that time known for successfully growing eel and penaeid shrimp. The major problem with the shrimp was very low survival of the offspring (juveniles, F1 generation) produced in the National Aquaculture Research Institute, showing that too little was known about the conditions necessary for gonad maturation. It was, therefore, contemplated to release a great number of juveniles obtained through controlled reproduction of wild breeders (the P generation) into an area where fishing would be banned for a while in order to give the released shrimp (F1) time to mature. After the ban, a high price would be paid for each egg-bearing female encountered in the catches, in order to obtain material for further research on controlled reproduction.

Although I do not know whether this idea was realised, the discussion let me understand how important it is to know how to raise offspring not only from wild, but also from cultured parents. Obviously, only this could make sure that the production was at least biologically sustainable. From then on I have used every opportunity, during my extensive travelling for development cooperation purposes, to question the biological sustainability of the production of new species through aquaculture. This endeavour has finally led to the present paper.

Gathering of information

Most of the information contained in this paper was obtained by e-mail correspondence and through personal discussion. It was hoped that this approach could provide the most recent information available, including the possibility to check in immediate discussions common understanding of terms and the reliability and adequate interpretation of facts.

Unfortunately, my e-mail requests for species-related pertinent information did not always get the response that I had hoped for. This may have been due to otherwise already heavy work load. It is also possible that precise knowledge about domestication is not considered an important issue, in particular, as long as the supply of broodstock or seed from the wild is no serious and imminent limitation to an economically viable production of the target species. In such cases, producing economically sufficient commercial-size offspring from wild broodstock may be seen as the most important success to be achieved.

Moreover, there has been disagreement and misunderstanding about the meaning of domestication and its prerequisites not only among farmers but also among scientists. It was not always understood that controlled reproduction must be continuous (or that breeding in captivity must be unlimited) if it is to become independent from any further supplies from wild populations. Only when such independence is achieved, farming of the species involved has prospects of sustainability.

In some cases it has been thought that repeated controlled reproduction of the same broodstock (P) kept in captivity means continuous controlled reproduction of several generations (actually several F1 from the same P) and thus progress towards domestication. Another misunderstanding is the belief that continuous controlled reproduction means taking broodstock or seed repeatedly from the wild (different P) as soon as the preceding offspring (F1) has been harvested and sold and so on. Such disagreements and misunderstandings have made it necessary to define the terms to be used in the present paper in a possibly unequivocal, unmistakable way.

The more theoretical contributions from other colleagues to the present paper (in addition to or instead of the mainly requested species-related practical information) will be referred to in the Discussion chapter (Part II).

TERMINOLOGY

Principles

A useful definition of a technical or scientific term should satisfy the following conditions:

- If the term is derived from a colloquial word or term, it should essentially correspond to the meaning of this word or term and at least not contradict it. (Obviously not relevant when a completely new term is created.)
- The meaning of the term that is to be technically or scientifically defined, should be so clearly described and delimited that no confusion with other, similar or contradictory, words or terms is possible.
- The definition should show that the term is useful to better understand an idea, a concept or an instrument.
- Ideally, the definition should follow the logic of a technical or scientific terminology describing the context into which the newly defined term is to be integrated.
- The defined term should be easily applicable from a linguistic point of view and understandable without too much additional information.

Three terms are of essential importance for the understanding of table 1 around which this article is centred: continuous controlled reproduction; domestication; and biotechnological genetic improvement.

Continuous controlled reproduction

The reproduction of living organisms is controlled when it occurs in captivity (animals) or in cultivation (plants) in order to serve man's purposes. The purposes can be the production of food or other commodities, amenities (ornamental organisms), and seed for populating natural or artificial sites. The control can be limited to the pairing of mature organisms or their released sexual products (eggs and sperm). It can include embryonic development, birth or hatching, and larval rearing until metamorphosis. Once the offspring obtained under controlled conditions have matured and have themselves succesfully been paired and reproduced under controlled conditions, one cycle of controlled reproduction is completed. To achieve independence from wild supplies (larvae, fingerlings, broodstock), the control of reproduction must go on for more than just one cycle. When this is reached, the control of reproduction can be called continuous.

The importance of the continuous control of reproduction can be demonstrated by the case of the eel. Until recently, in spite of great efforts, eels had been induced to reproduce in captivity (*Anguilla anguilla* in Europe as well as *A. japonica* in Japan), whereas larvae rearing until metamorphosis could not be completed. This has now become possible in Japan (*A. japonica*), where even elvers could be produced. A final breakthrough, however, is still pending. On the other hand, during the last two decades the availability of wild glass eels for stocking farm ponds and open waters, has dramatically decreased for reasons so far not fully understood. In Europe (*A. anguilla*) the decrease went down to 5% of its original level (Hilge, pers. comm.).

The original level even included an export for human consumption from France to Spain of at least 1000 but probably >1500 t (Bilio 1980). The biological sustainability of eel culture thus remains uncertain.

Domestication

The original meaning of the term domestication is the gradual adaptation of an organism to living conditions that are determined by some form of human intervention. Any new definition should not deviate too much from the way the term was used in the professional literature of the past. Keeping this in mind, a definition which is easily understandable, simply applicable, and hence generally acceptable, should include any terrestrial or aquatic organism (see, e.g., Darwin 1868).

There is sufficient evidence that some sort of habituation to the environment of captivity or cultivation, and a selection of traits for better survival under such conditions takes place at the time of first reproduction and individual development. Some authors, therefore, speak of a phase of "unintentional" domestication (Dunham et al., 2001). This can be the more effective, the more numerous the offspring of one pair of broodstock is, which, obviously, holds particularly true for many aquatic organisms. However, such unintentional selection is at best a first step preceding real domestication, and should better be seen as a form of natural adaptation to a new environment.

Real domestication in the sense of intentional (or "deliberate", Dunham et al. 2001) adaptation was traditionally brought about through selective breeding. According to Dunham et al., intensive use of genetic selection in aquaculture has only been made since about 1970. This does not only include cross-breeding among different strains within one species (intraspecific crossbreeding), but also between different species (interspecific hybridisation) – be the offspring fertile, partly fertile or infertile. A well-known traditional cross-breed between terrestrial species is the mule, with either the horse as the sire and the donkey as the dam or vice versa. A number of aquatic examples are referred to by Dunham et al. (2001). Note, however, that individuals of those cross-breeds which are fertile only exceptionally or not at all, have to be bred anew each time such a cross-breed is needed. In normal cases, the properties of the offspring of traditional selective breeding and cross-breeding are expected to be at least partially passed on to, and maintained by, subsequent generations, or even increased through further selective breeding.

Domestication requires continuous controlled reproduction (unlimited breeding; i.e. the sequence P->F1->F2->F3, etc. must be kept free of further wild inputs) as a *conditio sine qua non*, since otherwise no further captive generations would be produced to which new genetic properties could be passed on. Where interspecific cross-breeds with totally infertile offspring are desired on a permanent basis, their production remains dependent on continuous controlled reproduction of the parent species. An important limitation to continuous controlled reproduction, and thus to permanent domestication, is extreme inbreeding.

Once continuous controlled reproduction is achieved, the domestication process can continue towards the selection and production of pure breeds with all known ancestors of the same type. When the desired characters have thus been sufficiently stabilised, showing only minimal variation, pedigrees can be established and pedigree registration certificates issued, as in terrestrial animal husbandry.

Biotechnological genetic improvement

A new era began when some 25 years ago it became possible to intervene biotechnologically in the processes of heredity. A prerequisite to this advancement was the long-available knowledge of the rules and laws of heredity, as well as the more recently achieved insight into the biochemical and biophysical character of the genes, their position on the chromosomes, and the possibilities and ways of structural change and exchange, etc.

Typical avenues (so far mostly experimental) of technological genetic improvement are chromosome set manipulation, sex manipulation (uniparental chromosome inheritance, genetic material of one parent inactivated), nuclear and gene transfer ("genetic engineering") (Colombo et al., 1998; Dunham et al., 2001). Genetic engineering requires sufficient knowledge about the position of the genes on the chromosomes. Consequently, genome-and linkage-mapping (for marker-assisted selection of gene sites) have gained basic importance.

When looking at the fundamental difference in approach between the traditional indirect genetic improvement achieved in captivity and the new possiblities of exerting immediate and direct influence on the genetic properties of an organism, it seems adequate that this be reflected by the terminology applied. It appears recommendable, therefore, to confine the term "domestication" to traditional genetic influences in the sense characterised above, and to call further improvement based on different forms of biotechnical intervention "biotechnological genetic improvement".

Including biotechnological methods of genetic improvement in the term domestication would bring us far away from the original meaning of the term, i.e. the traditional ways of adapting an organism to the human farm and household environment by selecting the most promising breeders. Biotechnological intervention is a different methodological quality of exerting human influence on an organism. Moreover, a separation of traditional domestication from biotechnological genetic improvement appears useful also from a practical point of view helping farmers and scientists to understand each other more easily. This is not contradicted but rather supported by the fact that methods of both domestication and biotechnological genetic improvement, will increasingly be combined in order to enhance production or improve the product. It could even turn out that such a distinction helps to keep the public from confusing traditional domestication with those issues that are so controversial at present and distort the image of aquaculture more than is already the case without this confusion.

Another advantage of the distinction is that it does not essentially modify any previous definition of domestication as it does not add a new concept but simply sharpens the terminological instruments. It must be stressed, however, that continuous controlled reproduction, or unlimited breeding, are equally important for both traditional domestication and modern technological improvement. Where the offspring are fertile, these must carry the new traits into new generations, and when the offspring are infertile and have to be created anew, the parent species have to be continuously available through unlimited breeding (once they are no longer available from the wild).

The final success of biotechnological genetic improvement is achieved when the biotechnological intervention leads to hereditary new characters or properties, without the need to be repeated for each generation anew. Otherwise, the same holds true as for totally infertile hybrids (see above).

RESULTS

The present situation is summarised in Table 1. In this table, species are considered as domesticated when they show first results of selective breeding. Where no such evidence is found in the literature or through personal communication, it is assumed that pertinent alterations are achieved after at least three successive cycles of reproduction (generations) under controlled conditions. In order to give some indication of the next candidates for domestication, a number of species are included which have completed only one reproduction cycle under controlled conditions. Controlled conditions include rearing in earth ponds.

Even where spontaneous spawning can be obtained in ponds, hypophysation in hatcheries and spawning by stripping is often applied in order to secure regular spawning success (e.g., in central Europe with the three plant-eating cyprinids grass, silver and bighead carp and also with common carp, see Schaeperclaus & v.Lukowicz 1998). This is also done to obtain offspring outside the natural spawning seasons. When there is sufficient evidence that controlled reproduction and domestication has been achieved under commercial conditions, the situation at the laboratory or experimental level is, as a rule, ignored in the table.

Only partly included in Table 1 (cross for domestication in parentheses, see legend), are species which are reproduced in captivity exclusively for the stocking of open waters, i.e. natural water bodies and those artificial ones (e.g. dams) where fish populations can also develop naturally (e.g., in Europe, Salmo trutta, coregonids and others). This criterion is applied, as long as the broodstock is not kept in captivity for more than one generation. In Europe, several freshwater fishes are bred in captivity mainly for stocking purposes, but some of the produced offspring are used to substitute for the parent broodstock that no longer serve for reproduction purposes. This means that the broodstock is becoming increasingly domesticated, and the populations in the stocked waters are increasingly different from natural populations. After some time, wild individuals of the same species may be in the minority or completely absent. As a consequence, the fish could be less fit to survive under natural conditions and show similarities to fish produced in farm ponds. This is a major concern in the management of natural fish resources, and in Europe regulations are being applied to maintain a clear separation of broodstock and offspring for the enhancement of natural populations, from others serving exclusively for the production of fish for direct human consumption. While the former must be kept free from domestication ("hatchery") effects, the latter are fully exposed to breeding selection and thus domestication pressure.

This chapter will be continued in Part II, where Table 1 will be followed by Tables 2 and 3 with special information from China and Australia, respectively.

Table 1. Continuous controlled reproduction as an essential prerequisite of both domestication and biotechnological genetic improvement

Explanations:

Species names	According to Froese & Pauly FishBase (2006)
World production	According to FAO Fishstat Plus (2006), aquaculture production 2004
Level	Lab. = laboratory (experimental) Com. = commercial
Spawning	The release of eggs and sperm in captivity can be: Ind. = induced (through hormone injection, temperature shock, manipulation of the photoperiod, etc.) Spont. = spontaneous (spawning occurs in captivity under circumstances that are very close to natural conditions) (Spont.)= maturation spontaneous, spawning by stripping
Larvae rearing	From hatching to metamorphosis (fingerling stage)
Gonad maturation	The entire process (endocrinological sequence) of gonad maturation occurs under controlled conditions (offspring reaches maturity in captivity)
Cycles	Number of successive reproduction cycles (generations, P⇒F1⇒Fx) completed under controlled conditions (∞ = innumerable)
Domestication	Properties altered through traditional intentional breeding selection (assumed to be achieved when ≥3 consecutive generations have been reproduced under controlled conditions; see Part II, Results chapter); • pedigrees established; (+) domestication effects restricted to broodstock which is mainly or exclusively used for the production of seedfish for the enhancement of natural populations
Biotechnological genetic improvement	Properties improved through direct genetic intervention (gene manipulation, genetic engineering, etc.; see Terminology chapter)
-/+	Not achieved/achieved
Sources	Personal communications (author only); publications and reports (authors & years)

Species	World production (t)	Level	Reproduction under controlled conditions				Domestication (-/+/•)	Biotechnol. genetic Improvem. (-/+)	Main sources of information
			Spawning (ind./ spont.)	Larvae rearing (-/+)	Gonad matur. (-/+)	Number of cycles			
A. Freshwater finfish in Europe									
Common carp	3,387,918	**Lab.**							Schäpercl./v.Lukow.1998, Beck R., Flajshans, Tölg, Woynarovich E., Horvat
(Cyprinus carpio)		**Com.**	Spont./ind.	+	+	∞	●[1]		
Grass carp	3,876,868	**Lab.**							Schäpercl./v.Lukow.1998, Beck R., Woynarovich E., Horvat, Tölg
(Ctenopharyngodon idella)		**Com.**	Ind.	+	+	∞	●[2]		
Silver carp	3,979,292	**Lab.**							Schäpercl./v.Lukow.1998, Beck R., Woynarovich E., Horvat, Tölg
(Hypophthalmichthys molitrix)		**Com.**	Ind.	+	+	∞	●[2]		
Bighead carp	2,101,688	**Lab.**							Schäpercl./v.Lukow.1998, Beck R, v.Lukowicz,Tölg, Woynarovich E., Horvat
(Aristichthys nobilis)		**Com.**	Ind.	+	+	∞	●[2]		
Northern pike	302	**Lab.**							Schäpercl./v.Lukow.1998, Beck R., Horvat
(Esox lucius)		**Com.**	Spont./ind.[3]	+	+	∞	+	-	
Zander	313	**Lab.**							Beck R., v.Lukowicz, Wedekind, Horvat
(Sander lucioperca)		**Com.**	Spont./ind.	+	+	∞	(+)	-	
Tench	1,296	**Lab.**							Schäpercl./v.Lukow.1998, Beck R., Flajshans
(Tinca tinca)		**Com.**	Ind./spont.	+	+	∞	●[4]	-	
Wels catfish	731	**Lab.**							Beck R., v.Lukowicz, Wedekind, Horvat
(Silurus glanis)		**Com.**	Spont./ind.	+	+	∞	+	-	
(North) African catfish	23,115	**Lab.**							Beck R., Woynarovich A., Horvat, Radics
(Clarias gariepinus)		**Com.**	Ind./spont.	+	+	∞	+	?	
Grayling	-	**Lab.**							Schäpercl./v.Lukow.1998, Beck R., Kiuru & Mölsä
(Thymallus thymallus.)		**Com.**	(Spont.)	+	+	>3	(+)	-	
Common whitefish	445	**Lab.**							Schäpercl./v.Lukow.1998, Kiuru & Mölsä
(Coregonus lavaretus)		**Com.**	(Spont.)	+	+	>5	●[5]	-	
Peled whitefish	3	**Lab.**							Boguerouk 2005, Kiuru & Mölsä
(Coregonus peled)		**Com.**	(Spont.)	+	+	>5	●[2]	-	
Huchen	1	**Lab.**							Schäpercl./v.Lukow.1998, Beck R.
(Hucho hucho)		**Com.**	(Spont.)	+	+	∞	(+)	-	
Atlantic salmon	1,244,637	**Lab.**							Gjedrem 1979, Dunham *et al.* 2001, Beck R.
(Salmo salar)		**Com.**	(Spont.)	+	+	∞	+	?	
Rainbow trout	504,876	**Lab.**						+	Schäpercl./v.Lukow.1998, Beck R., v.Lukowicz, Flajshans
(Oncorhynchus mykiss)		**Com.**	Spont./ind.	+	+	∞	●[6]	+	
Brook trout	977	**Lab.**							Schäpercl./v.Lukow.1998, Beck R., v.Lukowicz
(Salvelinus fontinalis)		**Com.**	(Spont.)	+	+	∞	+	-	
Sea trout	22,183	**Lab.**							Beck R., v.Lukowicz
(Salmo trutta)		**Com.**	(Spont.)	+	+	∞	+		
Charr	1,468	**Lab.**							Pitkänen *et al.* 2001, Horvat, Radics
(Salvelinus alpinus)	(2002)	**Com.**	(Spont.)	+	+	∞	+	+	

[1] Pedigree establishment: Hungary (Váradi), Russian Federation (Boguerouk 2005), Czech Republic (Flajshans)
[2] Pedigree establishment: Russian Federation (Boguerouk 2005)
[3] Induced ovulation in Hungary (Woynarovich A.)
[4] Pedigree establishment: Czech Republic (Flajshans)
[5] Pedigree establishment: Finland (Quinton et al. 2006)
[6] Pedigree establishment: Finland (Kiuru), Czech Republic (Flajshans)

B. Marine finfish in Europe

Species	World production (t)	Level	Reproduction under controlled conditions				Domestication (-/+/•)	Biotechnol. genetic Improvem. (-/+)	Main sources of information
			Spawning (ind./ spont.)	Larvae rearing (-/+)	Gonad matur. (-/+)	Number of cycles			
Turbot	6,138	**Lab.**	Ind./spont	+	+				Bell
(Psetta maxima)		**Com.**	Ind./spont	+	+	∞	+		Jonassen, Gjedrem
Wedge sole	?	**Lab.**	Spont.	+	+	1			Herrera, Hachero, Ferrer, Márquez, Rosano, Navas 2005
(Dicologlossa cuneata)		**Com.**							
Atlantic halibut	187	**Lab.**	Ind./spont						Bell
(Hippoglossus hippoglossus)		**Com.**	Ind./spont	+	+	>3	+ [7]		Jonassen, Gjedrem
Atlantic cod	3,812	**Lab.**	Ind./spont	+	+				Bell
(Gadus morhua)		**Com.**	Ind./spont	+	+	>3	+[7]		Jonassen, Gjedrem
Spotted wolffish	100	**Lab.**	Ind./spont.	+	+				Bell
(Anarhichas minor)	(2005[8])	**Com.**	Ind./spont.	+	+	>3	+[7]		Jonassen, Gjedrem
European seabass	49,103	**Lab.**	Ind./spont.	+	+	>3	+		Divanach 2002, Cittolin
(Dicentrarchus labrax)		**Com.**	Ind./spont.	+	+	>3	+		Barbaro A.& A., Gjedrem
Gilthead seabream	90,995	**Lab.**	Ind./spont.	+	+	>3	+		Divanach 2002, Cittolin
(Sparus aurata)		**Com.**	Ind./spont.	+	+	>5	+		Barbaro A.& A., Gjedrem
Sharpsnout seabream	-	**Lab.**	Ind.	+	+	1	-		Divanach 2002, Barbaro A.& A.
(Diplodus puntazzo)		**Com.**	Spont.	+	+	>3	+		
Common seabream	400 [9]	**Lab.**	Ind./spont.	+	+	>5	+	-	Spedicato 2005
(Pagrus pagrus)		**Com.**	Ind./spont.	+	+	>5	+	-	Mylonas *et al.* 2004, Tort
Red seabream	?	**Lab.**	Spont./ind.	+	+	>3?			Divanach 2002, Barbaro A.& A.
(Pagrus major)		**Com.**	Spont./ind.	+	+	5	+		
Common pandora	181	**Lab.**	Ind./spont.	+	+	4			Divanach 2002, Spedicato *et al.* 2004
(Pagellus erythrinus)		**Com.**	Spont.	+	+	1	-		Mylonas
Common dentex	-	**Lab.**	Ind./spont.	+	+	1	-		Divanach 2002, Pavlidis *et al.* 20'04, Barbaro A.& A.
(Dentex dentex)		**Com.**	Spont.	+	+	1	-		
Brown meagre		**Lab.**	Spont.	+	+	1	-		Mylonas
(Sciaena umbra)		**Com.**	Spont.	+	+	1	-		
Meagre		**Lab.**		+	+		-		Mylonas
(Argyrosomus regius)		**Com.**	Spont./ind.	+	+	1	-		
Shi drum		**Lab.**	Spont./ind.	+	+	1	-		Mylonas *et al.* 2000, Barbaro *et al.* 2002, Mylonas *et al.* 2004
(Umbrina cirrhosa)		**Com.**	Spont./ind.	+			-		

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[7] "Wild broodstock partly replaced by domesticated fish" (Jonassen)
[8] Provided by Jonassen
[9] Provided by Tort

Species	World production (t)	Level	Reproduction under controlled conditions				Domesti-cation (-/+/•)	Biotechnol. genetic Improvem. (-/+)	Main sources of information
			Spawning (ind./ spont.)[10]	Larvae rearing (-/+)	Gonad matur. (-/+)[11]	Number of cycles			
C. Sturgeons (world-wide)									
Beluga	<0.5	**Lab.**	Ind.	+	+	>2	-	+	Chebanov, Debus; Boguerouk 2005
(Huso huso)		**Com.**	Ind.	+	+	>1	●[12]	-	
Russian sturgeon	?	**Lab.**	Ind.	+	+	>2	+	+	Chebanov, Debus; Boguerouk 2005
(Acipenser gueldenstaedtii)		**Com.**	Ind.	+	+	>2	●[12]		
Starry sturgeon	1	**Lab.**	Ind.	+	+	>2	+	+	Chebanov, Debus
(Acipenser stellatus)		**Com.**	Ind.	+	+	>2			
White sturgeon	2,500	**Lab.**	Ind.	+	+				Doroshov, Chebanov, Debus, Cancellieri
(Acipenser transmontanus)		**Com.**	Ind.	+	+	3	+		
Fringebarbel sturgeon	?	**Lab.**	Ind.	+	+	1			Chebanov, Debus
(Acipenser nudiventris)		**Com.**	Ind.	+	+	1			
Siberian sturgeon	185	**Lab.**	Ind.	+	+	>3	+	+	Chebanov, Debus; Boguerouk 2005
(Acipenser baerii)		**Com.**	Ind.	+	+	>3	●[12]	-	
Sterlet	<0.5	**Lab.**	Ind.	+	+	>3	+	+	Chebanov, Debus, Wedekind; Boguerouk 2005
(Acipenser ruthenus)		**Com.**	Ind.	+	+	>3	●[12]	-	
Mississippi paddlefish	?	**Lab.**	Ind.	+	+			+	Chebanov, Debus; Boguerouk 2005
(Polyodon spathula)		**Com.**	Ind.	+	+	>2	●[12]	+	
Adriatic sturgeon	?	**Lab.**	Ind.	+	+	>2		-	Debus
(Acipenser naccarii)		**Com.**	Ind.	+	+	>2			
Lake sturgeon		**Lab.**	-	+	+	0	-	-	Chebanov, Bruch
(Acipenser fulvescens)		**Com.**	Ind.?	+	+	>1?		-	
Amur sturgeon		**Lab.**							
(Acipenser schrenckii)		**Com.**	Ind.	+	+	>1			Chebanov
Bester	?	**Lab.**	Ind.	+	+	-		-	Chebanov, Debus
(Huso huso x A.ruthenus)		**Com.**	Ind.	+	+	>3	+	-	
		Lab.							
(Acipenser gueldenst. x baerii)		**Com.**	Ind.	+	+	>2		+	Chebanov

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[10] In Russia eggs are obtained through small oviduct incision and stripping (Chebanov)

[11] Egg production (final maturation stage) in all species by hormonal stimulation (Chebanov)

[12] Pedigree establishment: Russian Federation (Boguerouk 2005)

D. Non-European finfish (world-wide)

Species	World production (t)	Level	Reproduction under controlled conditions				Domestication (-/+/•)	Biotechnol. genetic Improvem. (-/+)	Main sources of information
			Spawning (ind./ spont.)	Larvae rearing (-/+)	Gonad matur. (-/+)	Number of cycles			
Channel catfish	351,357	**Lab.**						+	Dunham *et al.* 2001
(Ictalurus punctatus)		**Com.**	Ind.	+	+	∞	+	?	
Broadhead catfish	?	**Lab.**	Ind.?	+	+	≥4	+	?	Dunham *et al.* 2001
(Clarias macrocephalus)		**Com.**							
Walking catfish	?	**Lab.**							
(Clarias batrachus)		**Com.**	Ind.	+	+	?	?	?	Dunham *et al.* 2001
Rohu (Roho labeo)	761,123	**Lab.**							Beck R., Woynarovich A., Gjedrem
(Labeo rohita)		**Com.**	Ind.[13]	+	+	6	+		
Mrigal carp	573,657	**Lab.**							
(Cirrhinus cirrhosus)		**Com.**	Ind.[13]	+	+	∞	+		Beck R. , Woynarovich A.
Catla	615,576	**Lab.**							
(Catla catla)		**Com.**	Ind.[13]	+	+	∞	+		Beck R. , Woynarovich A.
Fring.-lipp. penin. carp	?	**Lab.**							
(Labeo fimbriatus)		**Com.**	Ind.	+	+	∞	+		Beck R.
Java barb	23,541	**Lab.**							
(Barbonymus gonionotus)		**Com.**	Ind.	+	+	∞	+		Beck R.
Chum salmon	1	**Lab.**							
(Oncorhynchus keta)		**Com.**	(Spont.)	+	+	∞	+		Beck R.
Coho (Silver) salmon	100,967	**Lab.**						?	
(Oncorhynchus kisutch)		**Com.**	(Spont.)	+	+	∞	+		Beck R.
Nile tilapa	1,495,744	**Lab.**						?	
(Oreochromis niloticus)		**Com.**	Spont.	+	+	∞	+		Beck R., Kubitza
Blue tilapia	1,883	**Lab.**						?	
(Oreochromis aureus)		**Com.**	Spont.	+	+	∞	+		Beck R., Kubitza
Threespot tilapia	2,000	**Lab.**							
(Oreochromis andersonii)		**Com.**	Spont.	+	+	∞	+		Flynn F., Woynarovich A.
Greenhead tilapia	?	**Lab.**							
(Oreochromis macrochir)		**Com.**	Spont.	+	+	>3	+		Woynarovich A.
Redbreast tilapia	?	**Lab.**							
(Tilapia rendalli)		**Com.**	Spont.	+	+	>3	+		Woynarovich A.
Cobia	20,461	**Lab.**							
(Rachycentron canadum)		**Com.**	Ind/spont.	+	+	>2	-		Schwarz M.
Mahimahi	2,770	**Lab.**	Spont.	+	+	∞	+		Kraul; Nel 1990, 1995, 1996
(Coryphaena hippurus)		**Com.**	Spont.	+	+	∞	+		
Pacific bluefin tuna		**Lab.**	Spont.	+	+	1	-		Sawada *et al.* 2005
(Thunnus orientalis)		**Com.**	Spont.	+			-		

[13] Induced ovulation as well as induced spawning in Bangladesh (Woynarovich A.)

Species	World production (t)	Level	Reproduction under controlled conditions				Domestication (-/+/•)	Biotechnol. genetic Improvem. (-/+)	Main sources of information
			Spawning (ind./ spont.)	Larvae rearing (-/+)	Gonad matur. (-/+)	Number of cycles			

D. Non-European finfish (world-wide, continued)

Species	World production (t)	Level	Spawning (ind./ spont.)	Larvae rearing (-/+)	Gonad matur. (-/+)	Number of cycles	Domestication (-/+/•)	Biotechnol. genetic Improvem. (-/+)	Main sources of information
Kona kampachi	?	**Lab.**	Spont.		+	3	+	-	Nel
(Seriola rivoliana)		**Com.**	Spont.	+	+	2	-	-	Sims
Kissing gourami	8,475	**Lab.**							
(Helostoma temminckii)		**Com.**	Ind.	+	+	>3	+	-	Woynarovich A.
Tambaqui	?	**Lab.**							
(Colossoma macropomum)		**Com.**	Ind.[14]	+	+	>3	+	-	Woynarovich E., Woynarovich A.
Pirapitinga/Pacu	87,961	**Lab.**							
(Piaractus mesopotamicus)		**Com.**	Spont/Ind[14]	+	+	∞	+	-	Beck R., Woynarovich A.,
Curimata pacu	?	**Lab.**							
(Prochilodus argenteus[15]*)*		**Com.**	Ind.[14]	+	+	>3	+	-	Woynarovich A.
Sutchi catfish	?	**Lab.**							
(Pangasius hypophthalmus)		**Com.**	Ind.	+	+	>3	+	-	CB International 2006
?	?	**Lab.**	Ind.	+	+	>1		-	CB International 2006
(Pangasius bocourti)		**Com.**							
Barramundi	29,899	**Lab.**	Ind/spont.	+	+	3	+	-	Gasnier
(Lates calcarifer)		**Com.**	Ind/spont.	+	+	3	+	-	
African catfish		**Lab.**	Ind.	+	+	1			Gasnier
(Heterobranchus longifilis)		**Com.**							
Bagrid catfish	1,000[16]	**Lab.**							
(Chrysichthys nigrodigitatus)		**Com.**	Ind.	+	+	4	+		Gasnier
Red drum	46,072	**Lab.**							
(Sciaenops ocellatus)		**Com.**	Ind.	+	+	3	+		Gasnier

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[14] Induced ovulation (Woynarovich A.)
[15] *Prochilodus marggravii* (Walbaum) not available on FishBase (Froese)
[16] Annual production in Ivory Coast until 1997 (Gasnier)

E. Crustaceans, bivalves and abalones (world-wide)

Species	World production (t)	Level	Reproduction under controlled conditions				Domestication (-/+/•)	Biotechnol. genetic Improvem. (-/+)	Main sources of information
			Spawning (ind./ spont.)	Larvae rearing (-/+)	Gonad matur. (-/+)	Number of cycles			
European crayfish	?	**Lab.**							
(Astacus astacus)		**Com.**	Spont.	+	+	∞	+		v.Lukowicz
Signal crayfish	<0.5	**Lab.**							
(Pacifastac. leniuscul.)		**Com.**	Spont.	+	+	∞	+		v.Lukowicz
Giant river prawn	194,159	**Lab.**							
(Macrobrach. rosenb).		**Com.**	Spont.	+	+	>30	+		FAO, Gjedrem, Brown J.
Kuruma prawn	47,647	**Lab.**							
(Penaeus japonicus)		**Com.**	Ind.?	+	+	>6	+		Briggs *et al.* 2004
Giant tiger prawn	721,793	**Lab.**							
(Penaeus monodon)		**Com.**	Ind.	+	+	5-10	+		Clifford & Preston 2006; Dunham *et al.* 2001
Whiteleg shrimp	1,386,382	**Lab.**							
(Penaeus vannamei)		**Com.**	Ind./spont.	+	+	>20	+		Briggs *et al.*2004; Gjedrem, Clifford & Preston 2006
Blue shrimp	3,132	**Lab.**							
(Penaeus stylirostris)		**Com.**	Ind./spont.	+	+	>30	+		Briggs *et al.* 2004; Clifford & Preston 2006
Fleshy prawn	56,806	**Lab.**							
(Penaeus chinensis)		**Com.**	Spont.	+	+	2	-		Gjedrem
Chinese shrimp	>200,000	**Lab.**							
(Penaeus orientalis)		**Com.**	Ind.	+	+	>30	+		Guo
(Penaeus indicus)	5,000	**Lab.**	Ind.	+	+	3	+		Gasnier[17]
		Com.		+	+	6	+		
Grass shrimp		**Lab.**	Spont.	+	+	3	+		Zaharia *et al.* 2005
(Palaemon adspers.)		**Com.**							
Rock shrimp		**Lab.**	Spont.	+	+	3	+		Zaharia *et al.* 2005
(Palaemon elegans)		**Com.**							
Blue mussel	526,987	**Lab.**							
(Mytilus edulis)		**Com.**	Spont./ind.	+	+	2			Brown J., Gjedrem
Mussel		**Lab.**	Spont.	+	+	1			Nicolaev *et al.* 2005
(Mytilus galloprovinc.)		**Com.**	Spont.	+	+	3			
European flat oyster	5,071	**Lab.**							
(Ostrea edulis)		**Com.**	Spont./ind.	+	+	>10?	+		Laing, Gjedrem
Pacific oyster	4,429,337	**Lab.**	Ind.	+	+	∞	+		Zaharia *et al.* 2003 Allen, Langdon FAO, Gjedrem; Guo
(Crassostrea gigas)		**Com.**	Spt./ind.	+	+	>30	+		
Eastern oyster	?	**Lab.**	Extr.	+	+				
(Crassostrea virginica)		**Com.**	Ind.	+	+	<10	●	-	Guo, Canzonier
Hard clam		**Lab.**							
(Mercenaria mercen.)		**Com.**	Ind.	+	+	>10	+		Guo
Bay scallop	450,000[18]	**Lab.**							
(Argopecten irradians)		**Com.**	Ind.	+	+	>20	+	-	Guo & Luo 2006
Pacific abalone	8,000	**Lab.**							
(Haliotis discus hannai)		**Com.**	Ind.	+	+	>10	+		Guo
Atlantic abalone	8,000	**Lab.**							
(Haliotis tuberculata)		**Com.**	Spont./ind.	+	+	2			Gasnier

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[17] According to Gasnier (August 2006) "domestication was also performed for several years in Tahiti" and (February 2007) the species "is produced for several years in Iran ... but domestication is not yet realised".

[18] (Guo)

PART II

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Controlled reproduction and domestication in aquaculture

- the current state of the art. Part II

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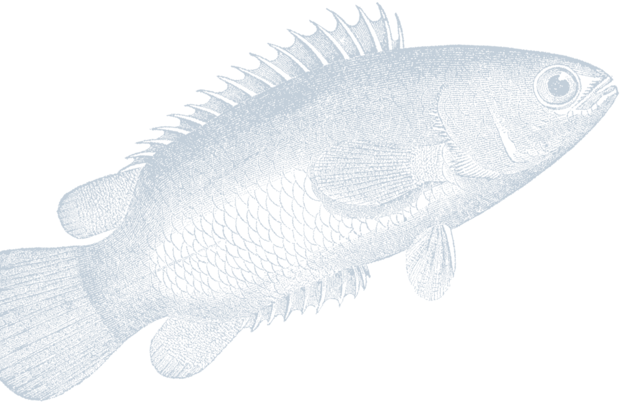

Controlled reproduction and domestication in aquaculture

THE CURRENT STATE OF THE ART PART II

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RESULTS

(continuation from Part I, *Aquaculture Europe* 32 (1), March 2007)

The following continuation of the Results starts with supplementary information. Thereafter, it summarises the information of Table 1 (Part I) following its column headings, thereby utilising explanatory information obtained in the correspondence on the subject of this paper and from the literature.

Supplements to Part I

Table 1.A, Northern pike and Rainbow trout: M.v.Lukowicz (pers. com.) drew my attention to the need for stripping, without which controlled mating and thus spawning in these two species can hardly be achieved.

Table 1.D, Barramundi: Important information was contributed by M. Rimmer (pers. com.), according to whom the number of cycles at commercial level was even exceeding 3 and selective breeding schemes use wild-sourced broodstock.

An interesting table was put at my disposal by Q. Wang and H. Liu (pers. com.) showing the situation with marine and brackishwater species in China (**Table 2**). Nearly all the production data can also be found in Fishstat 2006, but there are some differences (apart from rounding off effects). Some of the species do not seem to be considered by FAO at all (or are hidden under a completely different name); others are lumped together with related species assigning their total production to only one of them. The most important aspects will be dealt with together with the comments on Table 1.

Another new table containing data from Australia, was kindly provided by G. Mair (**Table 3**; pers. com.). Australia represents the other end of a scale, where China is certainly the country with not only the highest production worldwide but also many species domesticated for a long time, whereas Australia finds itself only at the beginning, with a still low national production and no indigenous species well advanced in the domestication process.

ON THE COVER

1 Krasnodar warm water fish farm at Krasnodar power station, of "Russian Sturgeon – Kuban Ltd.", used for commercial rearing of sturgeons and for live gene bank holding by the Federal Centre of Selection and Genetics for Aquaculture, South Branch. Courtesy: Prof. M. Chebanov, Director.
2 Ship sturgeon (*Acipenser nudiventris*), progeny obtained on farm of Russian Sturgeon – Adygheya Ltd. also used by the South Branch of the Federal Centre. Courtesy: Prof. M. Chebanov.
3 Mature Beluga (*Huso huso*) obtained during the autumn season and spawned in spring (May). Courtesy: Dr. Elena Galich, Krasnodar.
4 Mature Sevruga (*Acipenser stellatus*) obtained during the autumn season and spawned in spring (May). Courtesy: Dr. Elena Galich, Krasnodar.

Summarising comments on Table 1

Table 1 contains information mainly received through personal communication. Due to the limitations of this approach (see Part I, p. 5), the information is not complete. However, it is considered sufficient to obtain an overall impression of the situation and, on this basis, to renew the discussion as to what domestication really is or should be seen as. Contrary to what some authors think, it should not be left as it is and, in particular, there should not be a separate aquaculture definition of domestication, different from that used in terrestrial animal husbandry and agriculture in general. The contents of Table 1 will not be commented on in too much detail. Instead, subsequent to the summarising comments, some aspects considered as of special importance, will be dealt with more extensively: the distribution of domesticated species among continents, the different phases of domestication, and some aspects of the overall situation of biotechnological genetic improvement.

Names

While the finfish are covered by FishBase (Froese & Pauly 2006), crustaceans and molluscs as yet lack a similarly comprehensive and reliable reference basis. It is to be hoped that efforts to provide such a system will soon be successful and the results available in the internet.

World production

All statistical data are from FAO's Fishstat Plus 2006, covering the period 1950-2004. Exceptionally included in the present Part II are data for 2005 from Fishstat Plus 2007, published when Table 1 of the manuscript was already compiled. The extra data for China (Table 2) and Australia (Table 3) also refer to 2005.

It is well known that Fishstat has deficiencies as to precision and reliability. Many of the estimates are provided by government officials, only part of them by experts. Often they refer to species groups instead of single species. Table 2 for China can be seen as an example of some of the difficulties.

However, since there is no alternative, the Fishstat data are accepted as roughly correct, at least as far as the order of magnitude is concerned. In specific cases, also the context is considered in order to evaluate the degree of reliability. As for the rest, it is up to the reader to judge how far conclusions partly or entirely based on these data may be sound, at least regarding the issues to which they refer.

Laboratory and commercial level

The distinction is useful as long as the process of domestication is still either in its pre-domestication phase or at the beginning of the domestication phase proper. Where the Lab. level is filled in, it can be an indication of still ongoing experimental work. In cases of advanced domestication, the Lab. level is, as a rule, left open (see Table 1.A, Freshwater finfish in Europe and Table 1.D, Non-European finfish world-wide with few exceptions). This applies also for Tables 2 and 3 for China and Australia, respectively.

Reproduction under controlled conditions

Spawning

There is a considerable number of species in which spawning is not spontaneous but induced by various methods, such as hormone injection, photoperiod variation, temperature change, eyestalk ablation in penaeid shrimps, etc. My inquiries did not regularly include questions about the type of induction. M. Rimmer (pers. com.), e.g., let me know that most spawnings of Barramundi (laboratory level) in Australia are induced by hormone injection, but that some spawnings occur spontaneously, while in Asia most spawnings are spontaneous. **Table 4** shows how induced and spontaneous spawning are distributed among the various species considered in Table 1 (Part I). No clearly visible correlation appears to exist between the mode of spawning and the degree of domestication. In several cases maturation is spontaneous, but to extrude the sexual products stripping is performed, in particular when an exact timing is to be achieved. In sturgeons in Russia, egg production (the final maturation stage) is in all species induced by hormonal stimulation and eggs are obtained through small oviduct incision and stripping (Chebanov, pers. com.).

In Table 2 for China, induced spawning is indicated for two finfish species and spontaneous spawning for another two; both possibilities (spt/ind.) appear to exist for 9 finfish species and for all crustaceans (6) and molluscs (11). In Australia (Table 3), only three crustaceans spawn spontaneously in captivity, for all other species both possibilities are indicated. According to G. Coman (pers. com.) most of the Australian "prawn" (penaeid shrimp) farms "rely on eyestalk ablation to synchronise spawning of their broodstock".

Larval rearing and gonad maturation

The questions for larval rearing and gonad maturation were asked in order to get additional factual hints concerning the achievement of continuous controlled reproduction. There are six species without any entry at commercial level and one species (Pacific bluefin tuna) without an entry in the column for gonad maturation at Com. level. For three of the six species as well as for the tuna, the number of continuous controlled reproduction cycles is less than three even at laboratory level. Among the remaining three species, the number of cycles at laboratory level is ≥4 for Broadhead catfish and 3 for both Grass shrimp and Rock shrimp. The achievements at laboratory level only, as well as a small number of species with less than three cycles at commercial level were included in Table 1 because the data were supplied and it was considered useful to dispose of some information

Table 2. Domestication of marine and brackishwater species in China

(according to Q. Wang & H. Liu, pers. com.)

Table explanations and column headings as for Table 1 (Part I); blue values and species denominations from FAO Fishstat (2007, for 2005) for comparison

Species	China production (t)	Level	Reproduction under controlled conditions				Domestication (-/+/•)	Biotechnol. genetic improvem. (-/+)^{1}	Main sources of information
			Spawning (ind./ spont.)	Larvae rearing (-/+)	Gonad matur. (-/+)	Number of cycles			
Finfish									
Tongue sole	500	**Lab.**	Ind.	+	+	1			Fishery statistic annals of China, 2005
(Cynoglossus semilaevis)		**Com.**	Spont./ind.	+	+	1			
Olive flounder	76,900	**Lab.**	Spont./ind.	+	+	∞		undergoing	Fishery statistic annals of China, 2005
(Paralichthys olivaceus)		**Com.**	Spont./ind.	+	+	>5^{2}	+	+	
Stone flounder		**Lab.**	Ind.	+	+	>5	+		Fishery statistic annals of China, 2005
(Kareius bicoloratus)		**Com.**	Ind.	+	+	>5^{2}	+	-	
Turbot		**Lab.**	Ind.	+	+	>5	+	undergoing	Fishery statistic annals of China, 2005
(Psetta maxima)		**Com.**	Ind.	+	+	4	+	-	
Japanese seabass	88,000	**Lab.**	Ind.						Fishery statistic annals of China, 2005
(Lateolabrax japonicus)	249,170^{3}	**Com.**	Spont./ind.^{3}	+	+	∞	+	-	
Schlegel's black rockfish	1,000	**Lab.**							Fishery statistic annals of China, 2005
(Sebastes schlegelii)		**Com.**	Spont.	+	+	∞	+	-	
Red seabream	44,200 44,222^{4}	**Lab.**							Fishery statistic annals of China, 2005
(Pagrus major)		**Com.**	Spont./ind.	+	+	>5^{2}	+	-	
Black porgy		**Lab.**							Fishery statistic annals of China, 2005
(Acanthopagrus schlegelii)		**Com.**	Spont./ind.	+	+	∞	+	-	
Croceine croaker	69,600	**Lab.**							Fishery statistic annals of China, 2005
(Larimichthys crocea)	69,641	**Com.**	Spont./ind.	+	+	∞	+	-	
Red drum	45,700	**Lab.**							Fishery statistic annals of China, 2005
(Sciaenops ocellatus)	45,742	**Com.**	Spont.	+	+	∞	+	-	
Tiger puffer	18,800	**Lab.**							Fishery statistic annals of China, 2005
(Takifugu rubripes)		**Com.**	Spont./ind.	+	+	>5^{2}	+	-	
Cobia	18,900	**Lab.**							Fishery statistic annals of China, 2005
(Rachycentron canadum)	18,882	**Com.**	Spont./ind.	+	+	∞	+	-	
Yellowtail amberjack	12,000	**Lab.**							Fishery statistic annals of China, 2005
(Seriola lalandi/S. spp.)	11,973	**Com.**	Spont./ind.	+	+	∞	+	-	

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[1] - = no relevant work done; empty space = no information available

[2] With wild broodstock inputs

[3] Includes 161,176 t of inland freshwater production

[4] Blue value refers to Sparidae

Table 2. Domestication of marine and brackishwater species in China
(continued)

Species	China production (t)	Level	Reproduction under controlled conditions				Domestication (-/+/•)	Biotechnol. genetic improvem. (-/+)[1]	Main sources of information
			Spawning (ind./ spont.)	Larvae rearing (-/+)	Gonad matur. (-/+)	Number of cycles			
Crustaceans									
Chinese Shrimp	49,901	**Lab.**							Fishery statistic annals of China, 2005
(Fenneropenaeus chinensis)	49,901	**Com.**	Spont./ind.	+	+	∞	+[5]	+	
Kuruma prawn	41,000	**Lab.**							Fishery statistic annals of China, 2005
(Marsupenaeus japonicusi)	41,090	**Com.**	Spont./ind.	+	+	∞	+	-	
Giant tiger prawn	75,700	**Lab.**							Fishery statistic annals of China, 2005
(Penaeus monodon)	75,731	**Com.**	Spont./ind.	+	+	∞	+	-	
Whiteleg shrimp	407,600	**Lab.**							Fishery statistic annals of China, 2005
(Litopenaeus vannamei)	808,433[6]	**Com.**	Spont./ind.	+	+	∞	+	-	
Swimming crab[7]	79,100	**Lab.**							Fishery statistic annals of China, 2005
(Portunus trituberculatus)		**Com.**	Spont./ind.	+	+	∞	+	-	
Mud crab	111,400	**Lab.**							Fishery statistic annals of China, 2005
(Scylla serrata)	111,423	**Com.**	Spont./ind.	+	+	∞	+	-	
Bivalves									
Pacific cupped oyster	3,826,363 3,826,363	**Lab.**	Spont./ind.	+					Fishery statistic annals of China, 2005
(Crassostrea gigas[8])		**Com.**	Spont./ind.	+	+	∞	+	+	
(Crassostrea rivularis)		**Lab.**							
		Com.	Spont./ind.	+	+	∞	+		
(Crassostrea plicatula)		**Lab.**							
		Com.	Spont./ind.	+	+	∞	+		
Blue mussel	772,173	**Lab.**							Fishery statistic annals of China, 2005
(Mytilus edulis)		**Com.**	Spont./ind.	+	+	∞	+		
Bay scallop	1,035,796 1,035,796	**Lab.**							Fishery statistic annals of China, 2005
(Argopecten irradians)		**Com.**	Spont./ind.	+	+	∞	+	+	
Scallop		**Lab.**							
(Chlamys farreri)		**Com.**	Spont./ind.	+	+	∞	+	+	
Japanese scallop		**Lab.**						+	
(Patinopecten/Mizuhop. yessoensis)		**Com.**	Spont./ind.	+	+	∞	+		
Blood clam/Blood cockle	303,727	**Lab.**							Fishery statistic annals of China, 2005
(Scapharca subcrenata[8])	303,727	**Com.**	Spont./ind.	+	+	∞	+		
Clam/Jap. carpet shell	2,857,376	**Lab.**							Fishery statistic annals of China, 2005
(Ruditapes philippinarum)	2,857,376	**Com.**	Spont./ind.	+	+	∞	+		
Constricted tagelus	713,846 713,846	**Lab.**							Fishery statistic annals of China, 2005
(Sinonovacula constricta[9])		**Com.**	Spont./ind.	+	+	∞	+		
Tagelus		**Lab.**							
(Solen strictus)		**Com.**	Spont./ind.	+	+	∞	+		

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[5] Pedigree being established

[6] Includes 400,791 t of inland brackishwater production

[7] Production corresponds to FAO 2005 value for Portunidae (=79,068)

[8] Fishstat: *Anadara granosa*

[9] Blue value refers to this species only

from the transition area between laboratory and commercial level. Table 2 for China comprises very few data at laboratory level (only for the first four finfish species), while in Table 3 the many laboratory indications reflect the early state of development in Australia.

Number of cycles and domestication

The number of at least three full life cycles achieved under controlled conditions (= in captivity) is arbitrarily chosen, since in many cases no information was available as to whether the process of deliberate selection had already been started, which by the time of statement might not really have been the case yet. The definition concerning the absence of wild inputs during the first cycles, given in Part I, is problematic since the wild input could have been necessary to achieve continuous controlled reproduction as well as to provide a broader genetic basis for selection during the domestication phase proper. During the true domestication phase, wild inputs can still serve to avoid inbreeding and to increase the choice for genetic properties helping to realise the domestication goals, such as improved growth rate, better resistance to diseases and parasites as well as to extreme environmental conditions, etc. “Wild broodstock were partly replaced by domesticated fish” with Atlantic halibut and Atlantic cod in Norway, and “wild broodstock inputs” were used for Olive flounder, Stone flounder, Red seabream and Tiger puffer in China (see Table 2). Commercial selective breeding schemes for Barramundi also still rely to some extent on “wild-sourced broodstock” (M. Rimmer, pers. com.) and “most if not all hatchery stocks are still occasionally supplemented from the wild” (G. Mair, pers. com.).

Pedigree establishment

Information about the achievement of genetically stable strains was obtained from China, Czech Republic, Finland, Germany, Hungary, Norway, the Russian Federation, and the USA. Official recognition of clearly distinguishable strains is a rather recent achievement, obtained during the second half of the last and the present century (details under Phases of domestication further below).

In China a pedigree is being established for Chinese shrimp (*Fenneropenaeus chinensis*; H. Liu, pers. com.).

In the Czech Republic, according to M. Flajshans (pers. com.), the first breeds of Common carp (*Cyprinus carpio*) were established in the period 1880’s to 1930’s, those of the Tench (*Tinca tinca*) during the late 1970’s. Rainbow trout (*Oncorhynchus mykiss*) was first imported in 1888 and “since 1946… at least 15 times either for aquaculture or for restocking”. First breeding records date back to 1946/47, 1966, 1975 and 1988 and have led to four well-established commercial aquaculture breeds of known origin.

In Finland, the situation is somewhat complicated because of the great importance of biodiversity protection in nature. Selective breeding programmes for the domestication of aquaculture species are so far restricted to Rainbow trout and Whitefish (*Coregonus lavaretus* and *C. peled;* see Table 1.A). Finland’s Rainbow trout programme - the largest in Europe - includes more than 400 individually marked family lines with full pedigree information (H. Mölsä, pers. com.).

In Germany, efforts are made to document the existing variety of cultured strains of mainly Common carp and Rainbow trout. This is done in the context of a national programme aiming at conservation and sustainable utilisation of aquatic genetic resources (K. Kohlmann, pers. com.).

In Hungary, a new Animal Breeding Act came into force after 1993 including for the first time pedigree registration of a fish species, Common carp. Various carp lines were registered also before, but only at farm level (L. Váradi, pers. com.).

In Norway, (T. Gjedrem, pers. com.) pedigree records for Atlantic salmon comprise eight generations and similar records are kept for Rainbow trout. Both breeding programmes have been run by a private company since 1992. A breeding programme for Atlantic cod includes at present pedigree records for two generations.

In the Russian Federation, according to A. Boguerouk (2005; see Table 1.C of this paper and the Section on Phasing of domestication further below), the State Register includes 10 species of “domesticated” finfish, 5 of which belong to the sturgeon group, 4 are Chinese carps and one is *Coregonus peled*. In addition, by 2004 a list of “prospective aquaculture species” totals 23 strains, including 11 of Common carp (*Cyprinus carpio*) and 4 of Rainbow trout (*O. mykiss*).

In the USA, as reported further above among the Corrections and supplements to Part I, also the Eastern oyster (*Crassostrea virginica*) must be considered here. When at the Oyster Research Laboratory at Rutgers University in New Jersey there was evidence that selected strains of this species carried a stable MSX resistance trait (MSX, a Protozoan parasite), the product was patented and released to commercial enterprises for a fee (W. Canzonier, pers. com.).

Biotechnological genetic improvement

In the pertinent column of Table 1, crosses were made for the following species: Rainbow trout and Charr (Tabl 1.A); 7 species of sturgeon (including Mississippi paddlefish; Table 1.C); and Channel catfish (Table 1.D). Table 2 on domestication in China contains crosses for Olive flounder, Chinese shrimp, Pacific cupped oyster, Bay scallop, another scallop (*Chlamys farreri*), all at commercial level, and Japanese scallop (*Patinopecten yessoensis*) at laboratory level. In Table 3 for Australia there are crosses at commercial level for the Pacific oyster and Abalone, at laboratory level for 6 additional species.

Since I did not define early enough the prerequisites for a species to be included in this column, it is not possible to tell where the results of the great amount of experimental work done in this field have already led to commercially viable application. Improved growth seems to be among such achievements in several species (see also special Section further below).

Table 3. Domestication of finfish and shellfish in Australia

(according to G. Mair, pers. com.)

Table explanations and column headings as for Table 1 (Part I); blue production values from FAO Fishstat (2007, for 2005) for comparison

Species	Australian production[1] (t)	Level	Reproduction under controlled conditions				Domestication (-/+/•)	Biotechnol. genetic improvem. (-/+)	Main sources of information
			Spawning (ind./ spont.)	Larvae rearing (-/+)	Gonad matur. (-/+)	Number of cycles			
				Finfish					
Atlantic salmon	16,033	**Lab.**	ind./Spont.	+	+	-	-	-	
(Salmo salar)	123,975	**Com.**	ind./Spont.	+	+	∞	+	-	
Barramundi	1,763	**Lab.**	ind./Spont.	+	+	3	-	+	
(Lates calcarifer)	31,000	**Com.**	ind./Spont.	+	+	3	-	-	
Murray cod	26	**Lab.**	ind./Spont.	+	+	1	-	+	
(Maccullochella peelii)	26	**Com.**	ind./Spont.	+	+	1	-	-	
Silver perch	314	**Lab.**	ind./Spont.	+	+	2	-	-	
(Bidyanus bidyanus)	314	**Com.**	ind./Spont.	+	+	2	-	-	
Yellowtail kingfish[2]	~1,500	**Lab.**	ind./Spont.	+	+	0	-	-	
(Seriola lalandi)	156,000[3]	**Com.**	ind./Spont.	+	+	0	-	-	
Mulloway	~50[3]	**Lab.**	ind./Spont.	+	+	0	-	-	
(Argyrosoma japonicus)	~50	**Com.**	ind./Spont.	+	+	0	-	-	
Southern bluefin tuna	7,500	**Lab.**	-	-	-	-	-	-	
(Thunnus maccoyii)	7,500	**Com.**	-	-	-	-	-	-	
				Shellfish					
Pacific oyster	7,295	**Lab.**	ind./Spont.	+	+	>3	+	+	
(Crassostrea gigas)	4,497,085	**Com.**	ind./Spont.	+	+	>3	+	+	
Sydney rock oyster	4,500	**Lab.**	ind./Spont.	+	+	>3	+	+	
(Saccostrea glomera)	4,500	**Com.**	ind./Spont.	+	+	>3	+	-	
Blue mussel	2,845	**Lab.**	ind./Spont.	+	+	0	-	-	
(Mytilus sp.)	394,055	**Com.**	-	-	+	0	-	-	
Gold-lipped pearl oyster	n.a.[4]	**Lab.**	ind./Spont.	+	+	2	-	+	
(Pinctada maxima)		**Com.**	ind./Spont.	+	+	2	-	-	
Green-/Black-lip Abalone	300	**Lab.**	ind./Spont.	+	+	2	-	+	
(Haliotis laevigata/rubra[5]*)*	300	**Com.**	ind./Spont.	+	+	2	-	+	
Giant Tiger Prawn	294	**Lab.**	ind./Spont.	+	+	3	+	+	
(Penaeus monodon)	723,172	**Com.**	ind./Spont.	+	+	5	+	-	
Banana Prawn		**Lab.**	ind./Spont.	+	+	4[6]	+	-	Burke[7]
(Penaeus merguiensis)		**Com.**							
Yabby	120	**Lab.**	Spont.	+	+	?	+	+	
(Cherax destructor)	120	**Com.**	Spont.	+	+	>3	+	-	
Marron	77	**Lab.**	Spont.	+	+	?	+	-	
(Cherax tenuimanus)	79	**Com.**	Spont.	+	+	>3	+	-	
Red Claw	100	**Lab.**	Spont.	+	+	?	+	+	
(Cherax quadricarinatus)	123	**Com.**	Spont.	+	+	>3	+	-	

[1] Black values from ABARE 2006 (for 2005)
[2] Also known as Yellowtail amberjack
[3] Australian and/or world production are estimates as species production is not yet formally reported
[4] = not applicable (production not reported in t – mainly in value or some other specific measure)
[5] The two species are both farmed with different emphasis on species across the southern states; the production figures include some production of the hybrid between the two species
[6] "Held on a semi commercial basis"
[7] Directly obtained information

Aquaculture production and domestication

What is the share of domesticated species in the total of aquaculture species? **Tables 5 and 6** are intended to give answers. Whereas Table 5 includes all species of finfish, crustaceans and molluscs of Table 1 with a world production of ≥10,000 t, Table 6 considers only finfish with a world production of ≥100,000 t. While Table 5 is based on Table 1, Table 6 presents the FAO data (Fishstat 2006) for species for which I was not in a position to include information on domestication. Table 6 is intended as a check-test for the finfish species.

The last row of Table 5 for finfish shows that the species of this table comprise more than 60 % of the world production and of the production for each continent as well. In order to put the comparison on an equal scale, sums and percentages have been calculated separately for the 12 species with a world production of ≥100,000 t each, resulting in percentages only slightly smaller than for the sums of all 21 species of Table 5.

The 12 domesticated species with a world production of ≥100,000 t each of Table 5 make up about two thirds of the world production as well as of the production of each continent, whereas the sums of all 17 species of Table 6 remain well below one third. If we consider that Crucian carp can almost certainly be taken as domesticated, whereas Japanese amberjack and Japanese eel cannot, the achievement of domestication remains questionable for only 14 species of Table 6 with a total world production of 5,195,501 t. Moreover, some of the “species” are (spp.) or may include (nei[1]) more than just one species but would, if split, probably lose their weight rank.

As far as the number of species is concerned, Fishstat indicates aquaculture production figures for 2004 of 202 species comprised between <0.5 and almost 4 million t. 99 species remain below an annual production of 1,000 t, and 135 below a production of 10,000 t. 38 species cover the range between 10,000 and 100,000 t, and only 21+8 species range between 100,000 and 4,000,000 t. This situation is shown in detail in **Table 7**.

As reflected in Table 7, the percentage of domesticated species is increasing with the production level. It may be appropriate, therefore, to assume that the share of domesticated species is close to zero as long as the production per species remains less than 100 t and close to 100 % for species reaching a production of 1 million tons.

The representative value of the domestication data of Table 1 (Part I) remains to be dealt with in the DISCUSSION chapter (Part III).

Distribution of domesticated species among continents

In Table 5 all species of Table 1 with a world production of ≥10,000 t are placed in a decreasing order showing their distribution among continents, together with their degree of domestication and the environment in which they are cultured. The table shows that all species with a world production of more than one million metric tonnes are either at the point of pedigree establishment (4 species: the three Chinese carps and Common carp) or have achieved innumerable generations through continuous controlled reproduction (2 species: Nile tilapia and Atlantic salmon). Only 5 out of the 21 species of the table can be classified as being only at the start of domestication.

Domestication of a species appears as a favourable condition for massive production increases as well as for the transfer and distribution of highly productive species among countries and even continents. Indications of such developments can be drawn from Table 5. A successful transfer of farmed organisms over long distances, in particular overseas, can be facilitated when domestication permits the production of offspring in the area of destination immediately upon arrival. However, this possibility can be limited by the number of individuals being transferred. If it is too low, the genetic basis could be too small to warrant satisfactory performance, in particular when an adaptation to an entire new set of culture environments is at stake. This can only be overcome by additional supplies from the country/continent of origin.

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[1] FAO Fishstat: nei = not elsewhere included (referring to an anonymous species or species group)

Table 4. Mode of spawning (according to table 1). “Lab. level only” not considered in the % values.

Part of Table 1	A		B		C		D		E (Crust.)		E (Moll.)	
	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%
Induced	3	17	-	-	13[1]	100	13	50	3	33	4	44
Ind./Spont.[2]	2	11	7	50	-	-	2	8	2	22	-	
Spont./Ind.[2]	5	28	3	21	-	-	1	4	-	-	4	44
(Spont.)	8	44	-	-	-	-	2	8	-	-	-	-
Spontaneous	-	-	4	29	-	-	8	30	4	45	1	12
Lab. level only	-	☒	1	☒	-	☒	3	☒	3	☒	-	☒
Total[3]	18	100	15	100	13	100	29	100	12	100	9	100

[1] Lake sturgeon: induced?
[2] As indicated by the resource person
[3] Lab. Level not considered

Table 5. Distribution of production and domestication among continents

(only species with a world production of ≥10,000 t considered; production, continent and environment according to Fishstat Plus 2006, domestication according to Table 1)

Environment:
F freshwater
B brackishwater
M marine

Domestication:
≥3 number of full cycles achieved (= domestication started)
∞ innumerable number of cycles (= domestication well on the way)
• pedigree established

Colour, signature:
red, bold vertical maximum = species maximum
red, normal second vertical maximum
underlined horizontal maximum = regional maximum

No.	Species	World production (t)	Regional Production (,000 t)						Environment (F/B/M)	Domestication (≥/∞/•)
			Africa	North America	South America	Asia	Europe	Oceania		
	Finfish									
01	Silver carp *(Hypophthalmichthys molitrix)*	3,979,292	75.8	15.0	-	**3,842.5**	46.0	-	F(B,M)	●
02	Grass carp (= White amur) *(Ctenopharyngodon idella)*	3,876,868	41.1	-	-	3,832.7	3.0	-	F(B)	●
03	Common carp *(Cyprinus carpio)*	3,387,918	22.3	13.1	46.1	3,159.7	146.8	-	F(B,M)	●
04	Bighead carp *(Aristichthys nobilis)*	2,101,688	-	-	-	2,097.2	4.5	-	F	●
05	Nile tilapia *(Oreochromis niloticus)*	1,495,744	**209.5**	24.6	17.7	1,243.6	0.4	0.1	F,B	∞
06	Atlantic salmon *(Salmo salar)*	1,244,637	-	97.5	**349.3**	-	**783.0**	**14.8**	M,F,B	∞
07	Rohu (Roho labeo) *(Labeo rohita)*	761,123	-	-	-	761.1	-	-	F	6
08	Catla *(Catla catla)*	615,576	-	-	-	615.6	-	-	F	∞
09	Mrigal carp *(Cirrhinus cirrosus)*	573,657	-	-	-	573.7	-	-	F	∞
10	Rainbow trout *(Oncorhynchus mykiss)*	504,876	1.1	29.1	139.5	44.0	289.3	1.9	F,M,B	●
11	Channel catfish *(Ictalurus punctatus)*	351,357	-	**287.1**	1.5	62.6	0.1	-	F	∞
12	Coho (= Silver) salmon *(Oncorhynchus kisutch)*	100,967	-	1.2	90.2	9.6	-	-	M,F	∞
13	Gilthead seabream *(Sparus aurata)*	90,995	3.6	0.1	-	25.3	62.1	-	M(B,F)	>5
14	Pirapatinga *(Piaractus mesopotamicus)*	87,636	-	-	1.2	86.4	-	-	F	∞
15	European seabass *(Dicentrarchus labrax)*	49,103	2.8	-	-	1.3	45.0	-	M,B(F)	>3
16	Red drum *(Sciaenops ocellatus)*	46,072	0.5	1.4	-	44.1	-	-	M(B)	3
17	Barramundi (=Giant seaperch) *(Lates calcarifer)*	29,899	-	-	-	28.3	-	1.6	B,M(F)	3
18	Java barb *(Barbonymus gonionotus)*	23,541	-	-	-	23.5	-	-	F,B	∞
19	North African catfish *(Clarias gariepinus)*	23,115	16.8	-	0.2	0.8	5.3	-	F	∞
20	Sea trout *(Salmo trutta)*	22,183	-	-	-	11.9	10.3	-	F(M,B)	∞
21	Cobia *(Rachycentron canadum)*	20,461	-	-	-	20.5	-	-	M	>2
	Sums	19,386,708	373.5	469.0	645.8	16,484.3	1,395.8	18.3		
	World and continent totals	28,165,039	551.1	538.3	815.2	24,757.7	1,473.9	28.9		
	Sums in % of totals	68.8	67.8	87.1	79.2	66.6	94.7	63.3		

Table 5. Distribution of production and domestication among continents

(continued)

No.	Species	World production (t)	Regional Production (,000 t)						Environ-ment (F/B/M)	Domesti-cation (≥/∞/•)
			Africa	North America	South America	Asia	Europe	Oceania		
	Finfish (continued)									
	Sums species 1-12	18,993,703	349.8	467.6	644.3	16,242.3	1,273.1	16.8		
	World and continent totals	28,165,039	551.1	538.3	815.2	24,757.7	1,473.9	28.9		
	Sums in % of totals	67.4	63.5	86.9	79.0	65.6	86.4	58.1		
	Crustaceans									
01	Whiteleg shrimp *(Penaeus vannamei)*	1,386,382	-	**98.5**	**172.1**	**1,115.8**	-	-	B,M(F)	∞
02	Giant tiger prawn *(Penaeus monodon)*	721,793	7.6	-	-	710.9	-	3.2	B,M(F)	5-10
03	Giant river prawn *(Macrobrachium rosenbergi)*	194,159	-	0.3	0.4	193.5	-	-	F,B(M)	∞
04	Fleshy prawn *(Penaeus chinensis)*	56,806	-	-	-	56.8	-	-	B,M	2
05	Chinese shrimp *(Penaeus orientalis)*	>200,000	-	-	-	>200.0	-	-		∞
	Sums	**>2,559,140**	**7.6**	**98.8**	**172.5**	**>2,277.0**	**-**	**3.2**		
	World and continent totals	3,679,753	7.9	154.2	172.7	3,338.7	0.2	6.1		
	Sums in % of totals	>69.5	96.2	64.1	99.9	68.2	0.0	52.5		
	Molluscs									
01	Pacific oyster *(Crassostrea gigas)*	4,429,337	**0.4**	**52.9**	**2.4**	**4,246.2**	121.8	5.6	M,B	∞
02	Blue mussel *(Mytilus edulis)*	526,987	-	24.2	0.1	-	**502.7**	-	M	2
03	Bay scallop *(Argopecten irradians)*	450,000	-	-	-	450.0	-	-		∞
	Sums	**5,406,324**	**0.4**	**77.1**	**2.5**	**4,696.2**	**624.5**	**5.6**		
	World and continent totals	13,255,852	2.0	262.6	129.6	11,998.3	764.3	99.0		
	Sums in % of totals	40.8	20.0	29.4	1.9	39.1	81.7	5.7		

In Table 5, the sequence of the world production figures for the first four species is strongly reflected by the figures for Asia making up between 93 and almost 100 % of the world production for each of the four species. Three of these species are Chinese carps: Silver carp, Grass carp and Bighead carp. The fourth species, Common carp is known to have been the first cultured aquatic species ever (according to Chinese literature of 475 B.C.; after Bardach et al. 1972). The only other species exceeding a world production of 500,000 t, are the Nile tilapia, the two salmonids Atlantic salmon and Rainbow trout, and the three Indian carps Rohu, Catla and Mrigal. However, whereas Nile tilapia and Rainbow trout have been distributed all over the world, there is no appreciable production of Indian carps outside Asia.

The world production of the three Indian carps amounts to almost 2 million tons in 2004. India's share thereof is 71.6 %, followed by Bangladesh (21.9 %), Myanmar (5.6 %), and Laos, Nepal and Thailand (<0.5 each). Indian production is present in FAO's Fishstat since 1950 (8,326 t), the beginning of the registration. An appreciable production of other countries (≥500 t) started in Myanmar in the second half of the 1960s with Rohu only.

In the following only two species are dealt with in more detail: Nile tilapia, the "aquatic chicken", and North African catfish, a so-called "boutique fish". Both species originate from Africa, have a special intercontinental history, and differ considerably in their domestication pattern.

Nile tilapia (*Oreochromis niloticus*)

The Nile tilapia was originally an African species, as all its Tilapia kinship. It started its aquaculture "world career" in Asia (see **Table 8**), long before it became the "aquatic chicken" so intensively and appropriately promoted as food for the poor in tropical and sub-tropical countries of the so-called third world, or more adequately termed: the countries of the South. At the start of the Fishstat statistics, in 1950, it was already present in China, Thailand and Indonesia, followed by the Philippines in the next decade (**Table 9**). In 1950 China with a production of 700 t, equalled already Egypt (the only African country then producing the Nile tilapia at a level of >500 t). Egypt's production came, according to Fishstat, from brackishwater, whereas in other countries the species was almost exclusively farmed in freshwater (Tables 8 and 9).

When noting what reasons were named for choosing the Nile tilapia as particularly suitable for strategic genetic research in aquaculture (ADB 2005, p. 16: "importance in freshwater aquaculture, short generation time"), I sometimes miss one: the ease and efficiency of reproduction. This is almost unequalled in other species, in particular marine ones. In addition, when targeted genetic research in tilapias finally began in the 1980s, most of the possible difficulties, such as the modalities of controlled spawning, larval rearing, and maturation, had, at least in principle, already been solved and, moreover, there was the extensive experience with the genetics of salmonids. An important prerequisite of domestication was, therefore, already fulfilled when the efforts of the GIFT (Genetically Improved Farmed Tilapia) programme started: there was no need any more for much of a pre-domestication phase (see the following section on phasing of domestication). It had already turned out, instead, that the Asian aquaculture stocks, due to the introduction of only few individuals, were genetically exhausted and needed replenishing. One of the subsequent logical efforts was to look at the availability of the ancestral African resources for such replenishment (see Pullin 1988). This was done in addition to making the best possible use of the impoverished genetic material already available in several parts of Asia.

The GIFT concept was based on two pillars: (1) the use of exclusively conventional breeding methods (without recourse to genetic modification by gene transfer); (2) increased provision of animal protein for rural and urban consumers, including the poor. As to pillar (2), according to the ADB (2005) the success in the Philippines and Thailand was exemplary: "At least 280,000 people in the Philippines and 200,000 people in Thailand, inclusive of their families, directly and indirectly benefit annually from employment generated by tilapia farming alone", and among those are "the poor and small-scale farmers".

North African catfish (*Clarias gariepinus*)

Trials to reproduce the North African catfish *Clarias gariepinus* (then still *C. lazera*) under controlled conditions were first made in the second half of the 70's by H. Hogendoorn (1979) in Cameroon, following Pillay's principle to start aquaculture with local species (J. Verreth, pers. com.). He must have come close to domestication in the sense of the present paper, i.e. achievement of at least three consecutive cycles reproduced under controlled conditions. When he went back to the Netherlands to work in the famous Dutch aquaculture research institute at the Agricultural University of Wageningen, he was able to establish an aquaculture population of the species without further supply of wild inputs from Africa. It was here, in Europe, where an industrial production of domesticated *C. gariepinus* started, not in Africa. Marketing in the Netherlands, a country with a great variety of its own fish products from national and adjacent waters, was helped by launching the species as a "boutique" product (Huisman, pers. com.), i.e. directed towards consumers who liked to try something new and fancy (to be compared with the equally clever later introduction into the Dutch market of the Nile perch, *Lates niloticus*, from Lake Victoria in East Africa as "Victoria baars", a product of capture fisheries, not aquaculture).

A number of African countries have tried to make use of Hogendoorn's achievement; however, their success was limited, as can be seen from Fishstat Plus (2006). Between 1976 and 2000, 14 African countries appeared in the FAO statistics with only four countries reaching higher levels. Three of them remained at an intermediate state: Ghana reached 1,510 t in 2001 and 2002, South Africa 1,150 t in 1991, and Mali 300 t from 2002 to 2004. Only Nigeria's production increased beyond that of all other countries, The Netherlands and Hungary included. This was due to the establishment of joint

Table 6. Finfish species, or species groups (nei = not elsewhere included), with a world production of ≥100,000 t for which precise information on domestication was not available

(production, continent and environment data according to Fishstat Plus 2006, names according to Froese & Pauly, FishBase 2006)

Environment:

F	freshwater
B	brackishwater
M	marine

Domestication:

+	probably achieved
-	not achieved
?	no information available

Colour, signature:

red, bold	vertical maximum = species maximum
red, normal	second vertical maximum
underlined	horizontal maximum = regional maximum

No.	Species	World production (t)	Regional Production (,000 t)						Environment (F/B/M)	Domestication (+/−/?)
			Africa	North America	South America	Asia	Europe	Oceania		
	Finfish									
01	Crucian carp *(Carassius carassius)*	1,949,758	-	-	-	**1,949.0**	0.8	-	F	+
02	Freshwater fishes nei *(Osteichthyes)*	1,925,082	1.3	14.8	9.1	1,888.7	**10.2**	**1.0**	F(B)	?
03	Milkfish *(Chanos chanos)*	573,732	-	-	-	573.7	-	<0.1	B(F,M)	?
04	White amur bream *(Parabramis pekinensis)*	516,869	-	-	-	516.9	-	-	F	?
05	Black carp *(Mylopharyngodon piceus)*	296,446	-	-	-	296.4	<0.1	-	F	?
06	Tilapias nei *(Oreochromis (Tilapia) spp.)*	276,100	10.8	**20.9**	**90.0**	154.3	0.2	-	F(B)	?
07	Amur catfish *(Silurus asotus)*	246,857	-	-	-	246.9	-	-	F	?
08	Snakehead *(Channa argus)*	239,056	-	-	-	239.1	-	-	F	?
09	Japanese eel *(Anguilla japonica)*	238,637	-	-	-	238.6	-	-	F(B)	-
10	Marine fishes nei *(Osteichthyes)*	220,506	<0.1	<0.1	-	219.1	1.4	-	M(B,F)	?
11	Japanese seabass *(Lateolabrax japonicus)*	219,341	-	-	-	219.3	-	-	F(M)	?
12	Mandarin fish *(Siniperca chuatsi)*	168,650	-	-	-	168.7	-	-	F	?
13	Japanese amberjack *(Seriola quinqueradiata)*	150,113	-	-	-	150.1	-	-	M	-
14	Flathead grey mullet *(Mugil cephalus)*	142,853	**133.0**	-	-	9.2	0.6	-	B(F,M)	?
15	Swamp eel *(Ophisternon aenigmaticum)*	137,486	-	-	-	137.5	-	-	F	?
16	Torpedo-shaped catf. nei *(Clarias ssp.)*	129,720	14.9	-	-	114.5	0.3	-	F	?
17	Catfish, hybrid *(Clarias gariep. x macroc.)*	102,803	-	-	-	102.8	-	-	F	?
Sums		7,534,009	160.0	35.8	99.0	7,224.8	13.4	1.1		
World and continent totals		28,165,039	551.1	538.3	815.2	24,757.7	1,473.9	28.9		
Above sums in % of totals		26.7	29.0	6.7	12.1	29.2	0.9	3.8		

Table 7. Percentage of domesticated finfish species in relation to world production per species

World production for 2004 and number of aquaculture species according to Fishstat 2006; number of domesticated species according to Table 1 (Part I) of the present paper

World production 2004 (t)	Number of species	Domesticated	Percentage domesticated
<0.5 – 9	24	3(?)[1]	12.5(?)
10 – 99	29	-	-
100 – 999	46	9	19.6
1,000 – 9,999	36	10	27.8
10,000 – 99,999	38	8	21.1
100,000 – 999,999	21	6	28.6
≥1,000,000	8	6	75.0
Total	**202**	**42**	**20.8**

[1] In at least two of these species (sturgeons) domestication is apparently not production-oriented

ventures between the Netherlands and Nigeria (J. Verreth, pers. com.).

Hungary received the first fry (12 individuals of 3-4 g) in 1984 from the Netherlands and 2000 feeding larvae in 1987 from the same European country. Interest in commercial production of the species rose with export outlets first and increasing sales within the country later. The abundant geothermal water resources in Hungary make it possible to produce this species throughout the year. Active marketing and adequate product development also had their share in the success. (All information pertinent to Hungary from L.Váradi, pers. com.) From reliable other personal communications it appears that the establishment of an independent production in Brazil was connected with the success in the Netherlands and Hungary.

The development of *Clarias gariepinus* farming in Europe, Africa and elsewhere in the world is shown in **Tables 10 and 11**. From the above, it is obvious that without continuous controlled reproduction as a prerequisite of domestication, the various transfers could hardly have been successful.

Phases of domestication

Following the terminological definitions used for this paper (see Part I, p. 7), the process of traditional domestication can be divided into three main phases:

- pre-domestication (adaptation to the culture environment and achievement of continuous controlled reproduction);
- “Uncontrolled” and “targeted” domestication (selection for desired characters and, possibly, elimination of unwanted features);
- establishment of pedigrees (genetic stabilisation of strains most suited to meeting future production requirements).

In addition to the terms defined in Part I, there is thus another aspect to be considered: *uncontrolled* as compared to *targeted domestication*. This is what has been seen in terrestrial animal breeding as one of the major consequences of domestication, i.e. the survival of traits which, as a rule, are not – or only rarely – manifested in nature. This has led to a much wider (visible, i.e. phenotypical) variety of morphological and behavioural characters than observed in the ancestral wild forms, e.g. in dogs as compared to wolves, and in domestic pigeon. Man has often stabilised such variations as pedigree races because of the desirability of certain characters.

An attempt to introduce some phasing into the concept of domestication was made by Boguerouk (2005). In the present paper I go into further detail, trying to improve the concept by analysing, deepening and modifying it. There is, however, little use in defining the different phases too rigorously since there are various transitions. Well-defined terms can, nevertheless, be helpful in differentiating among various phenomena.

Pre-domestication

Stress reduction through improved communication

The essential requirement of domestication is continuous controlled reproduction (see Part I). This requirement has to be met in this phase, since otherwise one cannot speak of domestication in the next phase. A major additional consideration accompanying and even ruling the entire domestication process, at least during the pre-domestication phase, should be the reduction of all types of stress hampering or disturbing feeding, maturation, health and/or behaviour.

Among the first reactions of animals to captivity is a strong tendency to flee or escape from the unknown or directly frightening conditions of the new environment. Such reactions can be increased by being touched, grabbed or seized and retained by man. Even minor types of stress can have noticeable effects. Rosenthal (pers. com.) once noted nocturnal peaks in O_2 consumption (indicator of stress) in his experimental recirculation tanks and finally found out that a nosy person had visited the room at night without being authorised to do so!

To reduce the impact of stress resulting from fear, great efforts should be made – not only but mainly in this phase – to communicate with the cultured animals either by intervening into their intra-specific communication or

Table 8. Nile tilapia (*Oreochromis niloticus*), world production and production per continent (t)

F = Freshwater, B = Brackishwater; all data from Fishstat Plus 2006

Continent		1950	1960	1970	1980	1990	2000	2004
Asia,	F	890	5,636	9,464	31,781	197,053	851,994	1,240,309
	B	-	-	-	-	3,761	1,636	3,277
Africa,	F	-	50	344	1,347	6,991	27,048	32,578
	B	700	2,050	2,250	8,100	20,005	138,433	176,879
North America,	F	-	-	-	6	166	10,643	24,559
	B	-	-	-	-	-	-	-
South America,	F	-	-	-	103	2,244	12,999	17,521
	B	-	-	-	-	-	183	183
Europe,	F	-	-	-	-	-	-	355
	B	-	-	-	-	2	-	-
Oceania,	F	-	-	-	-	14	304	83
	B	-	-	-	-	1	<0.5	-
World totals		1,590	7,736	12,058	41,337	230,237	1,043,250	1,495,744

Table 9. Nile tilapia (*Oreochromis niloticus*), countries with an annual production in 2004 of ≥10,000 t

Quantities in 1,000 t; Shadowed: Asian countries; no brakishwater data in countries other than Egypt in Fishstat Plus 2006

Country		1950	1960	1970	1980	1990	2000	2004
Egypt	Brackishwater	0.7	2.1	2.3	8.1	20.0	137.9	176.9
	Freshwater	-	0.1	0.3	0.9	4.9	19.5	22.2
China		0.7	5.0	5.8	9.0	106.1	629.2	897.3
Philippines		-	0.1	1.4	9.4	51.6	76.0	116.1
Thailand		0.1	0.4	1.6	5.3	22.9	82.4	97.6
Indonesia		0.1	0.1	0.1	5.8	12.1	40.8	97.1
Laos		-	-	<0.1	0.2	1.3	18.9	29.9
Costa Rica		-	-	-	-	-	7.7	18.0
Sums		**1.6**	**7.7**	**11.5**	**38.7**	**218.9**	**1,012.4**	**1,455.1**
World totals		1.6	7.7	12.1	41.3	230.2	1,043.3	1,495.7
Sums in % of totals		100	100	95	94	95	97	97.3

by trying to establish some sort of direct communication between the cultured species and the human beings physically involved in the process. It could even be useful to be aware of a more recent discovery in terrestrial animal husbandry, namely that horses seem to be better understood (and available for peak performance?) by people having the capacity of a "horse whisperer". This capacity is based on the knowledge of the specific reaction schemes of an animal, different between a prey, such as a horse, or a big enough predator, such as a tiger - which means knowing, e.g., which type of body language can help reduce fear and flight reaction. This type of knowledge must, of course, be specific to an animal group, or to the position in the food web it normally occupies. Also, it will probably be easier between mammals (man and horse) than across great taxonomic distances like those between man and fish.

The following observation (Bilio, unpublished; evidence: A. Gnes) is interpreted by the author as an intervention into intra-specific communication through pheromones, with the effect of reducing stress. When once a load of new elvers (young eels) were received in a plant in Italy and put into a circular aluminium tank with black plastic lining, the elvers immediately tried hard to escape, using the folds of the lining as channels to get out of the water first and of the tank next. Following a sudden inspiration, the author asked a collaborator to take some buckets of water out of one of the other tanks where the elvers had long since calmed down, and pour it into the tank with the newcomers. The effect was a surprise: the newcomers now remained quietly in their newly arranged tank! Unfortunately, because of time constraints the finding could not be confirmed by duly repeating the trial. If replicable, a clue for avoiding losses or damage caused by transport could be obtained from this observation, namely to put water from the tanks (or ponds) to which they are accustomed into the transport containers, not "clean" new water!

Table 10: North African catfish (*Clarias gariepinus*), annual production per continent

(according to Fishstat Plus 2006 until 2004; and according to Fishstat Plus 2007 for 2005)

Quantities in t; South America: Brazil only; no production in North America and Oceania

Continent	2000	2001	2002	2003	2004	2005
Europe	3,000	2,695	3,734	4,639	5,331	5,963
Africa	1,416	3,984	5,056	4,982	16,762	21,317
Asia	414	443	700	850	777	1,242
South America	-	-	-	-	245	224
World totals	4,830	7,122	9,490	10,471	23,115	28,746

Table 11. North African catfish (*Clarias gariepinus*), annual production per country for countries with an annual production of ≥1000 in 2005

(according to Fishstat Plus 2006 until 2004 and according to Fishstat Plus 2007 for 2005)

Quantities in t

Country	Since	2000	2001	2002	2003	2004	2005
Netherlands	1984 (20 t)[1]	2,600	1,456	2,606	3,200	3,600	4,200
Hungary	1998 (200 t)[2]	<300[3]	889	878	986	1,228	1,412
Nigeria	1992 (3,850 t)	-[4]	1,906	2,874	4,024	15,758	20,413
Syria	1996 (65 t)[5]	381	418	670	815	747	1,208
Sums		<3,281	4,669	7,028	9,025	21,333	27,233
In % of world totals (see Table 10)		<67.9	65.6	74.1	86.2	92.3	94.7

[1] Steady increase from 1984 to 2000 (only exception: from 900 t/1993 to 710 t/1994, 1995: 1019 t)

[2] Váradi, pers. com.

[3] Váradi, pers. com.: "Most probably it was below 300 tons"

[4] No production before 1992, no data from 1996 to 2000 (both years included)

[5] No production before 1996 (until 2000 <100 t)

Communication of air-breathing humans with aquatic animals is obviously more difficult than with land animals because of the difference in the medium reducing the opportunities to touch, hear and see, as well as because of the impediment or distortion of sensual perception by the water surface. However, the training successes with aquatic mammals (dolphins, beluga whales) show that a lot is possible, especially when the attracting (and rewarding) effect of food administration is used.

In my correspondence, several colleagues mentioned or drew my attention to behavioural changes during what I suggest to call the "pre-domestication" phase ("The behavior changed quite dramatically, particularly feeding and reaction to man", Doroshov, pers. com., in reference to white sturgeon; and "some times one particular species may not be 'fully domesticate' as these traits (behaviour, performance, and more specifically stressability) are not stabilized", Ll. Tort, pers. com.). Getting used not only to a new environment but also to the presence of human beings close to the culture tank or farm pond, can reduce and finally suppress the flight or hiding instinct thus eliminating an important source of stress, which in turn may favour feeding and growth, mating behaviour and reproduction, health and disease resistance. However, it remains a question whether such adaptation is a result of learning, or of unintentional selection for genetically fixed traits (see the additional considerations on terminology at the beginning of the DISCUSSION chapter).

Adaptation to the culture environment

The transfer of animals from their natural to the culture environment has a number of biological, physical and chemical consequences. Territoriality implies aggressive defence of a scarce resource. Such aggression, with its undesirable consequences, can be minimised by identifying the critical resource (food, shelter) and providing it adequately. When the natural territory of a species is small enough, it can be offered even in a rather small aquarium. Space limitation can be frightening but for some species be overcome, e.g. for small pelagics by putting them in a ring tank thus simulating an unlimited swimming space. The photoperiod can be manipulated at will. Water quality requirements, such as a certain temperature regime, optimal oxygen supply, suitable salinity, can be fulfilled. Shelter can be offered, as well as an adequate spawning substrate for certain species (carp). More specific conditions like smell or taste characterising rivers, lakes or sea areas, are more difficult to provide, not least because they are mostly not even known. Forced adaptation or acclimation to inadequate environmental conditions means stress and should be avoided as far as possible. Exposure to inadequate culture conditions may lead to the elimination of the "weaker" individuals of a group thus resulting in "unintentional" domestication (Dunham et al. 2001; see Part I, p. 7).

Biotic conditions, such as food availability, preferred population density and sufficient mating partners, can also be fulfilled, although the fulfilment of the latter two is not always in the economic interest of the farmer. Natural physiological rhythms can be facilitated, e.g. feeding rhythms through adaptive feeding systems avoiding feed wastage (Blyth 1992). While provision of enough food of appropriate quality is an absolute necessity for obtaining a satisfactory harvest, a very low population density requires a lot of costly space, and offering a number of mating partners similar to the ratio in the wild can also turn out to be too expensive.

Achievement of continuous controlled reproduction

The survival and growth requirements satisfied by the culture environment often do not suffice for reproduction. To induce gonad development and maturation, more specific prerequisites must be fulfilled. Here, only one example will be referred to, known for a long time from botany where it is called "vernalisation" (exposure to low temperatures to ensure subsequent flowering). In sturgeon culture, a similar phenomenon has been called "artificial wintering" by M. Chebanov (pers. com.).

An acclimation to lower temperatures could be seen in the context of changes from all year round reproduction in the tropics towards seasonal reproduction in temperate climates (Nile tilapia, Common carp). In sturgeons, being distributed in temperate (and subtropical) zones, reproducing seasonally is not only an opportunity but a requirement. According to Chebanov (pers. com.), the need for artificial wintering pertains to all spring-spawners. Some females could reach maturity without artificial wintering but, as a rule, with poor progeny quality and lower fecundity. In contrast to autumn-spawners, it could be experimentally proven that the photoperiod did not play any considerable role.

Moreover, not only temperature is involved in the phenomenon but also interruption of feeding for 1-2 months (provided that gonad maturation has reached stage IV). Otherwise, a considerable part of the individuals would not reach maturity and have fatty gonads, or female maturity could partly be delayed and become asynchronous, thus compromising spawning results by stripping. (All this information on sturgeons was kindly provided by M. Chebanov through personal correspondence.)

Continuous controlled reproduction ('controlled reproduction' understood as one composed term, further defined by the adjective 'continuous') can only be achieved when the endocrinological processes conditioning the sequence of phases in gonad maturation are allowed to occur. The types of difficulties to be overcome before reaching the domestication phase proper are very diverse. It is true that a lot has been achieved once at least one life cycle under controlled conditions could be closed. However, just one cycle does not mean that a success in breeding the next generation in captivity is also guaranteed.

The end of the pre-domestication phase would be marked by the achievement of continuous controlled reproduction and thus the availability of the captive population for selection and genetic improvement, enhanced by avoiding any stressful situation as much as possible.

Uncontrolled and targeted domestication

True domestication means genetic improvement through selection for desired characters, possibly the elimination of unwanted features, and certainly the development of strains carrying the desired traits. In some cases it has become necessary, after an initial success with continuous controlled reproduction, to freshen an impoverished genetic spectrum by introducing further broodstock from the wild. It appears adequate to include such measures in this second phase of the domestication process since the need for them cannot easily be detected earlier.

Nevertheless, recourse to wild broodstock is sometimes already made during the pre-domestication phase, when no clarity exists as to the reasons for failures in controlled reproduction, in particular in reaching gonad maturation. Such recourse is, obviously, only possible as long as wild populations of the species exist or are accessible. In Australia (according to G. Mair, pers. com.), access to wild populations of Silver perch is prohibited in connection with conservation regulations, thus favouring and accelerating the domestication process.

> True domestication has two aspects: the uncontrolled and the targeted one. When it all started, long ago in our prehistoric past, on land and with a wild man in a wild nature, domestication was hardly controlled. In recent times, with science and an enormously increased knowledge about how to manipulate nature and its living terrestrial and aquatic components, nearly all domestication is objective-oriented, thus targeted. Much domestication on land just happened, before it became understood, whereas in the water most of it was from the beginning a deliberate undertaking.

Consequently, domestication of terrestrial animals was for thousands of years "uncontrolled", leading to a great variety of morphological and behavioural characters, partly convenient for man, partly not. Later and especially with the enormous upswing of aquaculture in the last century, the entire new development had immediate objectives, to be achieved as quickly as possible, without losses due to uncontrolled processes – domestication in the aquatic environment was "targeted". The overriding interest was in providing food for the poor, and profit and "luxury" meals for the well-off segments of the society.

Along this line, the culture efforts were centred on an increase of biomass, which means on growth, with health care as an enabling condition and reproduction as a basic prerequisite of continuity. In principle, this means improving feed composition and food acceptance and conversion, saving energy by avoiding behavioural (and metabolic) expenses for escape from predators, competition for food and shelter, search for a mate and mating behaviour, counteracting disease and parasites - through offering culture conditions appropriate to achieve this. Growth can also be increased by avoiding unfavourable seasonal conditions, such as low winter temperatures. An overview of pertinent aspects was given by Thorpe (2004). During the domestication phase proper, it is desirable to find out how much of the reaction to the new conditions (better food conversion, reduced fear from predators, greater resistance to diseases and parasites, acclimation to non-seasonal growth conditions) can be genetically stabilised by selection. This, again, would be targeted domestication

However, there is at least one area in aquaculture, where uncontrolled domestication has occurred: in the farming of Common carp. From its long farming history, Common carp appears predestined for uncontrolled domestication. However, even if uncontrolled, the procedure could to a certain degree be a deliberate one when small-scale farmers, far from public control and just trying out what would happen if they did this or that, obtain haphazard results, sometimes useful, sometimes not.

The process is also targeted when by crossing different strains, or even species, a better use of the various possibilities of improvement inherent in the genetic spectrum is attempted, not least the exploitation of the heterosis effect. It must not be forgotten, however, that even the genetic spectrum, composed not only of visible and non-visible features, but also of expressed and non-expressed characters, is limited. These limits are overstepped only by mutations, which are not a quite frequent phenomenon. This is one of the determinant points where genetic engineering and the entire complex of “biotechnological genetic improvement” comes into play.

With the true traditional domestication process going on, a certain point will be reached where it becomes desirable to keep track of the achievements, either at the level of public authority when financial support is at stake or within private enterprise when the success of the undertaking must be economically streamlined in order to avoid wastage of time and money. These are among the major reasons why pedigrees are being established for more and more species.

Implications of pedigree establishment

Further above species and countries have been considered about which I was provided with pertinent information. The most important prerequisite for recognising a new strain is the achievement of genetic stability and homogeneity of its distinctive features. In the following the means will be dealt with by which such stability and homogeneity is proven, certified and maintained in countries where pedigree documentation is in an advanced state.

In the Russian Federation, pedigree establishment is ruled by legislation, on the basis of which patents can be issued. A set of tests is applied under the authority of the Federal Centre of Selection and Genetics for Aquaculture. A breed is considered homogeneous and stable if the number of animals having atypical qualities, does not amount to more than 4% of the number of individuals examined and, further, if the coefficient of variation of the quantitative characteristics of the examined breed is not more than 1.5 times higher than that of the reference breed (Chebanov, pers. com.).

In Hungary, the responsibility for pedigree establishment is with the National Institute for Agricultural Quality Control. Tests, carried out according to a Code for Carp Performance Tests, include an examination of the external appearance (body shape, profile index, scale characteristics, colour, etc.) and also investigations on the productive performance (survival, growth, feed conversion, dressing yield, fat content). They are carried out on farms and in hatcheries. Environmental and biodiversity protection, animal health and welfare, as well as conformity with international regulations, are considered important issues. (Information obtained personally from L. Váradi.)

In the Czech Republic (M. Flajshans, pers. com.), since 2000 a National Animal Breeding Act including fish, is in force covering broodstock and breeding, gametes and cryopreservation, not only for aquaculture but also for the conservation of genetic resources. Performance testing of productive strains of Common carp, Tench and hybrids as well as of Rainbow trout is conducted similarly as described for Hungary.

In Finland (T. Kiuru, pers. com.), the competent authority is the Finnish Game and Fisheries Research Institute with its Aquaculture Unit. Decision-making in private aquaculture appears to be with the entrepeneurs.

In Germany (BMELV 2006), the documentation of breeds of the two main aquaculture species Rainbow trout and Common carp is poor, but the awareness of the need for pedigree establishment is increasing. There is as yet no national authority in charge of pertinent undertakings, but international collaboration at the EU level is seen as of great importance.

While in “eastern” countries a tendency could be seen to have a state register or at least some central authority responsible for the establishment of pedigrees, in “western” countries a company-based more competition-oriented and thus secretive attitude towards this issue seems to prevail.

Pedigree establishment has two aspects: the producer-oriented and the consumer-oriented. While the producer’s advantages lie in the reliability of the productive properties of a strain, for the consumer it is desirable to distinguish strains according to their quality as a consumption item. For the time being, the producer aspect seems still to prevail.

Pedigree criteria include externally visible features, such as form and colour (see, e.g., Hungary above), an aspect which facilitates the distinction when a producer wants to buy reproductive material (breeders). The consumer, on the other hand, can tell by eye which is his preferred strain from the palatability point of view. In both cases a strong correlation between visible and hidden features is of considerable advantage. Pedigrees may also be useful for pet races (Koi carps) where amenity (form and colour) is the value that counts.

It would be understandable, therefore, if from the producer's point of view, pedigrees were considered most advantageous at the beginning of the domestication process, since they allow to keep track of the success of the selective measures thus showing ways to rationalise production, whereas later, when the sale of the product comes to the fore, the external appearance would gain attention.

Another reason for the producer to keep pedigree records is the need to avoid inbreeding in family-based breeding programmes (T. Gjedrem, pers. com.). Family-based is a selected line derived and maintained by single-pair matings thus increasing the probability of expressing the desired trait, but also of reducing the gene pool.

Pedigrees, in particular if established nationwide, offer useful opportunities for standardisation and can rationalise the exchange of reproductive material (breeders, eggs, larvae and fingerlings). Moreover, it provides an appropriate basis for granting financial support and controlling its utilisation.

Biotechnological genetic improvement (implications)

A lot of research is going on concerning the methods and techniques of biotechnological genetic improvement. These investigations have already enormously increased our knowledge of the structures and processes involved in inheritence, and their results have become indispensable prerequisites of designing targeted domestication projects in modern aquaculture. However, the relevance of such efforts for aquaculture must be measured according to criteria proving a successful application of the new findings in the production process.

Two essential indicators thereof are the following:

- Either (1) the new character/trait/feature/quality is hereditary, i.e. it is possible to pass it on to further generations, without disturbing other genetically determined traits or having other side effects;
- or (2) the procedure to achieve the trait is replicable and, again, free of side effects.

The final benefit of such genetic improvement must be an advantage as compared with traditional domestication obtained through selection over generations. This can be directly achieved or in combination with traditional procedures. It can consist in a short-cut of the genetic processes, a simplification, or a cost reduction. Among the effects contributing to cost reduction could also be the better understanding of traditional procedures due to genome- and linkage-mapping and the use of genetic markers such as micro-satellites.

True achievements of biotechnological genetic improvement, beyond what could be called improvement of understanding genetic structures and processes, must be judged according to the same criteria as the results of pedigree establishment. Similar to pedigree establishment, there is a need for testing the stability and homogeneity of biotechnologically created new strains. Criteria could be (1) a minimum number of generations through which a new trait remains unchanged or (2) a minimum number of replicates leading to the same result. And, of course, there must be sufficient guard against quality-, health- and environment-related prejudice.

According to L. Colombo (pers. com. of 19 January 2007), "the gene transfer technique is now well consolidated and along the 22 years of its use has been greatly refined to obtain different traits of interest, with the predominance of growth hormone (GH)-gene transfer for growth enhancement, and, to a minor extent, gene transfer for disease resistance and cold tolerance. At least, 35 teleost species, mostly of aquacultural interest, have been successfully engineered to promote growth." Colombo lists 28 species as examples, of which the following are of special interest for the present paper (considered in Table 5):

Rainbow trout (*Oncorhynchus mykiss*)
Coho salmon (*O. kisutch*)
Atlantic salmon (*Salmo salar*)
Brown trout (*S. trutta*)
North African catfish (*Clarias gariepinus*)
Channel catfish (*Ictalurus punctatus*)
Common carp (*Cyprinus carpio*)
Nile tilapia (*Oreochromis niloticus*)
Gilthead seabream (*Sparus auratus*)

The Blackhead bream (*Acanthopagrus schlegelii*) is contained in Table 2 (China) under the vernacular name "Black porgy".

"The data clearly show that the potential for growth improvement of the transgenic technology vastly exceeds the most optimistic anticipation of genetic gain in any classical genetic amelioration program based on selective breeding, even if prolonged for decades." (L. Colombo, pers. com.)

Comments on the foregoing citations and a wealth of information and arguments communicated and discussed personally by L. Colombo will be made in Part III of the present paper, in particular under the subheading "Domesticated, gene technologically improved and wild populations".

DISCUSSION

An adequate discussion of the prospects and implications of domestication in aquaculture can gain from putting it into a wider context including capture fisheries and the entire aquatic environment with the full range of its organisms. Dangers and opportunities to be expected from global change are also to be taken into consideration.

Terminology (additional considerations)

In spite of the rather extensive description of the terminological disposition of the present paper in Part I, it appears necessary to add some further clarification and also additional aspects. As was to be expected, the separation between traditional domestication and biotechnological genetic improvement has led to some questioning. However, there was less discussion concerning the separation as such than regarding the term "biotechnological genetic improvement" for which "genetic engineering" was suggested as an alternative. Since the acceptance of this suggestion would have made it necessary to distinguish between genetic engineering *s.str.* and *s.l.*, the suggestion was not followed.

An additional word should be said about certain other terms sometimes confused with domestication, even in popular dictionaries. First there is *taming* (to get the animal used to man as a partner) which is a useful and often unconsciously or unintentionally fulfilled condition favouring domestication (see the pre-domestication phase further above in the RESULTs chapter), overlapping with the French "*dompte*r" (at the extreme: to subdue with force). The German word "*dressieren*" (English: to train, to break in; French: dresser) also belongs to this context (see the trained dolphins further above). As with taming, this term should rather be seen as a pre-domestication effect. As an example, Japanese colleagues were able to attract schools of young red seabream (*Pagrus major*) to feeding places in an open natural environment by music, thus obtaining a herding effect keeping the fish within a certain area where fishing was forbidden (Rosenthal, pers. com.). The distinctive feature would be the lack of genetic fixing of such learning from experience, which otherwise would mean inheritance of acquired characteristics.

The choice of three full cycles of continuous controlled reproduction as a borderline between pre-domestication and true domestication is an arbitrary criterion. It should only be applied if no clear sign of a successful selection process has been reported or noted which, however, is rather frequently the case. In individual cases rather more than three cycles could be necessary to achieve real domestication, i.e. a strain with genetically fixed new traits. One could say that only after proven continuous controlled reproducibility the lane is free for selection and thus domestication.

Selection without having first achieved *continuous* controlled reproduction is a contradiction in itself. How can selection for a certain trait be successful as long as insurmountable difficulties are still encountered when trying to reproduce the offspring, too, under controlled conditions (and the process has to be continuously repeated with wild-caught breeders)? It is here where a lot of misunderstandings have been created and wrong conclusions are drawn. Calling the achievement of just one controlled reproduction of wild-caught broodstock "domestication" means jumping to conclusions. In this context it is irrelevant by which type of "artificial" induction the progress was achieved. The inheritance of one or more traits through generations must be proven before reproduction under controlled conditions can be considered "domestication".

Being aware of the above logic, it can hardly be considered appropriate when a renowned scientific journal publishes a paper in which the authors (Duarte et al. 2007) claim that "About 430 (97%) of the aquatic species presently in culture (table) have been domesticated since the start of the 20th century, and an estimated 106 aquatic species have been domesticated over the past decade (figure)." The only definition of domestication given within the article is the following: "Domestication of wild species to produce food means that the breeding, care and feeding of organisms are controlled by humans". As could be expected, the eye-catching contents of the article have been readily taken over by journalists, even at EC level (European Commission 2007).

Recent experiments with a land animal, the silver fox (a farm variant of the red fox, *Vulpes vulpes*), carried out since the 1960s (Trut et al. 2004, Trut 1999), were conducted in order to obtain hints on the domestication of the dog and domestication of land animals more in general. Apart from fundamental considerations regarding the evolution of neoteny (maintenance of juvenile characteristics until sexual maturation), I would like to refer to what is called "taming" in this context. "The prerequisite for setting up a selection experiment was the genetic character of polymorphism for the expression of defensive reactions to humans, which had been found in farm populations…" From the start, animals showing a fearful behaviour were sorted out with the effect that "In generation 4 of selection, the first pups appeared that did not form aggressive-fearful reactions to humans as a result of positive contacts with them."

It thus appears that fearful behaviour is a hereditary trait that can be eliminated through selection. However, what in my opinion is misleading, is calling it a "response to selection for *tameness*". Taming appears to be more a learning (see above) than a selection process and using the term "taming" for what in essence appears to be a result of selection for the lack of fearful behaviour, is confusing and should be avoided. What results as a consequence of the elimination of fearful behaviour should rather be seen as "affectionate behaviour" towards man ("freed" from flight instinct and aggressiveness), similar to what is shown by pups towards the mother fox, perhaps triggered by corresponding behaviour of the mother (and perhaps unconsciously imitated by the experimenter; see the remark about the "horse whisperer" further above).

Climate change, aquaculture and domestication

Climate change, and in particular global warming, can be expected to affect the further development of fisheries and aquaculture through changes in air and water temperature, salinity, water availability, water flow regimes and water levels due to strong rain falls or drought, sedimentation and synergies between these factors. A direct and general impact will certainly be exerted by increasing air and water temperatures. Other effects will be of a more local nature, depending on the orology (distribution of mountainous areas), the distribution of rainfall, the configuration of the coastline and the impact of large-scale human interventions, such as the construction of dams and canals. Not to forget the impact of an increasing number of hurricanes and gales as a consequence of climate change.

The most immediate influence on both fisheries and aquaculture through temperature changes could result in shifting areas of distribution. However, the more aquaculture is confined to water bodies without contact to open waters, the more it could, at least theoretically, be managed independently – though probably at higher costs, e.g. for water cooling. A gradient could be imagined between indoor tank culture, outdoor pond culture and cage culture, the latter being most directly subjected to climate change.

Domestication potentially offers a way out of the difficulties. While hitherto one of the objectives concerning temperature adaptation was cold resistance in warm-water species, it may soon be the opposite which must be aimed at. Will turbot farming remain successful in southern France, Spain and Portugal? How will the farming of distinctively cold-water species, such as the salmonids (Atlantic salmon and rainbow trout) and gadids (cod) be influenced? What measures should be taken in order to lead domestication towards anticipating the consequences of climate change? Could a more general strategy be elaborated? At least theoretically, a partial solution could be to choose wild broodstock from the warm water margins of their distribution areas and try to genetically increase their resistance to or favour a preference for higher temperatures.

A particularly interesting point was made by J. Thorpe (pers. com.) hinting at the discovery of a much wider thermal adaptation potential of Atlantic salmon than hitherto assumed. In coastal marine waters of Tasmania (Australia) industrial cage culture of this species is flourishing at temperatures of about 20 °C; whereas in its North Atlantic home area the temperatures considered optimal for growth are 8-10 °C! Thorpe's point is ”that there are evidently physiological extremes within the normal range of natural populations which are worth looking for, as starting points for broodfish to found aquaculture lines where physical conditions for culture are apparently less than favourable”.

While domestication and the establishment of adequate pedigree populations could probably help intensive aquaculture, certain types of extensive aquaculture (e.g., the Italian "vallicoltura") could suffer since undersized individuals of certain species might not leave the lagoon ponds ("valli") before maturation and reproduction which they do now in order to escape low winter temperatures. They would then be less subjected to control measures at the catching installations ("lavorieri"), where in autumn undersized fish are hitherto diverted to wintering channels from which they are released to the lagoon-ponds in spring to gain further weight (instead of being allowed to return to the sea and re-immigrate next spring). Perhaps something in this respect could be learned from the situation in Mediterranean areas south of the Northern Adriatic Sea, where the highly sophisticated "vallicoltura" system of the North Adriatic lagoons was of a less complex design.

The following types of consequences should be considered and possible solutions be contemplated and discussed:

- The temperature range of a species so far thought to be optimal, might no longer allow farming in certain countries, regions, or zones without successful domestication efforts directed towards resistance to (and possibly preference for) higher temperatures.

- Different species could be hit to a different degree and the preferable species composition of polyculture systems could change; problems could arise from food web changes in extensive cultures.

- The distribution of cage culture along north-south coasts (Norway), could be shifted from south to north, while pond farming could be taken to higher altitudes. (However, what would happen if scenarios predicting a slackening or even failure of the Gulf Stream were to come true?) The six fish farming zones distinguished by Boguerouk (2005, Fig. 1) in the Russian Federation could also be shifted northwards, maintaining or changing their species composition.

- Available warm water sources (in particular from deep wells) could become too cold and heating could be necessary in areas where relatively high water temperatures were hitherto appropriate.

- Areas of coastal pond culture (shrimps, finfish) at present close to sea level, could be partially or entirely lost (Bangladesh).

- Offshore aquaculture could be threatened by an increasing number of hurricanes and gales, increasing on the one hand the need for further improved anchorage and on the other hand the risk of an intermingling of already well domesticated fish with wild populations as a consequence of cage breaks and escape of substantial numbers of fish.

- The threat of more frequent and perhaps stronger hurricanes and gales could lead to a tendency to move cage culture systems from positions in seaward areas of bays and fiords to better protected landward areas with a higher likelihood of water pollution and contamination.

Concerning particular species, the originally tropical freshwater species *Oreochromis niloticus* (Nile tilapia) could in the future become a major outdoor farming subject in southern and central Europe, having been easy to domesticate due to its readiness to spawn spontaneously under continuous controlled conditions. Going to the extreme, pond culture of common carp (*Cyprinus carpio*) might become feasible and profitable in northern countries, such as Sweden and Finland.

Domestication could become a general tool to render species more independent from direct climatic influences and to stimulate the mass production of well-known and accepted species, offsetting others that might be lost. Such compensation might also become necessary as a consequence of losses of aquaculture opportunities as such, owing to a decrease in water availability or even the inundation of entire districts or regions due to sea-level rise.

PART III

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Controlled reproduction and domestication in aquaculture

- the current state of the art. Part III

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Controlled reproduction and domestication in aquaculture

THE CURRENT STATE OF THE ART PART III[1]

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DISCUSSION

(continuation of Part II, *aquaculture europe* 32 (3), September 2007)

Domesticated and wild populations

There is a series of indirect and direct relationships between domesticated and wild populations that should be kept in view:

- Domestication and intensively exploited wild populations
- Domestication and stock enhancement and replenishment
- Intermingling of domesticated individuals and wild populations
- Interactions between biotechnologically improved individuals and wild populations
- Domestication and conservation of genetic resources
- Domestication and saving species from extinction
- Domestication and capture-based aquaculture

While the first and the last topic are not directly related to domestication, the third and the fourth show how in the remaining three topics domestication effects as well as those of bio-genetically improved organisms could affect wild populations. However, traditional domestication (selective breeding) and biotechnological genetic improvement could also help avoid negative consequences of interaction. They should, therefore, be given high priority ranking not only in research and technological development, but also in conceiving strategies for the future of aquaculture and pertinent public and private funding.

Domestication and intensively exploited wild populations

The great concern about the stagnation and even decline of many capture fisheries has led to much discussion about the role of aquaculture in alleviating the catching pressure on wild fish populations. The demand for the extremely valuable protein source "fish" is continuously increasing as a consequence of the alarming growth of the world population of man and the ongoing accumulation of wealth in the industrialised countries. Can aquaculture make up for the losses due to overexploitation of the wild resources? What is the role of domestication in this context? How many choices to overcome the bottlenecks do we still have? And where are the limitations?

It is common practice to lump capture and aquaculture production together in order to show an overall increase in the availability of fish products in general. There seems to be little realistic prospect to improve the production of wild fish populations through better management, since many protection measures meet either with an extreme poverty of growing human populations, forced to exploit their natural resources right to the bitter end, or with people that just don't want to listen to reason. Moreover, it now seems that at the present state of exploitation of wild populations aquaculture can in certain cases produce quantities considerably beyond the level that capture fisheries can ever reach – provided that the increases are based on domestication, i.e. basically on continuous controlled reproduction allowing selection and the sustainability of further breeding.

ON THE COVER

Floating cages in the North Aegean Sea (coast of Turkey) where the North Atlantic bluefin tuna is farmed. The animals are caught wild in an advanced stage of life and fattened in the cages only for the last few months before being slaughtered and shipped to Japan by transport vessels ("reefers") like the one waiting in the background behind the cages. Courtesy: Dr. Sergi Tudela/WWF.
Bottom left: Northern bluefin tuna (*Thunnus thynnus*) caught off Tripoli, Lebanon.
Courtesy: Michel Bariche, American University of Beirut, FishBase collaborator.
Bottom right (under water): Southern bluefin tuna (*Thunnus maccoyii*) in a fish farm off Port Lincoln, Australia.
Courtesy: Kerstin Fritsches, FishBase collaborator.

Correction of and supplements to Part II

By an oversight, Black carp (*Myliopharyngodon piceus*) was included in Table 6, (p. 15) in spite of the fact that it is contained in a "List of domesticated fish – aquaculture objects, included in the State Register of Russia" (Bogueroukk 2005, Table 2, p. 30). This oversight has minor consequences for Tables 5, 6 and 7 of Part II.

Unfortunately, in spite of repeated attempts, it was not possible to obtain data on freshwater species from China in order to complement Table 2 (Part II, p. 7-8).

[1] *I dedicate this third part of the paper to my Italian friend Giancarlo Cittolin (Padova, Italy) who has helped and encouraged me in many respects.*

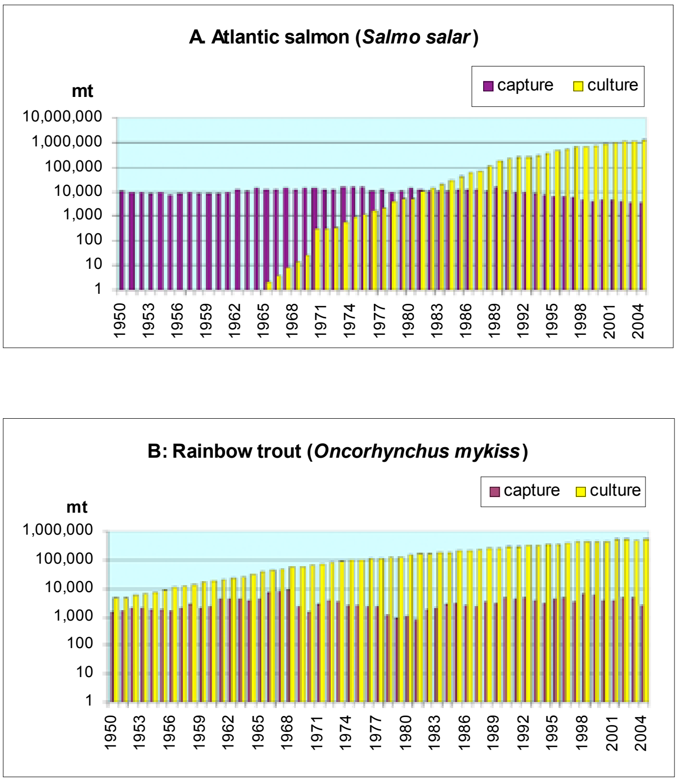

Fig. 1. Comparison between capture and culture fisheries (world production). The two domesticated salmonids with the highest aquaculture production worldwide. (Data from Fishstat 2006; note the logarithmic scale.)

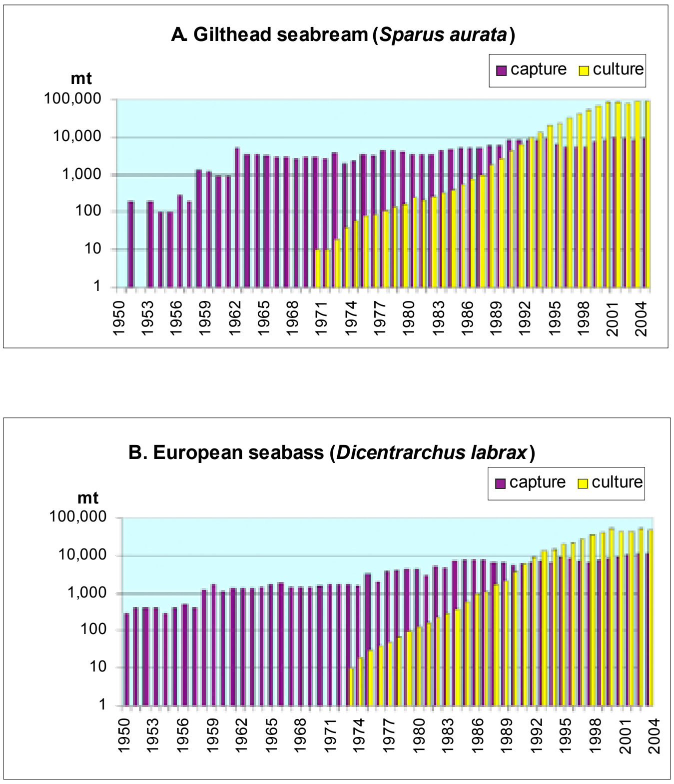

Fig. 2. Comparison between capture and culture fisheries (world production). Two newly domesticated European finfish species. (Data from Fishstat 2006; both at logarithmic scale!)

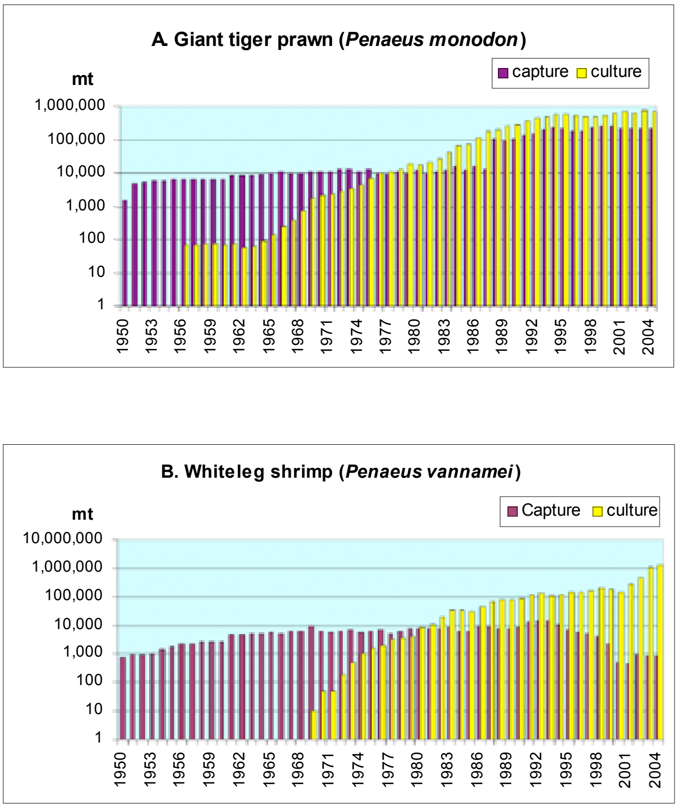

Fig. 3. Comparison between capture and culture fisheries (world production). The two domesticated penaeid shrimps with the highest aquaculture production. (Data from Fishstat 2006; logarithmic scale!)

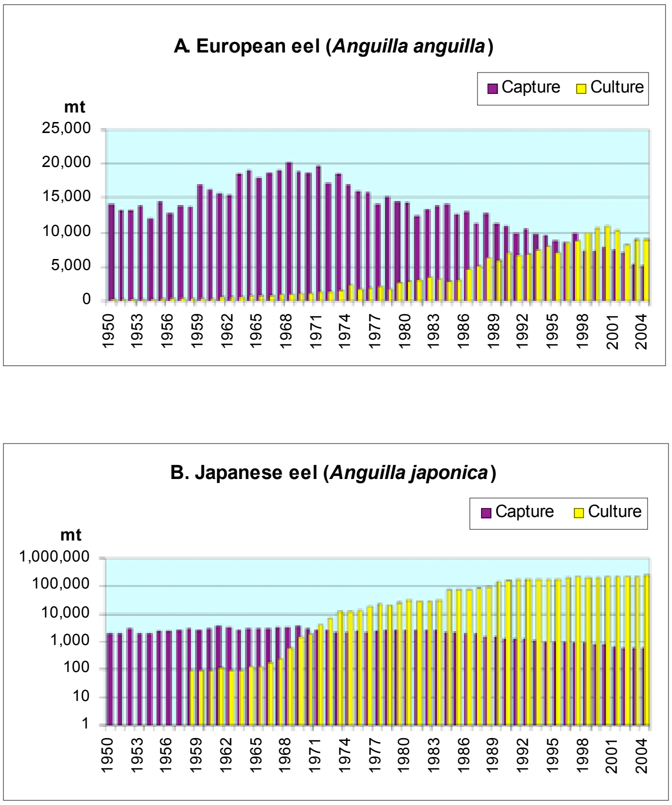

Fig. 4. Comparison between capture and culture fisheries (world production). The two eels of major importance. (Data from Fishstat 2006; only Japanese eel at logarithmic scale!)

Extreme examples of an aquaculture production exceeding the production of the capture fisheries are Atlantic salmon and rainbow trout, where aquaculture production surpasses the capture landings by orders of magnitude (Fig. 1). It should be realised, that both species are domesticated (Part I, Table 1.A, p. 9), rainbow trout for long and Atlantic salmon for a few decades. While wild Atlantic salmon is represented by a still considerable population in its natural distribution area on the coasts and inland waters of Europe and the American side of the North Atlantic, rainbow trout has even been widely transferred to natural waters outside its continent of origin (North America; see also Part II, Table 5, p. 12).

The *capture* production of Rainbow trout underwent considerable changes concerning the share of single countries. In 1950 there were only three players on the scene: Japan (890 t), USA (478 t), and Austria (150 t); in 2004, after coming in and dropping out of several countries, 10 countries were left with Finland at the top (653 t), followed by Peru (456 t), while Japan (347) and USA (153) had decreased considerably. Capture fisheries of Atlantic salmon were reported only for European countries in 1950, with a maximum for Sweden (678 t) followed by Finland (539 t). In 2004, the *aquaculture* production of rainbow trout reached 124,180 t in Chile and 63,177 t in Norway, whereas for Atlantic salmon in the same year the sequence was opposite: Norway 565,902 t; Chile 346,956 t.

Extending the comparison to two newly domesticated species, gilthead seabream and European seabass (Fig. 2; see also Part I, Table 1.B, p. 10), we see again a considerable increase of the aquaculture production beyond that of the still slightly increasing capture fisheries, a development reached in about three decades.

Fig. 3 allows the same comparison within two highly demanded and meanwhile domesticated penaeid shrimps, giant tiger prawn and whiteleg shrimp (Part I, Table 1.E, p. 14). In both species the capture landings are exceeded by the aquaculture production since 1980. However, while for the giant tiger prawn a considerable increase in the capture fisheries is still noticeable from 1988 onward following the aquaculture production, the whiteleg shrimp landings cannot keep step and decrease considerably from 1994 onward. Catches of the whiteleg shrimp are landed by two Pacific Latin American countries only, Ecuador and El Salvador, whereas the landings of the giant tiger prawn are shared by eight South and Southeast Asian and Oceanic countries.

The surprising upswing of the capture landings of the Giant tiger prawn in 1988 is due to India, that seems to have exploited its resources immediately at a very high level (89,382 t), reaching 223,703 t in 1999 and dominating the scene until 2004, though at a somewhat lower level.

While the two penaeids selected for the comparison make up only 6 % of the capture production of all shrimp- and prawn-like species, their share in the entire aquaculture production of the same group amounts to 85 %!

Two species still far from being domesticated are the European and the Japanese eel (see also Part I, p. 6). Comparing capture and culture production of these species, the result (Fig. 4) is different from the six afore-mentioned species. The capture landings have decreased in both since the end of the sixties, while their aquaculture production has increased, even beyond the capture landings. In the European eel, the decrease of the landings is dramatic and the aquaculture production has never exceeded the peak of the capture landings, which was reached at the end of the sixties. Since the year 2000 even the aquaculture production is decreasing.

For the Japanese eel the picture changes. The aquaculture production is by far exceeding the capture landings and is still maintaining its level. However, two factors must be taken into consideration: Japan's eel production from culture has at least temporarily in part been based on glass eels from Europe (*Anguilla anguilla*) yielding about 5,000 t when I visited Japan in 1978 (information from Japanese sources). Attempts were even made to obtain seed (*Anguilla rostrata*) from the USA. Moreover, eel production in Japan was based exclusively on glass eels obtaining a very high survival rate due to the great pains taken by the individual farmers over raising them, whereas in Europe (Italy) at least initially mostly elvers were used and much less care was applied to obtain high survival rates.

Aquaculture can thus, indeed, make up for losses in capture landings. Domestication appears as an important prerequisite for mass production, rendering the culture increasingly independent from wild populations (see Part II; p. 11, 14 and 16 and Tables 5 and 7). Regarding the aquaculture production of the six species of Fig 1-3, only a slight levelling off can be noticed in some, but no clear signs of market saturation (see also the section on *Domestication and value development* further below). Concerning the eels, the future appears rather gloomy. Capture and culture production of the European eel are in crisis, while in the far east the landings decreased and aquaculture production increased rather slightly in the last decade before 2004. Only the achievement of controlled reproduction and domestication could help, if it is not too late yet.

From the fact that aquaculture has the potential to achieve enormous production levels for certain species, several questions arise: (1) Is it necessary to realise such production for each species that is already suffering from or will soon be afflicted by overexploitation? (2) How many and which species are necessary to satisfy man's needs, those of the poor as well as those of the rich segments of the population? Where are the limits of aquaculture production as far as feedstuffs, water availability, space, markets, and its impact on wild populations are concerned? And what is the role that domestication could, or even should, play in this overall situation? These problems will be dealt with in the strategy subchapter to be included in Part IV of the present paper.

Domestication and stock enhancement and replenishment

In a previous paper (Bilio 2002, following Stickney 1994), it was pointed out why the genetic production requirements for direct human consumption on the one hand and stocking of open waters on the other hand are different and that such differing objectives must be taken into consideration right from the beginning of a controlled reproduction process. For the stocking of open inland waters (as well as for sea ranching) the seedfish should ideally be genetically unchanged as compared with wild populations, whereas consumption-oriented culture must select for improved survival and growth, better disease and parasite resistance, etc. It is advisable, therefore, to keep broodstock and hatcheries for the two purposes isolated from each other and avoid particularly the stocking of open waters with domesticated organisms.

Stocking of open waters can follow different objectives. If "enhancement" is intended, the objective is a production increase from the utilisation of wild populations through what has formerly been called "culture-based (capture) fisheries", i.e. the enrichment of wild fish populations subjected to fishery exploitation through hatchery-produced seedfish. Concern about this type of procedure has partly ecological and partly genetic reasons. Apart from the potential disturbance of the ecological equilibrium of the receiving water body, there is also concern about the possible genetic "interference" of the seedfish with wild individuals of the stocked species. Genetic implications of enhancements have received attention only more recently with the rising discovery of genetic markers (see section on *Interactions between biotechnologically improved individuals and wild populations* further below).

Genetic "interference" is of less concern as long as either the stocked species is not present at all in the water body to be stocked or it cannot reproduce in it. An example of the latter case is the stocking of "Major Indian Carps" in dams in Kerala (India; GTZ project in the nineties, see COFAD/GOPA 1993).*In such a case, stocking has to be repeated periodically. A special question is the introduction of suitable species into dams where in the initial phase of establishment of the new ecosystem certain niches are not yet occupied. Here, concern about genetic incompatibility can arise from the presence of the species to be stocked in the catchment basin of the river system into which the dam is inserted.

A special case is that of the Italian "valli". These lagoon ponds represent an early stage of aquaculture based on the (natural) periodic immigration of certain species into lagoon areas where they can satisfy their nutritional requirements better than in the sea. This "vallicoltura" system aims at maintaining control until harvest through preventing the immature fish from turning to the sea in autumn by keeping them in wintering channels and releasing them back to the lagoon ponds in the following spring. Lagoon-pond production, however, was limited by the number of fish returning to the lagoon ponds under natural conditions. When even the supplements provided by a special seed fishery became insufficient, Ravagnan (1978) recognising this, convinced himself and others of the necessity to maintain and increase the production of the "valli" by adding seedfish produced "artificially", i.e. under controlled conditions.

Obviously, at least a portion of the fish harvested from the lagoon ponds then stems from hatchery production. It now depends largely on the breeders used to produce the seedfish, to which degree the genetic composition of the seedlings has been changed as compared with wild individuals. If the breeders have undergone a selection process through several generations, also their offspring, i.e. the seedlings, can be "contaminated" by domestication effects and could thus influence the genetic composition of the lagoon-pond population.

Moreover, it seems possible that the controlled wintering has indirect selection effects, too, and that such effects could also ensue from other management measures applied to the "valli" (increased availability of food, less exposure to predation, etc.). Concerning the part of the population escaping back to the sea, selection could be favoured even through them if some sort of homing were involved (return to the lagoon areas where the fish have spent their first summer of life). True domestication, however, can only occur if full control over the life cycle of the entire population of a lagoon-pond is achieved continuously. If this were the objective, the immigration of individuals from the wild (i.e. the sea) in spring would have to be prevented, too, as well as the emigration in autumn.

In the USA there are so-called "mitigation hatcheries" which are designed for spawning and stocking large numbers of Pacific salmonids in compensation for the loss of spawning grounds due to dam construction. All Pacific salmonids, except for steelhead trout (anadromous rainbow trout), die after first spawning thus the broodstock cannot be used again, whereas steelhead trout is stripped and released back into the river. The only species of the sturgeon kinship in North America which has been produced in such mitigation hatcheries and stocked in large numbers in some catchment areas, is the Mississipi paddlefish (*Polyodon spathula*), reared to maturity also in ponds. (Doroshov, pers. com.)

The decisive question is: how can negative domestication effects on the hatchery-produced seedfish for stocking or ranching be avoided or at least minimised? Clearly, some of the unintentional consequences of hatchery production ("hatchery effects") can hardly be evaded, above all the losses due to non-adaptability to the conditions of captivity (see Part I, p. 7 and Part II, p. 18-19). Still, early life stages could perhaps find water quality conditions close to natural in "hapas", and appropriate bottom conditions in net pens.

The broodstock, however, should, if ever possible, come directly from the wild. This requirement is, e.g., fulfilled in the afore-mentioned example of the steelhead trout thrown back into its water of origin immediately after stripping. This principle is also followed in the controlled recovery of the sea trout (*Salmo trutta*) and maraena whitefish (*Coregonus maraena*)* stocks in the Baltic Sea area (Jennerich, pers. com.).

The lifetime period in captivity after hatching should be shortened as much as possible. The question is whether the release to an open water (preferably the natural environment of the population) can and should be done (a) already during yolk sac absorption, (b) between

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*It can, of course, not be definitively excluded that the stocked flow-adapted species can reproduce in the stagnant waters of dams; however, in the reference case it has never been observed.

**English and scientific name after FishBase (the species was formerly considered the Baltic subspecies of houting, *Coregonus oxyrhynchus*).

yolk-sac absorption and metamorphosis, (c) after the larval stage. Formerly, it was expected that post-larvae or fingerlings would have a better chance to survive and thus to enhance a population. However, in Germany it has been observed in rainbow trout (*Oncorhynchus mykiss*) as well as in brown trout (*Salmo trutta fario*) that hatchery-produced fingerlings do not compete well with the natural populations already present in the water where they have been released (Klein, pers. com.). On the other hand, how successful the stocking of larvae can be, is shown by the examples of sea trout (during yolk sac absorption) and maraena whitefish (after yolk sac absorption) in the Baltic (Jennerich, pers. com.).

The above principles hold also true when a population depleted by over-exploitation is to be restored, which is inherently demonstrated by several examples referred to above.

Intermingling of domesticated individuals and wild populations

Stock enhancement and replenishment, conservation of genetic resources and re-establishment of near-extinct populations must in practice follow similar principles, when genetic contamination from domestication effects is to be avoided. Before entering the discussion of procedures and limitations of conservation measures, it appears reasonable, therefore, to deal with the possible consequences of intermingling of domesticated and wild individuals.

The enormous success of Atlantic salmon farming in Norway, and to a lesser degree in Scotland, Canada, and Ireland, i.e. in countries with a highly developed pertinent research infrastructure, has led to an early awareness of the possible consequences of genetic intermingling of domesticated and wild populations. The first international symposium dealing with the subject was held in Norway as early as in 1990. The most recent overview of the state of pertinent knowledge was published in 2006, reporting on *Interactions between aquaculture and wild stocks of Atlantic salmon and other diadromous fish species: science and management, challenges and solutions* (Hansen & Windsor, 2006), where genetic interactions are an overriding topic.

Admittedly, the NINA/NASCO/ICES Symposium of 2005 in Bergen (Hansen & Windsor) concentrated and reported almost exclusively on Atlantic salmon. Priority reference to this report appears nevertheless justified, when considering that the vast experience with the extremely rapidly growing farming industry of this species can, and should, serve as a reference base for comparison when dealing with similar problems in the still less successful culture of other species.

The most serious problems of genetic intermingling are caused by uncontrolled active and passive movements of cultured fish: it is intelligible that among the uncontrolled movements the escape from cages must rank high, indicating that containment is of paramount importance. Another source of genetic intermingling is deliberate movement of broodstock and seedlings from one water to another in the absence of awareness of the possible consequences. Obviously, in both cases, the relation between the number of individuals escaping or being transported from one place to another and the size of the wild population contaminated (as well as its degree of exploitation or even depletion), is decisive for the degree of genetic impact of such movements. Consequences are also to be expected for enhancement through stocking and ranching (see preceding Section on *Domestication and stock enhancement and replenishment*).

In the case of Atlantic salmon, escapes (not only from cages) are by far the most direct and urgent concern. The situation is extremely alarming, not least because escapees could counteract the positive effects that an increased aquaculture production can have through alleviating the exploitation pressure on wild populations (see the above Section on *Domestication and intensively exploited wild populations*).

A low number of native individuals in a local population and a high number of intruding escapees can finally lead to the suppression of local populations and thus to substantial losses of intra-specific diversity. This diversity is due to the long-term adaptation of the local salmon populations to the specific ecological conditions of that system, indirectly based on, or connected with, the homing phenomenon. Hence, there is a lot of inter-population heterogeneity between river systems that could be impaired by a high percentage of intruding farm individuals and “hybrids”. Even the complete loss of a wild stock could eventually be caused when only a few or no purely wild spawners are left.*

The degree of interaction can be influenced by varying the distance of a farm complex from a salmon river system, which should lead to staying away as much as possible from still uncontaminated systems. Other solutions to the problem of escapes are mainly seen in technological improvements for better containment and in the creation of sterile farm fish. One can imagine how urgently needed such solutions are, when taking the rapidly growing amount of farm individuals into account: if the progress in escape reductions already achieved, is to be continued, it must exceed the rate of increase of the industry.

The importance of domestication is to be seen under two aspects: (a) at the beginning of the true domestication phase when interbreeding is still not impaired by a strong differentiation of properties, the altering of characteristics of the wild population through intermingling is a threat; (b) later, when true domestication has advanced, it could be that interbreeding is of less concern. The latter possibility may even open up an avenue towards reducing the effect of escapes substantially (see also section on *Interactions between biotechnologically improved individuals and wild populations* further below).

More recently, the genetic interactions between aquaculture and wild populations have been rather

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*It appears necessary to add that losses of wild Atlantic salmon stocks must not necessarily be an exclusive consequence of genetic intermingling, but could also be due to the exportation from farms of parasites such as sea-lice; and even climate change and consequent alterations of the North Atlantic Oscillation may contribute (for the latter see Boylan & Adams, 2006). In addition, there might be negative effects of escapees as a consequence of increased aggressiveness observed among cultured fish under certain circumstances (Jonsson & Jonsson 2006), which could put wild fish at a disadvantage in competitive encounters (Thorpe, pers. com.)

extensively discussed for a number of species cultured in Europe, including Atlantic salmon. The results are published in a compendium entitled "*Genetic impact of aquaculture activities on native populations*" (Svåsand et al. 2007, referred to as the Genimpact Compendium in the following in which the results are summarised and highlighted as far as deemed useful in the present context).

One piece of information on Atlantic salmon provided by the Genimpact Compendium (p. 129) illustrates the magnitude of losses to the wild: "~0.5-1.6 % of farm salmon (0.5-2 million) escape, equal to ~50 % of pre-fisheries abundance of wild fish, of which ~10 % enter rivers where many interbreed with wild salmon and trout." This corresponds to a concluding statement of the convenors of the NINA/NASCO/ICES Symposium in Bergen (Hansen & Windsor, p. 22) "that the escape to the marine environment of huge numbers of farmed fish (millions in some years) is accepted as 'normal'". It should not be forgotten, however, that there is still great variation among sites.

Further pieces of information in the Genimpact Compendium state that farm escapees can reduce the productivity of wild populations; that interbreeding can reduce mean fitness and have indirect effects through competitive, disease and parasite interactions; and that "farm fish in the wild have severely reduced life-time fitness compared to wild fish with intermediate hybrid fitness."

The bearings on domestication are explicitly acknowledged in the title of the first of four workshops constituting the basis of the Genimpact Compendium: *Genetics of* ***domestication****, breeding and enhancement of performance of fish and shellfish* (setting off by the present author). In the text, the term 'domestication' is also used here and there. However, what is meant by this term is explained only in the last article of the compendium (p. 162). The explanation is a rather loose and doubtful one: How can the number of "domesticated" terrestrial and aquatic species be compared, when on the terrestrial side only the final outcome of selective breeding is considered (after centuries or even millennia in some cases) and on the aquatic side all initial stages are included, whether they have already led to selective breeding or not?

The enormous success of salmon culture has put Norway in a leading position in many respects, not least in genetic research. In addition to Atlantic salmon, two other North Atlantic species are in the focus of Norwegian aquaculture: Atlantic cod (*Gadus morhua*) and Atlantic halibut (*Hippoglossus hippoglossus*). While the capture landings of salmon are in serious decline, its culture production today far exceeds the landings (see Fig. 1). The landings from most of the cod stocks are also in decline (many stocks have already collapsed) and halibut is following. The culture of cod being considered as the next species of great economic promise, even selective breeding programmes are already on the way in Norway as well as in Iceland. Halibut farming, however, is still mainly based upon wild captured broodstock.

The pace of development of cod farming is such that it very probably will follow the pioneering traces of salmon. The 2004 production was 3,800 t and for 2005 the preliminary result was already 7,000 t. The number of escapees was 75,000 in 2003 and 2004 and was expected to be more than twice this figure in 2005 (Genimpact Compendium, p. 12). The problems of containment are very similar to those of salmon farming. The spawning migration of Atlantic cod may cover great distances, according to the position of the spawning grounds, and includes the mouth of rivers. There seems to be evidence that maturing farm cod would need the guidance of adults to find the natural spawning grounds, thus diminishing the probability of genetic intermingling of farmed with wild spawners – if truly domesticated cod still maintain some migration instinct at all.

The two finfish species most important for Mediterranean aquaculture are gilthead seabream (*Sparus aurata*) of the family Sparidae and European sea bass (*Dicentrarchus labrax*) of the family Moronidae. Their area of distribution includes central and southern European coasts of the Atlantic Ocean. Both are traditional components of lagoon-pond aquaculture (called "vallicoltura" in Italy, see the enhancement section further above and Part II, p. 23). Capture production has been exceeded by aquaculture production since the first half of the nineties (see Fig. 2), the bulk of the latter being contributed by intensive forms (mostly cage farming). Both species can meanwhile be considered as truly domesticated, with breeding selection in its initial stages.

Intermingling between domesticated and wild populations can be expected above all from cage farming and can be increased additionally by indiscriminate transfer of seed, also for the enhancement of wild populations. However, detailed information is still largely lacking. The impact of lagoon-pond aquaculture has different implications, according to the degree of confinement and other control measures. Originally, the catching installations ("lavorieri") made of reed, wooden poles and brush, were completely open to immigration of all life-stages and more or less completely closed to the emigration of fish. The control on emigration became tighter with the introduction of more effective construction designs and materials of the "lavorieri". The productivity of the lagoon-ponds was maintained and enhanced by the establishment of special catching practices for juveniles, allowing stocking of the ponds additional to natural immigration (Pellizzato et al. 2005). This was in the eighties of the last century superseded by the growing availability of seed from hatcheries.

From the above, the following could be expected for aquaculture: containment in the lagoon-ponds becomes easier than in cages; this would favour the production success of lagoon-pond populations (continuing, nevertheless, to keep a semi-intensive level); it could accelerate domestication when fish matured in the ponds are used for hatchery production and their offspring is released to the ponds. Wild populations, however, would be deprived of the possibility to immigrate into the lagoon-ponds for better nutrition. Little is known about the importance of this possibility for the maturation and survival of wild populations. This could become noticeable when in its absence the wild population is forced to remain in the sea for its entire life-time. The study of such an interrelationship, and possible interdependence, could be facilitated by the increasing knowledge about genetic markers, not least through experimental releases of wild-caught seed in still pristine lagoon areas.

The Genimpact Compendium deals with two more finfish (turbot and common carp), one crustacean (European lobster), and six bivalves (two mussels, two oysters and two scallops). The natural distribution area of turbot, *Psetta maxima*, extends farther to the north than that of sea bass and includes the Baltic as well as the Black Sea (from where a subspecies, *maeotica*, was described). Turbot has been introduced for culture to Chile and China. Cage culture is of less importance than in the preceding cases. Culture problems are limited growth due to early maturation, lack of skin pigmentation and morphological deformations. Selective breeding appears still to be in its infancy. Studies on genetic interactions are lacking.

The only aquatic animal species whose domestication process can approximately be matched with that of terrestrial animals, is common carp. This regards the length of practical experience as well as its intra-specific diversity. While the genetic structure of wild carp is rather poorly understood, its domesticated strains are better known. Farmed carp have been extensively used for traditional breeding trials as well as for modern biotechnological improvement experiments. Genetic intermingling between wild and domesticated individuals must have taken place rather early, without leaving a possibility of tracing this back with sufficient clarity. Many areas and countries shelter feral* carp populations originating from introductions. Three subspecies are distinguished: the European (*Cyprinus carpio carpio*) of the Danube drainage system and two Asian ones (*C .c. haematopterus* and *C. c. viridivlaceus*) of the southeast and far east of the continent. Existence and geographical distribution of wild populations are little known and need to be investigated, not least in order to analyse and protect them.

An additional example of a freshwater species for which consequences of intermingling can be expected, is grayling (*Thymallus thymallus*). Since some natural populations of this species in southern Germany are becoming impoverished, stocking is seen as a remedy, thus broodstocks have been established in order to produce seedfish. Since the broodstocks are kept through generations, they might already have undergone some initial domestication, with the possible consequences of an intermingling of the offspring with wild individuals which, however, has not been studied yet. (M. Klein, pers. com.)

Following anew the Genimpact Compendium, the European lobster (*Homarus gammarus*) is even farther distributed towards the north of Europe than the European sea bass. It is absent from the Baltic but present along the northern coastal areas of the Mediterranean. This species is at present passing the threshold from enhancement practices to full grow out farming, overcoming the difficulties caused by its cannibalistic behaviour. Awareness of the genetic implications of ranching, in particular when using non-native or domesticated individuals, has increased recently. So far, conclusive studies on intermingling of domesticated and wild populations have not been conducted, but with the now available methods of genetic marking, future attempts have bright prospects, not least because of the more sedentary life of lobsters in comparison with many marine finfish species.

In passing from the lobster, a creeping long-tailed decapod crustacean (Macrura Reptantia), to bivalves, the sedentary nature of the adults increases. Two species of mussels, the blue mussel (*Mytilus edulis*) and the Mediterranean mussel (*M. galloprovincialis*) are of major importance to European aquaculture and included in the Genimpact Compendium. Based on genetic differences between the two species, of which the taxonomic status is still under debate, knowledge of their natural distribution has been revised. The area of the Mediterranean mussel includes now the entire Atlantic coast of Spain and is overlapping from the Atlantic coast of France until Scotland with the area of the blue mussel, which extends to Iceland and the north of Norway. It is supposed that a slow spread northwards of the Mediterranean mussel be partly connected with global warming. As natural spatfall still satisfies the culture needs in Europe, there is as yet no hatchery production on this continent. However, being aware of the selective breeding success in New Zealand, the interest in domestication and further genetic research is growing.

One of the two oysters, the flat oyster (*Ostrea edulis*), is a native European species, whereas the other, the Pacific cupped oyster (*Crassostrea gigas*), a meanwhile almost worldwide established foreign species, originates from north-eastern Asia. Different from the mussels, which are sexually separated (but similar to the gilthead seabream, *Sparus aurata*), oysters are alternate hermaphrodites, passing from one sex to the other during their lifetime. Due to a drastic decline of the production of the flat oyster caused by parasitic epizooites, the cupped oyster began to displace the flat oyster and finally dominated by far the production scene, above all in aquaculture. While the potential benefits from selective breeding, based on the results of some orientating experiments, are appreciated, selective breeding is more an option than a realised perspective. As long as many farms rely on natural recruitment instead of using hatchery-produced seed, domestication is not considered a necessary step forward, and intermingling of domesticated and wild, or feral, populations is not an urgent issue.

The distribution areas of the two scallops, the Atlantic *Pecten maximus* and the Mediterranean *P. jacobaeus*, do not seem to overlap. In the Genimpact Compendium the species are treated together and the species-related information refers mainly to the great scallop, *P. maximus*. This may be justified by the failure to identify deep genetic separation. What has been stated for the oysters regarding selective breeding and intermingling of domesticated and wild populations, holds largely true also for the scallops: a breeding programme is lacking and so are interaction studies.

Summarising this section, one can say the following:

There is a threat that the benefits of great production successes could be counterbalanced by escapes from farming installations, especially from net cages. This

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** A "feral" animal is understood here as one that has established a self-reproducing population originating from a transfer from its natural distribution area for aquaculture, fisheries or other purposes.*

is the most worrying outcome of Atlantic salmon farming so far, not only in view of the ongoing rapid increase in salmon production, but also regarding the next candidates to follow the salmon path, in particular Atlantic cod.

The most important avenues to be followed to minimise and eventually avert the danger are:

- develop technologies suitable to avoid escapes as much as possible;
- intensify selected breeding efforts (domestication) in order to increase the genetic distance between farmed and wild populations;
- intensify biotechnological genetic research aiming at creating barriers between farmed and wild aquatic animals without compromising quality and image of the aquaculture end product.

It is decisive for the final success of aquaculture as a food producing industry to demonstrate that the same errors of the past will not be committed either in the near or in the distant future. Otherwise, the public image of an industry compromising the natural resources could become a rather significant commercial and economic impediment.

Another conclusion to be drawn from this section is the importance to know existence and degree of intra-specific differentiation and its possible relationship to corresponding geographic and ecological barriers.

Interactions between biotechnologically improved individuals and wild populations

Currently, three issues are of paramount importance in the field of biotechnological genetic improvement that has given rise to so many expectations and preoccupations:

- genetic markers;
- transgenics;
- sterility.

Genetic markers

One of the major problems when the success of stocking and ranching measures remained doubtful, was tagging - difficult and costly with the means formerly available and particularly difficult to apply at early life stages. In addition, there was a need to ascertain the tagging mortality, in addition to natural and fishing mortality. With the discovery of genetic markers, such as microsatellites and allozymes, the situation has changed profoundly. The continuing increase of our pertinent knowledge opens up good prospects that it will become possible not only to discover intra-specific diversity within the overall distribution area of a species, but also to trace back individuals to their origin, including that of farms.

At present, the knowledge about the methodologies for discovering and characterising the different types of markers, their best application, their validity ranges and the limitations of their utilisation, is in full development. Urgently needed are not only baseline data from the wild as well as from farms in order to put comparisons on firm grounds, but also time series to monitor the degree of stability of such data. Among the limitations concerning the entire new field of research, are the differences between species and locations requiring a case by case approach and the need for standardisation among studies.

In the Genimpact Compendium (p. 132) priority is attributed to "identifying the genes involved in domestication, i.e. the changes in the genetic architecture of wild populations when brought under farming practices", allowing the identification of "the true functional differences" between wild and farmed individuals. The molecular markers available for the species dealt with in detail in the Genimpact Compendium are compiled in a useful table on p. 133, in which far more than 2500 microsatellite positions are numbered, with the maximum of ~1700 for Atlantic salmon.

Transgenics

The knowledge of genetic markers and their position on the chromosomes is an important prerequisite to what could be called "genetic engineering" in a broad sense of the word. However, deliberate alterations of the genetically fixed characters of an organism are among those most controversially discussed not only in the public but also among producers and scientists. Experience shows that less is known with certainty, the harsher and more divergent arguments and discussions are. This means that in the present field much more well targeted, time-consuming and expensive research is needed, as well as extensive information exchange and good coordination of efforts, to arrive at less controversial conclusions. Applying this criterion to transgenics, it is evident that we are just at the beginning of a long process.

Transgenics must be reliably described, genetically well confined, ecologically safe and harmless to consumers. One of the major reasons for the great concerns of large parts of the public is failure to demonstrate and communicate these prerequisites of economic success. As long as considerable parts of the public do not sufficiently understand what is going on in this field, apprehension and mistrust will prevail. Scientists and producers, not least the authorities (where public interests are involved), must do more in this respect, but are hindered from doing so as long as conclusive results are scarce.

Beyond what has been said in Part II, p. 21, in the following a few details are added (based on information contained in the Genimpact Compendium, p. 104 and 109) that show how complicated things can be and how much care must be taken not to jump to conclusions. Particularly revealing as far as the limitations of the hitherto achieved results are concerned, is a statement referring to the most often claimed growth improvement: "despite encouraging data from laboratory studies (Fig. 1, comparing normal salmon to those transformed with a growth hormone gene construct), a clear demonstration has not been made regarding the economic benefit of transgenic fish relative to existing strains which have been genetically improved by traditional methods, such as selective breeding." According to another finding, "GH transgenic fish display significantly enhanced feeding behaviour and prey capture rates", but may "succumb to predation mortality at a greater rate than controls and thus display lower fitness".

In a special article (Genimpact Compendium, p.123-125) L. Colombo scrutinises "The semantics of the term 'genetically modified organism'" (GMO) which has aroused much critique and misunderstandings and even distorted the image of biotechnological genetic improvement as a whole. Colombo characterises the EU Directive concerning this issue as process-based rather than product-based and as genotype-oriented without reference to the phenotype, although the real source of risk is the product, not the process. He, therefore, suggests that the emphasis be laid on the result of the risk evaluation, i.e. the terminal act of the process of a GMO generation, instead of the initial one. He pleads for a substitution of genetically *approved* (GA) or *improved* (GI) for *modified* and proposes a supplementary statement that the gene transfer must affect the germinal cell line, thus including fertile transgenics but not totally sterile ones.

Sterility

The enormous success of Atlantic salmon farming has brought to mind the great economic potentials of aquaculture as well as its shady sides. The basic question is how to save and further develop the benefits and, at the same time, reduce and possibly avoid the negative consequences. Keeping the farm environment completely apart from the natural, or wild, one, would be a radical solution, realisable, however, only in recirculation systems. While they, too (though to a much lesser degree), are subject to errors and hazards, they are expensive and so far used only for special purposes, e.g. in hatcheries. Cages are placed into the same waters in which wild animals live, and that is the core of the problem. How to exclude interaction between farm and wild, or feral, organisms? Thus, the major problem of genetically improved escapees is essentially the same as with domesticated and wild animals: interbreeding.

Apart from solutions securing separation between environments technologically, the most direct approach would be to render farmed organisms incapable of mating successfully with wild or feral ones. This could theoretically be done by creating artificially induced or otherwise established genetic barriers between farm and wild animals or by excluding mating at all, e.g. by sterilisation of farm animals. (It should be realised, however, that a fully effective genetic barrier would mean that no further input from the wild to broaden the genetic basis of domestication would be possible.)

Sterilisation through triploidy is at present seen as the most promising avenue. It is being tried with several species (seven out of the dozen specifically dealt with in the Genimpact Compendium), however, with mixed results. Sterility was found to be not total ("Triploid bivalves are generally almost sterile …", p. 67, and further, concerning several species of oysters: "Triploidy is not considered as a safe genetic confinement tool as triploids can effectively breed.", p. 80). In Atlantic salmon, the growth rate was reduced and deformities were a concern; in turbot the growth increase remained "relatively low" (p. 58). So far, "No commercial production of triploid or transgenic salmon occurs in Europe." (p. 28), and for carp this appears also to be true, although "Sterile triploid transgenics were produced to avoid environmental impacts." (p. 36).

In Australia, much research is directed towards polyploidy inducing sterility in penaeid shrimps, in particular (*Marsu-*)*Penaeus japonicus*. One of the objectives there is "to prevent unlicensed breeding", together with "the introduction of genetically improved strains into natural fisheries" (Sellars et al. 2006a, p. 631). However, total triploidy could not be achieved there either (Norris et al. 2005, Sellars et al. 2006b).

Domestication and conservation of genetic resources

Coming back to the initial statement of the preceding section on intermingling, it is now clear what the consequences of man-induced interferences of domesticated and biotechnologically improved individuals with natural populations could be. Enhancement through stocking and ranching has been discussed further above, demonstrating that the organisms used for such purposes should be kept free from domestication effects as much as possible and feasible. This is the more imperative when genetic resources are to be conserved, whatever the objective of such conservation is. The last paragraphs of the section on *Domestication and stock enhancement and replenishment* further above are, therefore, equally valid for conservation measures.

A reasonable approach to the conservation of threatened but still available genetic resources would certainly be to prevent or minimise their utilisation, or at least make sure that they are exploited at a biologically sustainable level. Equally important is the protection of the environment in which a resource lives. Any dam construction in a river can change the set of ecological niches available from a fluvial to a lacustrine character upstream and modify also the hydrological conditions downstream. If the responsibility for environmental protection is left to private enterprise, public authorities must have the ultimate control, preferably by law, including enforcement of the law and regulations derived from it. Unwanted or abusive introduction of domesticated individuals should be subjected to obligatory official notification and, where necessary and possible, penalising.

In Finland, conservation of the genetic fish resources is a major concern of the Finnish Game and Fisheries Research Institute, with ten fish farms all over the country, and includes a considerable number of species, and forms within species ("morphs"), belonging mainly to the genera *Salmo*, *Salvelinus* (Atlantic salmon, Arctic char, and trout), and *Coregonus* (whitefish). To avoid domestication effects, painstaking procedures are scrupulously followed for enhancement and replenishment stocking as well as for resource conservation and saving of species from extinction. (The following information was provided personally by Tapio Kiuru.)

Captive broodstock for seed production is established using eggs and sperm obtained from wild individuals. Fertilisation follows a complicated procedure in order to secure equal pairing of females and males as well as of different year classes, thus reducing inbreeding. Alternatively, when mature fish are not available, smolts and fingerlings are caught and raised to maturity in order to establish a captive brood stock as before. The cultivation of the fingerlings occurs in the same water body in which they were caught. Since during this period no attempt at selection is made, the rearing is considered "natural" or close-to natural.

Special cases are the land-locked Atlantic salmon (*Salmo salar* morph *sebago*) and one strain of Arctic char (*Salvelinus alpinus*). The salmon does no longer reproduce in the wild because its natural spawning areas have been destroyed or dams prevent access. Concerning the char population, there are difficulties to catch enough mature individuals. Where this is still possible, their sexual products are used to form a new broodstock. The offspring of this captive broodstock are released into their water of origin, migrate to their growing area and return to the vicinitiy of their traditional spawning places. There, some of them are caught and used to form a captive broodstock for another cycle of seedfish production under semi-natural conditions. In order to maximise the time under natural selection, the earliest possible life stages are used for stocking.

When not enough wild males are available for pairing, material from gene banks can be used. Cryopreserved sperm of the following species is available:

Native		
Atlantic salmon	(*Salmo salar*)	8 strains (including *sebago*)
Brown trout	(*Salmo trutta m. trutta*)	6 strains
Brown trout	(*S. trutta m. lacustris*)	10 strains
Brown trout	(*S. trutta m. fario*)	4 strains
Arctic char	(*Salvelinus alpinus*)	2 strains
White fish	(*Coregonus lavaretus*)	7 strains
Asp	(*Aspius aspius*)	1 strain
Introduced		
Rainbow trout	(*Oncorhynchus mykiss*)	1 strain
"Lake trout"	(*Salvelinus namycush*)	2 strains
Brook trout	(*Salvelinus fontinalis*)	1 strain
Broad whitefish	(*Coregonus pidschian*)	1 strain

This list comprises most of the threatened as well as of the commercially important species, which are kept separate according to their individual river or lake system of origin.

The Finnish policy of protecting genetic diversity is determined by local steering groups composed of governmental and local specialists. These groups act in compliance with the following principles: (a) no stocking at all in some cases; (b) use of only local seed in others; (c) marking of stocked fish in order to allow identification in commercial landings as well as in fish caught for broodstock establishment.

When the conservation of genetic resources is a concern, then also their intra-specific diversity must be considered, as is nicely demonstrated by the Finnish example. Population supplements with offspring from mixed wild broodstock, i.e. originating from different waters and thus potentially from sub-populations which are genetically heterogeneous, are to be avoided.

Domestication and saving species from extinction

Measures aiming at the conservation of genetic resources must be taken as long as the resource is present in its environment. Saving of populations already extinct, or threatened by extinction, can only rely on the presence of the species either in other parts of its distribution area or in captivity, i.e. in an environment controlled by man. This implies the danger that in the environment of origin, in particular captivity, the individuals used for restoration cannot be considered as representatives of a genetically uncontaminated wild population without examination, or are even already definitely affected by domestication or pre-domestication effects.

Among the species most threatened are the sturgeons (Williot et al. 2002), in particular the great sturgeon (*Huso huso*), Russian sturgeon (*Acipenser gueldenstaedtii*), stellate sturgeon (*A. stellatus*), ship sturgeon (*A. nudiventris*), and Persian sturgeon (*A. persicus*), all of which are classified as "endangered" at the international level by IUCN (1994), the great sturgeon even as "critically endangered". The most important waters harbouring these species were the Caspian, Azov and Black Sea and the major rivers draining into them, i.e. the Volga, the Ural, and the Kuban River. (See also cover photos of the issue of this magazine containing Part II of this paper; Bilio 2007b)

At the times of the Soviet Union, the Russian sturgeon resources were considered a national patrimony and subjected to intensive protection measures which, however, could not prevent them from being heavily exploited already then for their world-famous caviar. Consequently, extensive restocking was carried out with millions of offspring. Hatchery production was enormous and did formerly not raise concern about possible genetic consequences. Stocking success was then mainly evaluated on the basis of production increases as compared with the situation before stocking.

Today this has changed profoundly (see, e.g., Chebanov 1998). The situation in the Azov Sea can serve as a good example (Chebanov et al. 2002). Six species of sturgeon populated this extensive estuary of the Rivers Kuban and Don in the northeast of the Black Sea, but after dam construction natural propagation has been absent from this area for 25 years by the end of last century. This situation explains why also stellate and Russian sturgeon from the Caspian Sea have been used to restock the Azov Sea, thus changing the genetic composition of the species in this area.

Sturgeons are genetically heterogeneous not only geographically, but exhibit also different ecotypes connected with their spawning behaviour (spring or autumn spawners), and their spawning season lasts rather long in nature, which is not easy to simulate in captivity. Moreover, their migration instinct must be satisfied as well as their preference for clean gravel as spawning ground. All such requirements must be met when hatchery-produced seedlings are to be as similar to wild offspring as ever possible.

In the South Branch Federal Centre of Selection and Genetics for Aquaculture (Krasnodar, Russia) a system has been designed that takes the various ecological requirements into account (Chebanov 1998): its form of an oval ring (with controllable water flow) allows continuous swimming, imitating the conditions of the spawning migration; for spawning, gravel beds with a cleaning system are provided; it has a channel for the entrance of broodfish and a larvae outlet into a separate area for juvenile rearing; etc. (Chebanov et al., Fig. 2). The system is intended to be installed alongside the river and to be operated with captured broodfish first and to be reached by mature fish directly from the river later when the natural population will have been sufficiently restored. Meanwhile, however, in spite of a promising start, the realisation of the project suffered a delay. Being an integral part of a dam project that was rejected for hydrological and ecological reasons, it could not be realised either.

In Krasnodar a lot of emphasis is placed on the genetic and phenotypic quality of hatchery-produced juveniles used for restocking. Testing includes environmental tolerance and the incidence of deformities. Broodstock for stocking on the one hand and for meat and caviar production on the other hand are kept separate and individually recognisable by genetic markers (microsatellites) constituting a genetic passport and indicating the purpose for which they are retained (Chebanov, pers. com.). Among the objectives for establishing and maintaining a live gene bank are the preservation of the most heavily threatened species for a "potential restoration of wild stocks (…) in their native habitat", as well as the "optimisation of environmental and husbandry conditions for the intra-specific groups (populations and ecotypes)" (Chebanov et al., p. 6), thus for domestication.

A special case is that of the American Atlantic sturgeon (*Acipenser oxyrinchus*). It has been shown recently (Ludwig et al. 2002) that this species colonised the Baltic Sea in the Middle Ages, thus adding another species to the European Atlantic sturgeon (*A. sturio*) once inhabiting the northern, western and southern coasts of Europe including the Black Sea. At present, only a very small relict population of *A. sturio* in south-western France is considered to have survived the extensive habitat deterioration, waste disposal and overfishing of the last centuries. Therefore, when restoration measures for sturgeon in the Baltic were contemplated, *A. oxyrinchus* became the species of choice, restricting such measures for *A. sturio* to the North Sea.

Among the priority prerequisites of a successful restoration attempt were a well-considered transfer of broodstock caught wild on the east coast of Canada to a quarantine station in Germany and a scrupulous choice of the release area for juveniles (Gessner et al. 2006). As release area, the watershed of the Oder/Odra River has been chosen by the Polish and German institutes involved, as it still offers presumably adequate ecological conditions. Currently, these conditions are carefully studied under various aspects, including potential food competition with other species and identifying the most suitable season for release. In addition, the mechanisms of the extinction of *A. sturio* and the establishment of *A. oxyrinchus* are being studied in order to permit a risk assessment of the envisaged re-introduction measures.

Obviously, saving a species from extinction when it is almost too late, is a demanding task and comprises many species-specific aspects, above all the assessment of the suitability and quality of the still available individuals or relict populations, as well as the environmental conditions of the waters where the captured adults or cultured juveniles (or larvae) are to be released. If only domesticated individuals have survived, attempts should be made to activate within the genome those perhaps now hidden (i.e. phenotypically not realised) properties that characterised the original wild form. It seems that on land similar efforts have led to the preservation, or re-creation, in zoos of individuals close to the original forms of the European bison and Przewalski's horse, now both successfully re-established in nature.

Domestication and capture-based aquaculture

The term "capture-based aquaculture" has been coined in an FAO document published a few years ago (Ottolenghi et al. 2004). Its formulation resembles the much older term "culture-based (capture) fishery", also launched through FAO. Both terms appear to imply rather optimistic expectations as far as aquaculture is concerned. However, the possible implications for the capture fisheries are less positive. As can be seen from the above (section on *Domestication and stock enhancement and replenishment*), culture-based fisheries can imply a serious threat to the sustainable management of wild fishery resources if the genetic aspects (together with others) are neglected.

Essentially, the new term describes an old practice, perhaps the initial forms of aquaculture when, in the absence of domestication successes, just weight increase through taking wild animals in captivity was intended. One might have expected that through better control in terms of avoidance of losses, better growth through the utilisation of household wastes as feed, one would have been able to better nourish a family or even be able to barter. In addition, until recently certain types of coastal brackish-water ponds (the "tambaks" in Indonesia and the "valli" in Italy) also represented traditional forms of capture-based aquaculture.

Ottolenghi et al. deal with four species groups: eels (4 species); groupers (8 species); bluefin tunas (2 species); and yellowtails (3 species). The species were chosen for their extraordinary market value, affordable mainly by the richer segments of the population in countries with a thriving economy and a long and deeply-rooted tradition in seafood consumption, above all Japan. To exemplify this, the species will be briefly dealt with in the following, concentrating on aspects relevant in the wider context of domestication.

Eels are mainly farmed in East Asia and Europe. Both species are far from being domesticated. Not one life cycle could be closed in captivity neither in the Japanese (*Anguilla japonica*) nor in the European eel (*A. anguilla*), though attempts at controlled reproduction were made since the sixties in Japan and since the seventies in Taiwan (Liao & Chang 2001), as well as in Europe (Denmark and Italy), with the respective species. Landings of both species have declined at least until 2004 (see Fig. 4), with the causes up to now not well understood (hypothesising overfishing, in particular of glass eels, and environmental degradation and also global change).

The different species of eels are transferred worldwide without much knowledge of the consequences, e.g. regarding their migratory and mating behaviour. As with the other species dealt with in the afore-mentioned FAO document (Ottolenghi et al.), eels mature late and, to abbreviate the period from the larval to the adult stage, much detailed knowledge is necessary and so far not available. The decline in landings indicates that it is late, perhaps already too late, to achieve true domestication of at least one species in order to maintain the aquaculture production and thus save the wild populations from further overexploitation. Capture-based aquaculture can hardly solve this problem, since sustainable management of the capture resources largely appears as an illusion seen the lacking success of long-lasting pertinent efforts dedicated to many other species and areas.

Groupers, too, are top predators growing slow and reproducing late, thus being among the species particularly vulnerable to over-exploitation. Another weakness in terms of such vulnerability are their predictable spawning aggregations in massive numbers in rather easily accessible areas. Some populations have already crashed because of the ease of getting hold of them. Not less worrying are the millions of pelagic seed caught in shallow coastal areas where they accumulate in sea-grass beds, mangroves, reefs and brackish-water areas. Another disturbing aspect are wasteful culture practices derivable from the excessive numbers of seed used up for the production of relatively small quantities of marketable fish. Overfishing is thus an immediate concern.

However, the considerable number of grouper species already involved in capture-based aquaculture indicates good prospects for concentrating on one or two species most suitable for pure aquaculture under biological, technological and market-related aspects, and finally for true domestication. To this end, the candidates to be chosen for sustainable aquaculture should be subjected to increased and internationally well-coordinated research efforts to achieve continuous controlled reproduction, thus paving the way for selective breeding and finally even pedigree establishment leading to well-defined reliable products (see the below section on *Strategies for future development*).

Out of the 47 species of the genus *Seriola*, only a few are used for the farming of yellowtails, or amberjacks. The species most often referred to is the Japanese amberjack (*Seriola quinqueradiata*) inhabiting the western central Pacific Ocean and famous for the taste of its “sashimi”. Its fishery yield in Japan peaked in 1995 (>70,000 t), but fell in the following years. The greater amberjack (*S. dumerili*) is a cosmopolitan species with 72% of the world catch (~2,000 t) obtained in the Mediterranean in 2000.

The supply of fry of the Japanese amberjack (*Seriola quinqueradiata*) as seed is declining in Japan and the fishing quota of domestic fry was limited to 40 million in 1966, but amounted in fact to about 50 million around 1980; until 1999 the domestic provision fell to less then 30 million and was supplemented by several million imported from Korea and Vietnam. The Mediterranean population of the greater amberjack (*S. dumerili*) yielded much less, but seemed to be under-exploited by the year 2000. Hatchery production of this species was achieved in Japan but, nevertheless, most of the seed came from other countries in Asia.

Yellowtail farming was originally carried out in ponds (still applied), coastal lagoons and lakes, later in net pens (bottom areas fenced off by nets), and since the fifties increasingly in floating or submersible cages. Aquaculture production of the Japanese amberjack (*Seriola quinqueradiata*) was around 140,000 t by the year 2000 in Japan (by far the main producer), exceeding the catches (which, however, fetch better prices on the market) by about 100,000 t. Among the key bottlenecks is juvenile supply. As with the eels, a question concerning the possible implications of worldwide transfers (*S. dumerili*) remains: what is the fate of the genes of escapees?

By far the most problematic of the four groups dealt with in the FAO document (Ottolenghi et al.), are the highly migratory bluefin tunas, the northern (*Thunnus thynnus*) and the southern (*T. maccoyii*). Both species have become massively over-utilised and the southern species has been considered a candidate to be included in the Endangered Species Act (1992) and also in CITES (the Convention on International Trade in Endangered Species of Wild Fauna and Flora). The Japanese custom to eat especially tuna, but also other fish, raw and the readiness to pay exorbitant prices for such enjoyment, is at the basis of the tremendous exploitation pressure on this resource, even as far away from the Japanese (and increasingly also Chinese) consumers as the Mediterranean Sea.

Within the distribution of the northern species, the Mediterranean area is of particular concern. Since it is the exclusive spawning area of the eastern Atlantic population, there was an old (medieval) tradition in southern Italy to catch the tuna in fixed installations, the “tonnare”, in places where the tunas used to pass. Only two of these installations are left in Sicily because the great aggregations of tunas fail to appear. The Mediterranean fisheries are also suffering from the lack of a political decision of the littoral states to claim EEZs (Exclusive Economic Zones) under the Law of the Sea, leaving all what lies beyond the traditional 12 nautical miles to international instead of national jurisdiction.

Fish-finding was, at least in the Mediterranean, not much of a problem when the migration routes to the spawning areas were maintained by the tunas and known by the fishermen. In the open ocean, where fishing with multiple rods became customary, the shoals were detected through their predatory behaviour at the surface (splashing around when in full action), from boat look-outs first and with the help of helicopters in some areas at present. The catching method now most applied is purse-seining, used also for seed fishing. Seedfish are transferred from the seine directly to the growing cages in slow-moving transport cages, sometimes over great distances.

The aspect of capture-based tuna aquaculture that worries resource protectionists most, is fattening fish only for the last months before reproduction (Tudela 2002). Removing considerable numbers of fish from an already threatened stock just before recruitment to the reproductive generation, endangers the population even more than fishing juveniles. Heavy complaints are, therefore, directed towards the representatives of the producer and political level, blamed for insufficiently respecting even the recommendations of the International

Commission for the Conservation of the Atlantic Tuna (ICCAT).

The only mid- or long-term solution would be to accelerate R&D efforts towards true domestication as much as possible. An important step forward was made in Japan when in June 2002 for the first time the full life cycle of bluefin tuna could be completed under controlled conditions. Although this is a significant achievement, one should not neglect that commercial hatchery production of seedfish can hardly be considered a final solution, since it means that broodstock has still to be taken from the wild, which would mitigate but probably not definitively solve the basic problem of conserving an already threatened resource.

Domestication and diversity

There has been an incredible overestimation of the number of already domesticated aquatic species due to a rather unsatisfactory definition of domestication. According to Duarte et al., "About 430 (97%) of the aquatic species presently in culture (see the table) have been domesticated since the start of the 20th century, and an estimated 106 aquatic species have been domesticated over the past decade (see the figure)." While it is stated that it took millennia for the land animals to become domesticated, it is claimed that in aquaculture the progress is much faster (see Part II, p. 22).

However, all land animals considered as domesticated can be reproduced at will under controlled conditions and without any limitation through generations. By contrast, out of the aquatic species kept in captivity, continuous controlled reproduction with the possibility of selective breeding, is achieved only in a rather restricted number of species, so far certainly not more than the number quoted for land animals: 44, presumably less. It seems, and this appears to be the present practice in a considerable part of the world, that completing successfully just one life cycle under controlled conditions be considered sufficient to call a species domesticated. As a rule, at this stage many of the species concerned are in what I call a "pre-domestication phase" (see Part II, p. 16-19; Bilio 2007b).

Selection at this stage can, if at all noticeable, be seen as an "unintentional" adaptation to culture conditions (see Part I, p. 7; Bilio 2007a), not as deliberate selective breeding, the decisive criterion for domestication. A hardly questionable indicator is the considerable number of species the aquaculture of which is still based on capture fisheries ("capture-based aquaculture", see Ottolenghi et al. and the preceding section of this paper), and even the completion of one life cycle alone does not mean that achieving the completion of further life cycles is guaranteed. This is, obviously, not contradicted by the fact that there are species immediately available for selective breeding, such as the tilapias.

Anyhow, a definition of domestication in aquaculture should not essentially differ from that in terrestrial animal husbandry.

Naturally, with the scientific knowledge achieved during the last two centuries and the development of new research methods and tools, domestication in aquatic organisms can be expected to take a more direct and quicker path than the almost subconsciously achieved traditional advancements of a distant past. This appears to offer a chance to try out many more species in aquaculture than have ever been considered for domestication in terrestrial animal husbandry and thus to arrive at better choices. It could be, however, that numerous trials with land animals that might have been made in the course of millennia, were unsuccessful under the given circumstances and are, therefore, not reported or remembered.

What has not been taken into account so far, is the enormous potential of an intra-specific diversity that has been available and exploited in terrestrial animal husbandry, which in aquaculture has just started to become visible in strain and pedigree establishment. Most encouraging in this respect is the enormous number of races developed in some domesticated land animals that we are most familiar with (according to WIKIPEDIA)[1]:

Species	Number of races
Cattle	~500
Pigs	47
Sheep	71
Goats	160
Horses	69
Dogs	388

Why should such a potential not be available also in aquatic animals (and plants)? It is already visible in common carp having a tradition similar to that of terrestrial domestic animals. In eastern countries where public pedigree establishment has begun some time ago, such intra-specific diversification has even obtained public recognition. In the State Register of Russia, 11 carp "breeds" are named and characterised, 4 of rainbow trout, 3 of *Acipenser nikoljukin*[2], and 1 each of five other species (Boguerouk 2005, Table 3, p. 31). In Hungary, 13 breeding farms work with 24 certified common carp varieties, and a live common carp gene bank, operating since 1962 in the Hungarian Research Institute for Fisheries, Aquaculture an Irrigation (HAKI), comprises 17 Hungarian and 15 foreign strains and races. (See also Part II, p. 20-21; Bilio 2002b.)

It has been mentioned further above in this paper that, e.g. in Atlantic salmon, there is considerable intra-specific genetic diversity also in the wild, expressed in the adaptation to the ecological conditions of different river systems. Moreover, there is the example of the Tasmanian Atlantic salmon displaying a temperature tolerance exceeding considerably the range of the species in the North Atlantic (see Part II, p.23; Bilio 2002b). This, together with the examples of domesticated land and some first aquatic species, seems to indicate that perhaps also in domesticated forms there might be hidden genetic

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[1] Obviously, the purpose of creating these races was not always food production, but also transport (riding, carrying, draughting), herding, the production of fur, wool and leather, etc. (The skin has been utilised also from aquatic animals, e.g. from eels for leather production.) These other objectives are mainly due to the fact that man and land animals live in the same terrestrial environment, exposed to air, not to water.

[2] This species name is misprinted in Boguerouk's publication as "*nikotjudini*" and refers to "bester", the famous cross between *Huso huso* and *Acipenser ruthenus*, and backcrosses of bester with either one of the parent species (Chebanov, pers. com.).

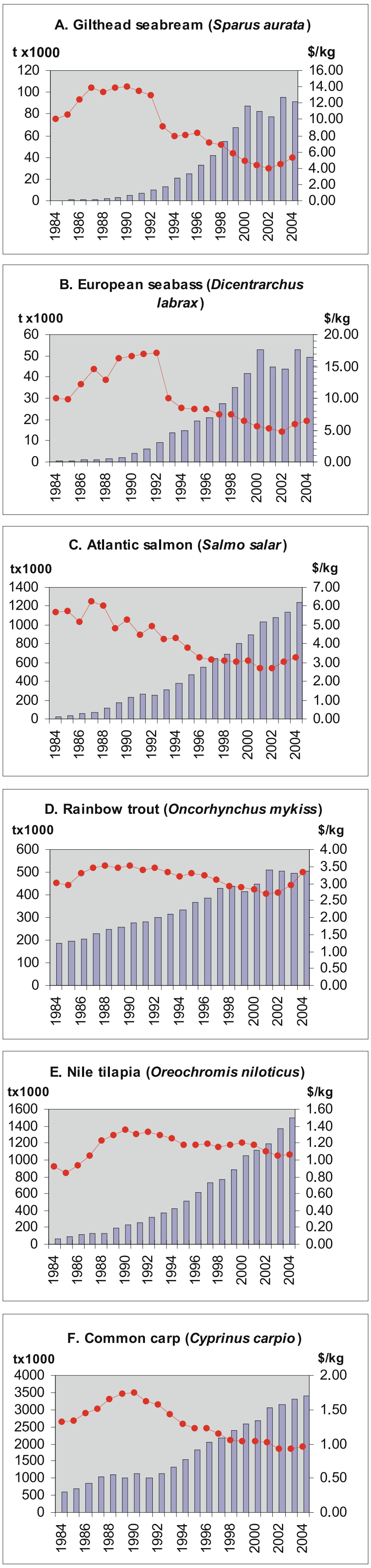

Fig. 5. Development of aquaculture production (mt, blue columns) and value (US$/kg, red line) in six different domesticated species (data from Fishstat 2006).

potentials which can be detected only occasionally or through long and painstaking test series.

It thus appears that the conditions of inbreeding, the occurrence of mutations, as well as hidden potentials within the genomes, should be better looked after in order to find out what the rules and limits of utilising intra-specific diversity also in domestic aquatic species are and how they could be influenced by man.

Domestication and value development

Value data are collected and compiled by FAO from 1984 onward. An evaluation of these data is, therefore, limited to the last three decades and might perhaps initially be less complete and reliable than later on, especially considering that they are compiled by public officials not immediately used to provide such calculations or estimates. Value data refer to the entire production of a country and do not reflect local market situations, which can sometimes differ considerably from overall annual estimates or calculations. This can be due to the offers influenced by the productive season and by seasonal differences in demand. Such differences can cause producers to adapt their productive season to that of maximum demand where this appears biologically and technologically feasible. Then it appears reasonable to speak of prices instead of values.

When looking at value development in the context of domestication, the main question is how much the values decrease when a production steadily increases. For the two recently domesticated Mediterranean species gilthead seabream (5.A) and European seabass (5.B), the entire process from the beginning of an industrial production until reaching 90,000 and 50,000 t, respectively, is covered by the two diagrams. Most striking is the value increase in the second half of the eighties when the production is still rather low. Another interesting feature is a small rise in value in the last three years included in the diagrams.

Atlantic salmon (5.C) and and rainbow trout (5.D) are chosen because one, Atlantic salmon, is a rather newly domesticated species, the other, rainbow trout, was formerly also a high-priced species, but is meanwhile since long easily affordable as a super-market product in industrialised countries. While the value of salmon is at present about half that of the eighties, rainbow trout has also suffered some decrease, but only from about 3.50 to about 2.80 US$, both experiencing a small increase between 2.50 and 3.50 US$ in the last three years as mentioned for A and B. While salmon showed a development similar to that of the two Mediterranean species dealt with above, though starting at a slightly higher production level in the diagram, rainbow trout production was in 1984 already well established at about 200,000 t, obtaining rather low prices similar to those of salmon in its end phase. Salmon might even have followed the path of the two Mediterranean species with an increase of the value in the beginning, but that cannot be deduced from the data.

The last pair is intended to show the development in two rather low-priced species considered food items of the poorer segments of the population in industrialised and so-called threshold countries, such as China. Nile tilapia (5.E) experienced a relatively small production, but a considerable value increase in the second half of the eighties (to almost 1.4 US$), whereupon along with a now strongly increasing production the value fell only to slightly more than 1 US$ in 2004. Common carp production (5.F) was already well-established at >500,000 t in 1984, but still increased to more than 3 million t in 2004. Also here, the value increased considerably around 1990 and fell with the continuously increasing production. In 2004, both species, tilapia and carp, ended up at prices of about 1 US$.

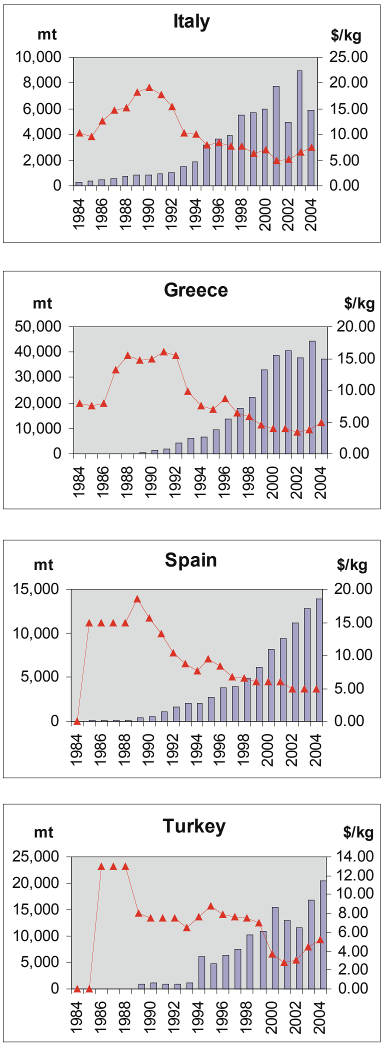

*Fig. 6. Gilthead seabream (*Sparus aurata*), value development in the four countries with the highest aquaculture production (data from Fishstat 2006)*

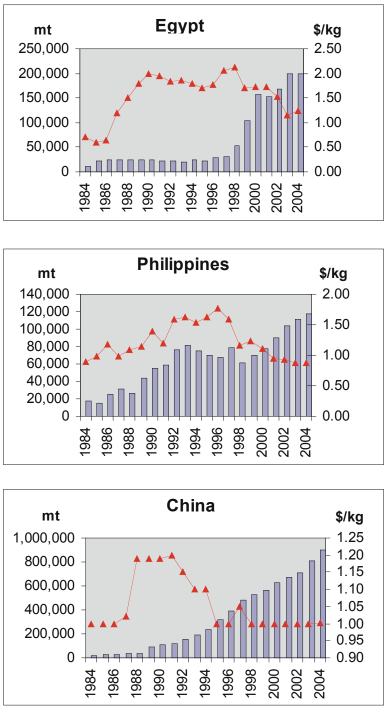

*Fig. 7. Nile tilapia (*Oreochromis niloticus*), aquaculture production and value development in different countries (data from Fishstat 2006)*

A more detailed analysis gives more insight. Fig. 6 shows the development of gilthead seabream in four Mediterranean countries (with Spain's production area including the Atlantic coast). Italy was the first country to produce at a level perceptible in the diagrams, with Greece meanwhile at the top because of so many areas suitable for cage culture. However, production and value development reflect the general course seen in Fig. 5.A. The most probable explanation is an orientation along the lines of a common Mediterranean market with the top prices paid, as usual for such seafood, in Italy (almost 20 $/kg in 1989-1991) and the lowest in the same period in Turkey (about 13 $ in 1986-1988).

More difficult to interpret are the values of tilapia in Egypt, The Philippines and China (Fig. 7). In Egypt, production remained low (~25,000 t) until 1987; instead, values increased until 1990 from a bit more than half a dollar to almost 2 US$ and remained at the same level even after an about 6-fold production increase (to ~150,000 t). In The Philippines, values followed the production increase for about ten years and only then fell with the further increasing production. In China, by contrast, production and value behaved in a way similar to that of the newly domesticated Mediterranean species (5.A and B), although the Nile tilapia could be considered domesticated right from the beginning.

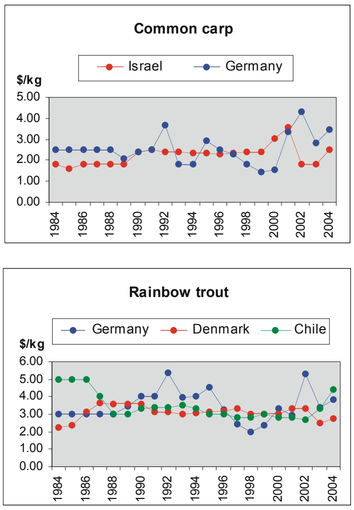

Fig. 8. Comparison of aquaculture values between countries (data from Fishstat 2006; US$/kg).

A last test was made by comparing the value in countries where one could perhaps expect differences according to food preferences (common carp in Israel and Germany) or to the distance from the main markets (rainbow trout in Germany, Denmark and Chile). However, neither in one nor in the other case the rather small differences at fairly low value levels corresponded to expectations (Fig. 8).

Summarising, three features can be observed:

(1) From a certain higher level onward, values decrease with increasing production, a trend following normal expectations and certainly favoured by true domestication (see Part II, Tables 5 and 7).
(2) There is a tendency during an initial, still moderate production increase for values to increase considerably, perhaps due to psychological reasons, i.e. a hope for high profit as long as demand is still relatively high and production rather low.
(3) An increase in value in spite of a still increasing production, observable in some species, but over a rather short period (2002-2004), thus needing a longer observation time.

There has been discussion as to point (2) suggesting that there could be an influence of inflation. One counterargument are the unchanged average values for common carp and rainbow trout in different countries (Fig. 8, possible exception: rainbow trout in Chile). To solve this question more definitely, detailed market research would be necessary, which, however, would go beyond the scope of the present paper.

PART IV

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Controlled reproduction and domestication in aquaculture -

the current state of the art.

Final Part

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Controlled reproduction and domestication in aquaculture

THE CURRENT STATE OF THE ART

PART IV (Final Discussion and Conclusions)[1]

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Domestication and value development (Supplement)

Further considerations have shown the usefulness of including additional comparisons between production and value development (Fig. 9-11)[2]. The most interesting feature is the sudden rise of white-leg shrimp (*Penaeus vannamei*) farming in Asia.[3] Originally this species was restricted to the western hemisphere, where landings from the capture fisheries began to decrease in 1994 (see Part III, Bilio 2008, p. 6 and 7). The first production of the species under culture in Asia (2,310 t) was registered in Taiwan by FAO in 2000, followed by mainland China (100,000 t in 2001), Thailand (60,000 t in 2002), and Indonesia (53,217 t in 2004:). The total production of these four countries in 2004 was 1,075,790 t, by far exceeding the production of the entire western hemisphere (Fig. 9, page 13).

Just prior to this enormous increase, shrimp farming in Latin America had reached a critical stage, which I had an opportunity to observe and discuss in Nicaragua. The business appeared to be threatened from two sides: pollution of the water taken into the farms, and rumours that the white spot disease had spread among the wild post-larvae (PL) resources (Bilio et al. 1999, p. 19). Guatemala had forbidden the export of its still-rich PL resources, however, not for fear of disease transfer but to maintain a competitive advantage over other Latin American countries. Nicaragua saw the need for recycling the water within the farms and for using larvae from hatcheries (realising a closed cycle, "ciclo cerrado"). A Taiwan Chinese delegation, present in the country with a "Misión China"[4] and studying the availability of PL from 1992-1994, could have taken advantage of the acquired knowledge and their access to the wild resources for developing farming of *Penaeus vannamei* in their own country.
In mainland China continuous controlled reproduction appears to have been achieved not later than in the early years of the new millennium (Part II, Bilio 2007b, Table 2, p. 8). This agrees roughly with the very thorough and comprehensive review by Briggs et al. (2004).

The average unit value of the world production of *Penaeus vannamei* decreased considerably during the production increase, ending below 4 US$/kg in 2004, which is about 1 US$/kg less than that of *Penaeus monodon* (Fig. 9.B), although both species had previously reached similar maximum values close to 8 US$/kg. The values of European and Japanese eels (Fig. 10, page 13) followed a different pattern, with a sharp decline for the Japanese species by the end of the eighties, but at a >20 times higher production level than that of the European eel. The production increase of the Pacific cupped oyster (Fig. 11, page 13), together with a certain revival of the European flat oyster, could indicate a relief situation for the much higher quoted flat oyster, having previously suffered a serious decline caused by parasitic epizooites (see Part III, Bilio 2008, p. 11). The considerable difference in production and value of the two species points to the different income levels of the respective consumer segments.

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[1] This final part of the paper is dedicated to Roland Beck (Tutzing, Germany), friend and source of a wealth of experience and knowledge.

[2] Although it is apparent from the figure legends, it remains to be pointed out that "value" in this context always means unit value (US$/kg), not the total production value.

[3] At logarithmic scale the sudden rise in production is much less conspicuous than at normal scale (cf. Fig. 9 of the present part and Fig. 3.B of Part III, Bilio 2008, p. 6).

[4] Misión Técnica Agropecuaria de la República de China

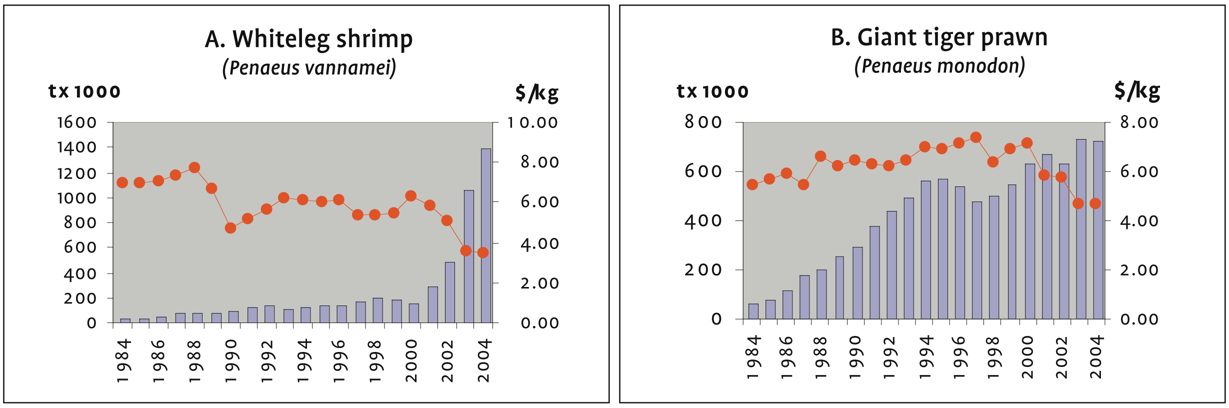

Fig. 9. Development of aquaculture production (world; mtx1000, blue columns) and value (US$/kg, red line) in the two penaeid shrimp species with the highest world production (data from Fishstat 2006).

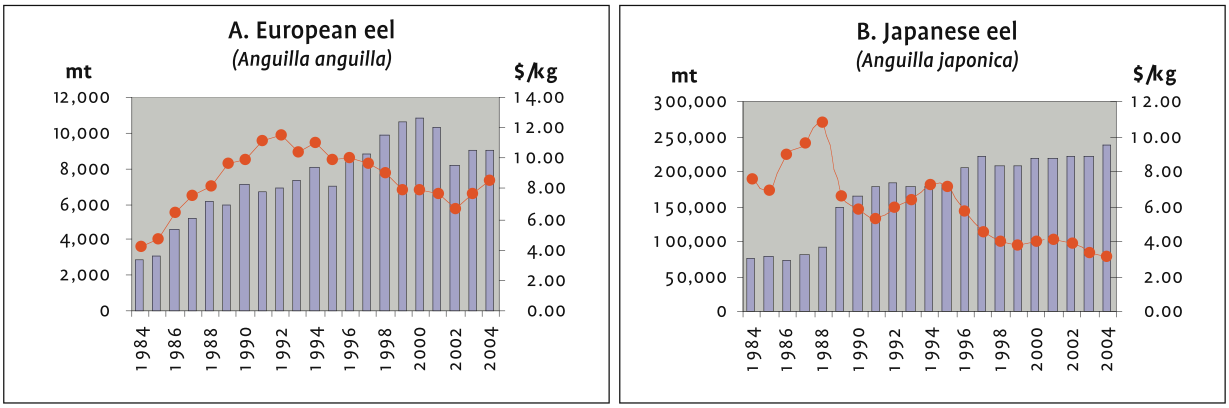

Fig. 10. Development of aquaculture production (world; mt, blue columns) and value (US$/kg, red line) in the two eel species of major importance (data from Fishstat 2006).

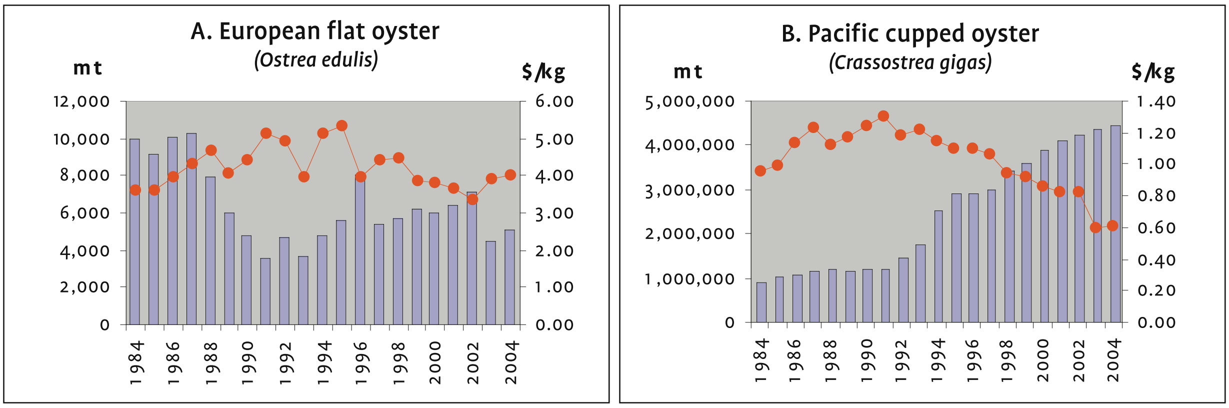

Fig. 11. Development of aquaculture production (world; mt, blue columns) and value (US$/kg, red line) in two oyster species cultured in Europe (data from Fishstat 2006).

Elements of a possible new strategy for future development

Contemplating the future of aquaculture, the starting point is the increase in demand for fish caused by an increasing world population. If solutions are to be found for the ensuing problems, it is necessary to consider all known practical and scientific facts. Speculation can help advance hypotheses based on known facts, and by wishful thinking a direction can be determined in which one prefers to proceed. However, speculation and wishful thinking must take reality into account, which often shows the limits of development based solely on theoretical considerations.

Practical experience and scientific research

When in the 1970's modern European aquaculture was still in its infancy, different directions were chosen by two countries: France and Italy, then in leading positions in Mediterranean brackish-water aquaculture, in particular of gilthead sea-bream and European sea-bass. The French chose to first solve the culture problems scientifically and then hand over a ready methodological concept to the prospective fish farmer (Mr. Perrot, CNEXO, the forerunner organisation of IFREMER). The Italians – backed by the long tradition of lagoon-pond aquaculture (the "vallicoltura") – did not consider scientific research to be of much use, instead, practical solutions for encountered difficulties were attributed the highest priority.

In Italy, it was realised only gradually what could be achieved when true scientific research was applied to solving problems. In France, it had to be acknowledged that exchange of scientific knowledge and practical experience was essential to bring technological development forward. Today this is recognised, though apparently not yet fully. Consequently, several expectations ("wishful thinking") had to be revised, above all the former conviction that the major driving force of aquaculture development would be the provision of food, rather than the attractiveness of economic profit (see also Bilio et al. 1989). Along this line, one could say that in industrialised and threshold countries, a growing segment of the population, intermediate between the poorest and the richest, can now afford fish products that are available at moderate prices. This is proven by the fact that some species once reserved for the rich are now available at ordinary supermarkets: (rainbow) trout and (Atlantic) salmon. Even the prices of gilthead sea-bream and European sea-bass have gone down considerably.

Demand stratification

The continuing success of aquaculture, however, is limited at both ends of societies and countries: the richest and the poorest. Both tend to overexploit wild resources, the poorest because of their increasing numbers, the richest because of their immense purchasing power and excessive demands. The poor need alternative food, employment and income, the rich exert pressure on capture- and culture fisheries to satisfy their luxury demands. The latter leads entrepreneurs to ever-more technological improvements in order to tap economic gains offered by the wealthy segments of the population, particularly in the most industrialised countries. New fishing technologies and overcapitalisation of fishing fleets as well as automation in aquaculture (e.g., feeding systems that allow the detection of diseases through feed-back from feed consumption) are among the major consequences. Such food production systems need organisational concentration to remain profitable, which in turn reduces the employment opportunities for the untrained poor.

The beneficiaries of aquaculture development are already, and will increasingly be, the intermediate segments of industrialised societies. This is clearly visible where mass production of prestigious species leads to decreasing prices and where species of formerly low status become affordable exotics. The driving force behind, and thus the real target, of modern aquaculture is the middle classes. Otherwise aquaculture would not have become a new "business" and a significant asset of local and national economies. If aquaculture is also to feed the most indigent, the farming of appropriate, preferably low trophic level species, must be funded by the better-off (i.e. the major tax-paying segments of society; see "*Remaining options for the poor*" further below).

Choice of species

Modern aquaculture became a new field of research activities only after World War II (see Bardach *et al.* 1972). It is for this reason that Dunham et al. (2001) were correct in stating that intensive use of genetic selection in aquaculture has only been made since about 1970 (see Part I, p. 7). Since that time many choices have been made (and put in doubt), culminating in the question: how many species do we need to cultivate, which ones, and why? Looking at what has happened in the recent past, it is obvious that a scrupulous screening of candidate species, and the establishment of some basic elements of a strategy for further development are desirable.

The unfortunate tendency to include yet more and more species in controlled reproduction trials, before the suitability of the first, perhaps even more promising species has been thoroughly tested, is obvious. Hormone injection to achieve the completion of the final maturity phase and the release (naturally or by stripping) of eggs and sperm is a tool that is easy to apply even with only scarce background information. Intensive investigation of the natural biology, ecology and behaviour of a species, with a view to exploiting such knowledge, seems too far-fetched to be undertaken regularly. Whereas in former times aquaculture was seen in the context of the culture environment ("vallicoltura", or lagoon-pond culture, in Italy; "Teichwirtschaft", or pond culture, in Germany), today "zootechnie" (French) and "zootecnia" (Italian) revel in attention, favouring narrower views and approaches, but neglecting the wealth of hints available through thorough investigation of a species in its natural environment.

Worth mentioning in this respect is the Genimpact Compendium (Svåsand et al. 2007, p. 51) where the need for a comprehensive approach to culture which includes "the life cycle and ecology of the species in the wild" is stressed, not least in order "to understand how the farmed individuals, depending on the life stages and places where they are intentionally or accidentally released, may interact with the wild ones" (see also Part III, section on "*Domestication and stock enhancement and replenishment*", Bilio 2007b, p. 7-9).

It should be realised that in terrestrial animal husbandry relatively few species were needed to fulfil man's needs (see Part III, sub-chapter on "*Domestication and diversity*", Bilio 2008). Domestication in terrestrial animal husbandry developed over thousands of years and was for the major part probably not based on deliberate choices but on trial and error. The basis for well-informed choices likely appeared when scientific investigation and analysis of the processes involved had paved the way, especially the laws of inheritance discovered by Mendel (1865) through his work on plants. Their use in animal husbandry came later.

In some countries there is still a tendency to insist on theoretical ("academic") approaches (see France, above), likely due to a basic misunderstanding that appears to persist among some scientists. Aquaculture is often perceived to be a science in its own right, and certain journals seem to confirm this view calling "Aquaculture" what in essence is "aquaculture (or even better: aquacultural) research". As with agriculture, aquaculture is a means of production, and the sciences applied to this field are aquacultural sciences, in the same sense as agricultural sciences are applied to agriculture. It is likely that this terminological misinterpretation has led to misunderstandings between scientists and producers, the former trying to be the pathfinders for the latter, where continuous interaction between the two would be more effective.

Apart from technical feasibility and ease of production, the prospects for farming a new species are determined by its acceptability and market demand. Since World War II, the potential of aquaculture for providing benefits for poor and rich people has been more fully appreciated, yielding two major but controversial options. One option was for small-scale, low-input production for the rural poor and mass production of low-priced species for the urban poor. The option for the richer segments of the population was for "niche" species, available in nature, as a rule, in rather small populations, easily over-exploited by the capture fisheries, thus rare and expensive on the market and often requiring sophisticated aquaculture techniques.

The "niche species" concept has stimulated the diversification of aquaculture to a degree where a comprehensive reconsideration of what has already been achieved, and what should be done further, is desirable. INRA and IFREMER have made such an attempt (INRA 2004), starting, however, with rather academic terminology (p. 159-165). There is, for reasons explained in the introduction to this paper (Part I, Bilio 2007a, p. 6 and 7), no convincing alternative to a definition of domestication that includes terrestrial animal husbandry and also considers practicality, as is used in this paper.

The INRA/IFREMER publication deals first with terminology, then with some species and species groups (frogs, cod and pollack, blue-fin tuna, Eurasian perch, and pangasiid catfishes of the Mekong), further with culture aspects in general (reproduction, nutrition, behaviour, and growth), and finally with three special questions: (1) diversification and product quality; (2) genetic management of fish domestication; (3) genetic improvement of French captive populations as considered by SYSAAF (organisation of French selective breeders of birds and aquatic species). One of the main objectives is the identification of rules and procedures that could eventually be applied to as many species as possible – *a priori*, not *a posteriori* (INRA 2004, p. 159).

However, at the current state of aquaculture development, it is no longer desirable to seek further diversification by subjecting yet more species to experimentation, but to exploit the intra-specific potential, i.e. the still largely unknown genetic diversity resources within truly domesticated species.

Moreover, we are still far from paying sufficient attention to including product-quality as a target for future diversification, as is referred to by Fauconneau (cf. INRA 2004, p. 227). This potential was nicely demonstrated in the 1980's in Central Europe where a high-quality smoked salmon product from Scotland began to compete successfully with an already famous brand from Switzerland known as "Balik salmon"*. The Scottish quality secret was fourfold: low stocking density of fish in large cages; feeding below the *ad libitum*-level; slaughtering before reaching maximum weight; and, last but not least, smoking in one of the well-known smoke-houses in the Spey Valley (south of Inverness, Scotland). The main objective during grow-out was to reduce the fat content to extremely low levels. Such fish fetch a relatively high price and attract richer consumers.

Liao & Huang (2000) have tried to give an overview of domestication in aquaculture, in particular regarding developments in Taiwan. The basic difference from a realistic concept of domestication is their understanding that one life-cycle completed successfully under controlled conditions is sufficient to allow the use of the term. According to these authors, "65 species of finfish have been domesticated (can be artificially propagated) so far". This apparently means that propagation under controlled conditions occurred at least once (i.e. eggs of the P generation taken from the wild could be obtained, fertilised with sperm of the same P generation, hatched, and the larvae and juveniles raised in captivity), without making sure that successive generations (F_1, F_2, etc.) would reproduce under controlled conditions. They state (p.104) that giant tiger prawn (*Penaeus monodon*, called "grass prawn" by the cited authors) were successfully propagated artificially in 1968. However, when I was in Taiwan in 1984, the problem of raising the offspring of such a first reproduction to maturity under controlled conditions had not yet been surmounted (see also Part I, Bilio 2007a, p. 5).

Special consideration must be given to species that are apparently difficult to be reproduced under controlled conditions, e.g. eels, yellowtails, groupers, etc. Sometimes it appears rather easy to induce spawning through hormone injection, since the fish seem to be forced to react physiologically, provided they have reached the maturation stage at which such treatment can be effective. However, it often seems impossible, or at least extremely difficult, to continue controlled reproduction. Gonad maturation or larval rearing can cause problems. Diamond (2002) attributed the small number of domesticated terrestrial animals, e.g. among the big African mammals, to extreme aggressiveness, of zebra in particular (p. 702), but put hopes in "recognizing the specific difficulties that previously derailed domestication of particular valuable wild species, and using modern science to overcome those difficulties" (p. 706). This is in agreement with Russian findings (Trut et al. 2004, Trut 1999) that aggressiveness in silver foxes could be suppressed (eliminated?) "in generation 4 of selection" (see citations and comments in Part II, Bilio 2007b, p. 22).

The lesson to be learnt for domestication in aquaculture is that of a very careful choice when restricting the number of species to be domesticated, and to consider all available knowledge, not least the results of such efforts as have been made by INRA and IFREMER (see above). To overcome difficulties encountered during the pre-maturation phase, it could be helpful to take the experience with ornamental fishes into account, in particular with those aquarium fishes that have more recently been reproduced continuously under controlled conditions.

* The word Balik means "fish" inTurkish and "dried sturgeon back" in Russian.

The two sides of aquaculture

Today, with all the practical experiences and research results at hand, a global concept could be based on the following two theses:

- Under favourable circumstances enormous quantities of certain aquatic species can already be produced through aquaculture.
- Wild populations of the same species can be threatened by aquaculture through uncontrolled mass production.

Aquaculture can thus have a double effect with regard to the future of the wild resources. It can accelerate the overexploitation of some (see section on capture-based aquaculture in Part III, Bilio 2008, p. 15-17) and even bring species close to extinction by intermingling with escapees from farms, but it can also help in saving others. The negative aspect of intermingling is aggravated by the finding that with the development of cod farming in Norway, new challenges to fish farming have arisen following spontaneous spawning in net cages (Jørstad et al. 2008; reported also for *Sparus aurata* in Greece, Dimitriou et al. 2007, cited after Jørstad et al.). The problem is thus no longer only one of escaping fish, but of eggs and larvae that could become potential recruits to the wild stocks. Thinning out of wild stocks through overexploitation could add to the problem. It remains to be seen whether the offspring from farms retain the instinct of migrating to natural spawning sites, led by their wild conspecifics.

Attempts at solving the antithesis call for an urgent change in the relationship between those exploiting the wild resources through capture fisheries, the fishermen, and those using them for aquaculture, the fish-farmers. It should finally be recognised that for a long time a number of fishers and resource biologists have held serious reservations about the promotion of fish farming, subliminally as well as openly. To overcome this opposition, an atmosphere of mutual understanding must be created through better communication between the opponents and among the stakeholders in general (Bilio 1996, 1998, 2002; see also under *Stakeholder involvement*, below).

A more rational approach

On the basis of the available practical experience and current scientific knowledge, it appears possible to design a more rational strategy for further development than has been followed so far. First, the number of species to be subjected to further trials should be substantially reduced and efforts concentrated on a few species only. Experience with shrimp culture has shown that the present worldwide demand for shrimp could be satisfied by farming only a few truly domesticated species instead of subjecting ever more shrimps and prawns to aquaculture trials (cf. Part III, Bilio 2008, p. 7). In the practical sense, by far the majority of consumers do not really distinguish between different shrimp and prawn species.

Such a restriction could be appropriate for other species groups such as the Sparidae, where cultivating species other than *Sparus aurata* could become superfluous. Any demand for an individual species could, in the long run, be satisfied by the capture fisheries, especially when species fetching higher prices are concerned. The role of the "niche" species could then be taken over by species exclusively "produced" by capture fisheries. Moreover, instead of threatening wild populations by driving the exploitation of different life stages for capture-based aquaculture to the extreme, true domestication of a limited number of species each representative of a whole group, could lead to their mass production, thus satisfying a growing, intermediate segment of the human population.

Switching, e.g., from bluefin tuna to Japanese yellowtail, could finally alleviate the deadly threat to the tuna, making it necessary, however, to succeed with research towards continuous controlled reproduction of the yellowtail. (Yellowtail "sashimi" is considered at least as tasty as that of blue-fin tuna.) Once the pressure on the wild bluefin tuna populations was reduced by such a switch, their populations could recover, and the small numbers of extremely rich people could have their "kick" eating sashimi from bluefin tuna captured just before the fish would have reached their final maturation stage – if such a demand remains. As another example, one or two out of the many species of groupers, the early life-stages of which are already heavily exploited for capture-based aquaculture (see Part III, Bilio 2008, p. 16) could, when fully domesticated and produced in high quantities, be sufficient for those who do not care which species they eat, as long as it is prestigious and well-tasting. Additionally, prices would go down when mass production begins (Part III, Bilio 2008, p. 18-19), favouring the consumption of the few domesticated species by the middle classes.

Among the alarming signals indicating a gloomy future for capture fisheries, are the arguments against targeting mainly high-priced species that occupy high trophic levels and have long generation times. Such targeting leads to what has been called "fishing down food webs" (Pauly et al. 1998). A more or less equal exploitation of all trophic levels, such as probably prevailed before the industrial revolution, could perhaps save wild resources and their top predators, including even man's interest in keeping their exploitation sustainable.

A way to achieve this objective could be by restricting aquaculture to just a few valuable high trophic level species, and through the simultaneous implementation of well-conceived programmes for culture-based fisheries aimed at replenishing and conserving wild resources (see Part III, Bilio 2008, p. 7-9). Prerequisites would be: (a) agreement among all stakeholders, with the informed middle classes of the industrialised countries as pressure groups; (b) a substantial replacement of fish meal in feeds; and (c) sufficient scope (comprising R&D funding for the final domestication of certain species) for the capture, and culture production, of inexpensive fish from low trophic levels (detritivores and filter-feeders) for the poorer segments of society.

A sad aspect of the proposed approach could be the possible final sacrifice of the wild status of a few species (the fewer, the better!) selected for full domestication and mass production; for the present situation (see cod!) is not encouraging with respect to avoiding adverse consequences for con-specific wild stocks.

Farming and domesticating fewer species

Choosing the foregoing avenue of restricting aquaculture development to a few representative species would require a focus on well-targeted *demand-led* research, instead of continuing along the path of free-choice, *curiosity-led* research. Such a new orientation should not be difficult, even for those who think that their scientific freedom might be in danger. Overcoming the many pre-domestication obstacles also requires creative thinking. In the early 1950's, I asked the Yugoslav ichthyologist Tonko Šoljan, author of the book "Ribe Jadrane" (Adriatic fishes) and then Director of the Institute for Oceanography and Fishery in Split, whether he felt restricted in his freedom to choose his research subjects under the (communist) rule of those days. He put it this way: "Whether I continue studying the behaviour of lipfish (Labridae) or switch to the behaviour of commercially important fish vis-à-vis fishing gear, does not make a great difference to me since the challenge is there anyhow and, in addition, my research is of societal value." This might have been said to please the rulers, but it is nevertheless worth contemplating.

Present-day thinking about the future of wild resources needs to acknowledge the "driven by profit" reality: make as much as possible as quickly as possible. A few years ago, at an international conference in Denmark, a Thai professor wanted to give me and other colleagues an idea of what people in his country thought about aquaculture. A farmer had come to him and asked him bluntly: Professor, how can I become rich, soonest? Obviously, when this is the starting point of development, regard for sustainable resource utilisation does not rank high, at least in the beginning. However, sustainability is indispensable when we want to save these resources for future generations. It would be unwise not to use the economic impulse as a motor for development. However, society has to make sure that the resource use is genuinely sustainable and warranted.

Again, aquaculture development on the Atlantic coasts of Europe can serve as an example. The farming of Atlantic salmon is the master-piece. Cod is following and probably halibut. But is there a need, or at least a worthwhile opportunity, to include the wolf-fish (*Anarhichas*)? Perhaps one should better wait and see what happens with cod. With cod, will it be possible to avoid what has so far remained a problem with salmon: the consequences of escapes from cages, of genetic intermingling, and of parasite transfer? This must be reconsidered from time to time by all stakeholders (see below), and the discussion should include all countries concerned. The final choice of species could be facilitated by designing standard procedures (with checklists and protocols) to assess acceptability and affordability on the market and the bio-technical feasibility with a view to prospects of economic efficiency.

The intra-specific potential

The agriculture experience shows that only a few species are needed to gain all the different benefits that man can obtain from domesticating terrestrial species. This has been achieved by exploiting the intra-specific genetic diversity inherent in truly domesticated species. The intra-specific potential has apparently also been sufficient to develop breeds adapted to different environments, which holds out good prospects for coping with climate change without necessarily shifting production to different geographical areas. It is of importance to understand that in the case of land animal husbandry the rise of new "landraces" occurred in the context of changing farming systems (Cunningham 1996).

Crossing and back-crossing of races played a significant role in this process, as is becoming increasingly clear with the discovery of different types of genetic markers. Applying genetic markers to African cattle, it was possible to find strong evidence for the separate domestication of the two subspecies *Bos taurus* and *Bos indicus*, the latter having been believed to have been developed as "a later variant from herded *Bos taurus"* (Cunningham l.c.). Perhaps this new methodology could help trace back the history of domestication of common carp (see Part III, Bilio 2008, p. 11). Analogous attempts have been made to distinguish between different origins of the more recently cultured and domesticated gilthead sea-bream (Genimpact Compendium, p. 48).

For domestication in aquaculture to proceed effectively, it appears advisable to consider carefully what has happened in agriculture, in particular regarding the final choice of species. Close attention to the intra-specific genetic potential of aquatic species will be rewarding, especially if ways can be found to assess such potential beforehand.

Much is being undertaken worldwide to conserve biodiversity. Increasing attention is being given to agricultural biodiversity. However, how stable can diversity be? Pedigree stability must be controlled to avoid aberration. Individuals deviating too much from the typical character must no longer be included in the pedigree – unless an interesting new type is discovered, due to a new combination of hereditary characters or even useful mutation, worthwhile to be considered as a new type. Such intra-specific diversity development is certainly faster than inter-specific evolution but - seen the phylogenetic changes – can it be considered completely absent from the inter-specific level in the foreseeable future? Is conservation of biodiversity justified at any cost? In terrestrial animal husbandry, a cost/benefit approach to conserving diversity at the breed level has been suggested (Cunningham l.c.). In aquatic animal husbandry (aquaculture) true domestication is generally not yet sufficiently advanced to apply such procedures, with the exception perhaps of common and some Chinese carps.

Awareness of limitations

Producers should not be criticised for seeking profit. However, they should be persuaded of the need (sometimes even obliged) to follow rules. This will not be too difficult when the sale of a product is hampered by quality deficiencies caused by inadequate disease treatment, unbalanced feed or obvious production failures. Recognition of deficiencies that limit producers' profits, and the need for improvement, are also rather easily recognised when environmental limitations compromise production, e.g. cage culture in shallow bays where pollution effects (deprivation of oxygen) finally damage production itself. More difficult (and much less common) is the recognition and avoidance of mistakes when environment or resources are damaged without affecting production or profit.

It is here where stakeholders other than producers and scientists become involved: consumers and the public in general. Creation of problem-awareness among these stakeholders is of utmost importance when a change of attitude, with a view to political decision-making and legislation, is to be achieved. Such achievements take time and it would, therefore, be necessary to start soon. In the long run, even habits of food consumption can be changed and consciousness of the need for resource protection created, as has been seen in Central and Northern Europe as well as in North America and even partially in Africa, where many terrestrial wild animals and plants are now protected by laws and no longer consumed as food, though mainly for biodiversity conservation and amenity reasons. New jobs and income sources are decisive in Africa, where such opportunities have been created through wild-life tourism. Here again, communication among stakeholders and concerted decision-making are of great importance.

Remaining options for the poor

Two problems arise from opting for targeting high-value species:

(a) Since the major commercial interest in farming aquatic organisms goes to species fetching the highest prices on the market, the need for producing food for the poor has been downgraded.

(b) The requirement for protein close in composition to that of farmed species has favoured the exploitation of "low-value" species, such as small pelagics (clupeids above all) landed by the capture fisheries, processed into fish meal and used as major feed component for high-value cultured species.

The exploitation of "low-value" small pelagics has different consequences. These species were once a major source of income, labour and food for the poorest segments of human populations worldwide. This holds true even for Europe where until the first half of the last century salted herring sustained the poor of many countries. Nowadays, these species are mainly caught by modern commercial fleets, in order to be converted into fish meal and integrated into animal feeds, used not only in aquaculture but, at least formerly, also in terrestrial animal husbandry. In the case of the recently developed tuna fattening in the Mediterranean, they are fed directly to the caged fish. Moreover, as the landings of fishes such as herring decrease, they can come to be regarded as delicacies demanded by the well-to-do. These consequences do not only affect the living conditions of artisanal fisherfolk in certain regions, especially in developing countries, but also the ecosystems in which the respective species is an integral component of lower trophic levels.

How can aquaculture, and in particular the domestication of selected species, provide food also for the poor, either directly or indirectly through the creation of employment opportunities, or by opening up sources of income? So far, incentives other than "big profit" are scarce. Backyard-farming in rural areas, using household and agricultural wastes, is one option and should be increasingly promoted in cooperative projects with developing countries, especially where no such tradition exists. Still not yet realised at large scale, is mass fish culture for the urban poor. The main problem is lack of funding for the true domestication of traditionally well-accepted species that rank low in their respective food webs, thus requiring low levels of animal protein in their feeds. Since the costs of achieving true domestication cannot be borne by the prospective producers, this could be a major objective of cooperative development. Candidate species could be grey mullets (Mugilidae), milkfish (*Chanos chanos*)* and others, in addition to already domesticated species such as the Chinese and Indian carps. Common carp (Indonesia) and tilapia (Africa, Southeast- and East Asia) will not be available as food for the urban poor in the respective regions as long as market prices remain high, at least locally. They need to be well below the 1 US$/kg level (cf. Part II, Bilio 2008, Fig. 5.E and 5.F), although their farming could be seen as an employment opportunity and an income source.

Another option of the rural poor in developing countries is a better use of opportunities offered by the periodical inundation of flat river banks. The natural productivity of such flood plains could be enhanced by constructing small barriers in order to extend the inundation period and thus natural aquatic productivity. The achieved increase in fish production could benefit the capture fisheries. Other examples are the brush parks in Benin ("acadjas") and Cambodia (Lake Tonlè Sap), where productivity is enhanced by the decomposition of branches from trees introduced to establish protected fish nurseries. In addition, large dams constructed for other purposes (power generation, irrigation and the like) could be better used for fish production if an exploitation of the fishery potential would be considered already during the planning phase. The opportunity for culture-based fisheries in such dams is obvious but should be thoroughly planned in view of the ecological compatibility of the species and the biodiversity affected. The former options could be called "ecological enhancement" to be distinguished from enhancement through culture-based capture fisheries. Enhancements should exclude the introduction or transfer of species alien to the continent or region of enhancement.

Urgent issues

The potential for the continuing development of aquaculture at the global level is considerable. However, one problem must be solved soon: the reduction and possibly replacement of fish meal in feeds. Research should be intensified, concerted and coordinated worldwide. At both regional and local levels the availability of water and space can also be problematic. Awareness of these limitations can help in finding timely solutions that will allow reliable planning. Controlled depuration of effluents from fish farms is essential, at least in industrialised countries, as is the availability of uncontaminated water for farming. And another question, concerning cage culture, arises: is the carrying capacity of the oceans really unlimited? Some people contemplating intensification of the oceans' biological

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* It is not clear whether the world aquaculture production of grey mullets (flathead grey mullet, *Mugil cephalus*, ~150,000 t) and milkfish (*Chanos chanos*, ~600,000 t) is mainly based on capture-based aquaculture or on true domestication (see Part II, Bilio 2007b, p. 15, Table 6).

production by fertilising them seem to think so. And what about the implications of offshore aquaculture in this and other respects? Finally, what are the consequences of ballast water exchanges at sea and the possible transfer of potential invaders, parasites and diseases to fish in offshore cages?

Obviously, in addition to their continuing availability, it is essential that feed stuffs and water be free from contaminants. This has long since been recognised, but is of increasing importance. Richardson (2003) has dealt with the effects of man-made changes in the environment on capture fisheries, which are relevant also for aquaculture as long as farms are not fully controlled recirculation systems using truly domesticated organisms. Richardson stresses the need for the principle of "responsible fisheries" to focus not only on the effects of fisheries, but also on the opposite direction, i.e. the consequences of environmental changes on fisheries (and aquaculture; addition by the present author).

A significant issue is the contamination with dioxin(s), known to a wider public in Europe from the Seveso accident. However, the Seveso dioxin can only be seen as a metaphor for a wide range of novel contaminants and pathogens meanwhile considered as being potentially harmful to humans consuming organisms from affected areas (CIESM 2004). Aquaculture is concerned particularly through feed components containing such substances (Tuominen & Esmark 2003). In 2001, at the EAS/WAS World Conference on Aquaculture in Venice, Italy, Kinne (1986) concluded that in the end aquaculture would have to resort to recycling of suitable wastes from different sources to solve the feed problem. What was not considered in this vision, is the need to decontaminate and depurate much of such wastes from toxins and germs. Suitable procedures are in demand already now (Betts 2004), seeing the present levels of contaminants, some of them perhaps still tolerable, detected in farmed salmon.

Is there, under the given circumstances and with the present knowledge, any opportunity for aquaculture to mitigate or overcome serious contamination threats to its products at least in the medium-term? The answer would, first of all, require conclusive research results as to concentrations and circumstances under which contaminants become harmful to the consumer. Only after pertinent and reliable tests, can it be decided to which degree the quality of feed and water must be monitored and which are the maximally tolerable levels. At present, it seems that substituting vegetable for fish protein could at least reduce dioxin and similar loads, but what remains is the issue of taste (Betts l.c.) – a problem opposite to that of land animals fed too high a percentage of fish or fish meal.

True domestication of a limited number of species could eventually reduce the problem by limiting its specific variability. How much of a vegetable component could be used, would depend on the species and the reaction of the consumers. To maintain the fishy taste of the final product, a transitional solution could be the admixture of fish meal and oil containing tolerable concentrations of contaminants. Apart from the taste, there is the present experience with producing fuel from vegetables that competes with food production (and indirectly even affects rain forest conservation through soybean plantations for feed production).

The future of the wild stocks

What about the wild populations, in particular those becoming "niche species" in case only a few species were fully domesticated, as envisaged further above? Once these wild resources were relieved from the present fishing pressure, those already overexploited or even threatened would have to be replenished, protected and, where necessary, saved from extinction. Culture-based fisheries, restricted to well-conceived hatchery production of seed as much as feasible and opportune, would have an important role to play in this context. Sustainable management of wild populations could become easier.

Unavoidable "pre-domestication" effects (e.g., unintentional selection through mortalities due to non-adaptability to hatchery conditions; see Part I, Bilio 2007a, p. 7 and Part II, Bilio 2007b, p. 16-19) would probably have to be accepted. Concerning Pacific salmon ranching in North America, Brannon et al. (2004) advocating hatchery production to maintain and enhance fisheries[1], emphasise the adequacy of releasing fish propagated under controlled conditions, into river systems from which their parent generation originated. This makes sure that, among other things, the released fish match their wild counterparts in emigration and spawning period as well as in juvenile size, and it would preserve local genetic diversity. (The need to avoid pre-domestication effects as much as possible is discussed in Part III, Bilio 2008, p. 7-12 and 13-15.)

Feral populations[2]

A subject that, for lack of time, has been deliberately omitted from this paper, should be raised by future authors. It is the complex question of those truly domesticated species being released or escaping from farms in continents, regions or countries outside their natural distribution area (cf. Part II, Bilio2008, Table 5, p. 12-13). What are the prerequisites and conditions for feral populations to develop? What are the dangers or even chances? As with the establishment of the Pacific cupped oyster in the Atlantic, what is the present situation of rainbow trout in Europe, Japan and Chile, of Atlantic salmon on the Pacific coast of North America and Chile, of the Chinese carps in eastern Europe? Which are the reasons why the Indian carps remained limited to the Indian subcontinent and adjacent countries? There is obviously a rather wide field to be covered, by a comprehensive review of the literature first and by further investigation later.

Stakeholder involvement

Any further development of aquaculture, considering or not an increase of true domestication efforts in a

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[1] The authors plead for a broadened concept of hatcheries including "stream-side gravel incubation boxes (reference), spawning channels (reference) and engineered streams (reference)" and say that "In any of these hatchery facilities, survival to the fry and advanced fingerling stages is greatly increased over that found under natural conditions."

[2] Definition in Part III, p. 11, footnote

restricted number of species and their implications for capture fisheries (as well as for combinations between these and aquaculture), should be discussed and agreed among all stakeholders – country-, region- and, where appropriate (blue-fin tuna), also worldwide. Stakeholder involvement should include capture- and culture-fisheries (see Hansen & Windsor 2006, p. 18), practice and scientific research, resource protection and management, producers and consumers, society segments concerned, and public authorities. All potential resource users must have a say in this context, as has already been envisaged and partially achieved with integrated coastal zone management (ICZM).

Appropriate stakeholder participation in planning and development is essential to anticipate and avoid dead ends or foresee and overcome bottle-necks, at least within the realm of possibility. Research and modelling require inputs from various sources having a bearing on the subject in question. Unnecessary controversies could be avoided, conflicts could be nipped in the bud and dangers diverted in advance. Expensive scientific research should only be applied where really necessary and helpful, and fundamental research limited to areas of basic importance (see also Bilio 1996). To obtain maximal benefit from stakeholder involvement, communication must be improved and adapted to the various levels of education involved ("multi-faceted communication", Bilio 1997 and 1999). Public authorities at the political level must be convinced of the need for mid- and long-term perspectives requiring reliability of R&D funding.

There is not much time left to save the remaining resources and to improve the life conditions of the poor, acting soon should be the motto of the present time. True domestication of a few wisely selected species could help save the wild resources for future generations and, by sharing know-how and R&D funding with developing countries, also provide animal protein and thus more quality of life for the most needy. Further development of aquaculture, in coordination with all stakeholders, will soon have to cope with the limited nature of all resources on earth, to be shared among its inhabitants in the most balanced and equitable way possible.

SUMMARISING CONCLUSIONS

In the following, the references to the three previous parts of this paper are restricted to part and page numbers, Part I being Bilio 2007a, Part II Bilio 2007b, Part III Bilio 2008.

1. **Range:** The paper is restricted to finfish, crustaceans, and bivalves; not considered are gastropods (with the exception of abalones), amphibians, reptiles, exclusively ornamental fishes, and plants. (Part I, p. 5, and Table 1, p. 8-14)
2. **Terminology:** For mainly practical reasons, it appears useful to subdivide the production of aquatic organisms in captivity (animals) or under cultivation (plants and bacteria) into pre-domestication, traditional domestication and biotechnological genetic improvement, and the traditional domestication into uncontrolled and targeted domestication. Wild inputs may be necessary also during he domestication phase proper in order to avoid inbreeding and to enlarge the genetic basis of intra-specific diversity (Part I, p. 6-8; Part II, p. 9, 16, and 21-22)
3. **Criteria:** The achievement of continuous controlled reproduction is suggested as the decisive criterion for the distinction between pre-domestication and traditional domestication, whereas for the distinction between traditional domestication and gene-technological improvement it appears appropriate to use "genetic engineering" in the widest sense of the term, including genetic marking (Part I, p. 7-8). The choice of three continuous reproductive cycles under controlled conditions as criterion for achieved domestication is arbitrary and preliminary for cases in which more specific information is lacking (Part I, p. 8 and Part II, p. 9).
4. **Practice and research:** Aquaculture is a field of production in need of scientific research; however, research can only be rationally applied when experience and information between practice and research are continuously exchanged through adequate communication channels. (The present part)
5. **Species domesticated:** According to the definition and results of this paper, the number of truly domesticated aquatic species hardly exceeds that of the number of domesticated terrestrial species. A positive correlation seems to exist between the level of production and true domestication. (Part I, Table 1, p. 8-14; Part II, Tables 5 and 7; Part III, p. 17)
6. **Stability:** Steps of domestication beyond continuous controlled reproduction are selective breeding and pedigree establishment; the results of selective breeding, as well as those of gene-technological improvement, must undergo stability tests before becoming acceptable at a commercial level. (Part II, p. 16-21)
7. **Mass production:** It has been demonstrated that aquaculture is capable of mass production far beyond the potential of the capture fisheries of the same species but, for the time being, this is accompanied by the danger of affecting the con-specific wild populations. (Part II, p. 11-16; Part III, p. 5-7)
8. **Threats:** The recent development of cage culture of Atlantic salmon, and the first experiences with Atlantic cod, show the potential negative genetic and other implications of mass production for the con-specific wild populations. (Part III, p. 11/12, and the present part)
9. **Interaction:** It is of paramount importance to avoid genetic and other interactions (such as parasite and disease transfer) between farmed organisms and wild populations through technological improvement of confinement as well as through the creation of genetic barriers by means of selective breeding or gene-technological intervention. (Part III, p. 9-13)
10. **Gene technology:** The most significant progress so far has been made through the discovery and utilisation of genetic markers for the distinction of subspecies and races (strains, morphs) and for the ascertainment of the origin of transferred batches of seed or breeders. Attempts at creating sterile farm fish were so far not fully successful; moreover, parallel raising of fertile fish would be needed for continuous controlled reproduction and selective breeding. An important objective for the creation of transgenics would be the establishment of genetic barriers

between farmed and wild fish. (Part III, p. 12-13, and the present part)

11. **Enhancement:** Interventions aiming at enhancement, replenishment, saving, and re-establishment of wild resources must make sure that the controlled reproduction of seed (culture-based fisheries) is kept free from domestication or pre-domestication effects as much as possible. (Part III, p. 7-9, 13-15)
12. **Capture-based:** Wild resources should not be continuously used for aquaculture production; capture-based aquaculture cannot realistically be considered more than a transition phase, historically as well as at present and in the future. (Part III, p. 15-17)*
13. **Diversity:** The future of diversifying aquaculture production should not be sought in subjecting ever more species to aquaculture experiments, but in developing intra-specific diversity through the creation of stable strains (pedigree establishment) and by diversifying culture and processing techniques. (Part III, p. 17-18, and the present part)
14. **Value and prices:** An important consequence of mass production through domestication is a value and price decrease, making originally high-priced species affordable to intermediate segments of the human population. (Part III, p. 18-19, and the present part of this paper)
15. **Target consumers:** The increasingly important target segments of the human population as consumers of aquaculture products are the classes at intermediate income levels, in particular in the industrialised countries. (The present part)
16. **Niche species:** As a consequence of an increasing affordability of formerly expensive species by the middle classes through mass production of truly domesticated species, the demand of the wealthiest segments of the human population could be satisfied by the capture fisheries, where rare species fetching particularly high prices could become "niche species". (The present part)
17. **The poor:** The lowest income levels of human populations and countries can benefit from fish production through *rural* low-input/low-output systems (backyard ponds), as well as through culture-based and "ecological" enhancement of capture fisheries. A substantial increase in the availability of fish for the *urban* poor through domestication and mass production of suitable species would require R&D assistance of the developed world. (The present part)
18. **Climate change:** True domestication could render species more independent of climatic influences through selective breeding, thus exploiting intra-specific potentials of diversity. (Part II, p. 22-23, and the present part)
19. **Strategy:** Full domestication and exploitation of the intra-specific diversity potential of a few species through selective breeding could satisfy most of the world's demand for fish, while well-conceived culture-based fisheries could save, replenish and enhance the wild stocks of the many other species. Such an approach could put the wild status of the con-specific stocks of the few fully domesticated species at risk, if measures of separation between farmed individuals and wild populations fail. (The present part)
20. **New feedstuffs:** Fish meal must increasingly be replaced by organic wastes and vegetables in order to sustain mass production of domesticated fish; where necessary new feed components must be decontaminated from toxins and adequately treated to eliminate pathogens. (The present part)
21. **Stakeholders:** It is necessary to involve all stakeholders in decisions on the future utilisation of the living aquatic resources, in particular those of the oceans, the sustainable exploitation of which must be recognised as a global concern. (The present part)
22. **Animal behaviour:** When trying to accelerate the domestication process, maximum attention should be paid to the fact that living beings are concerned, about whose conditions of well-being we still know very little, and that one should, therefore, treat them with particular care. (Part II, p. 16-18)
23. **Limited world resources:** Stakeholders of aquaculture should from time to time discuss the availability of feedstuffs, water and space on earth with other users of the same resources in order to recognise the future limits of development and to discuss how to cope with them. (The present part)

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* The document on capture-based aquaculture (Ottolenghi et al. 2004) is restricted to four species groups fetching extremely high prices, and its preparation was financially assisted by the government of a country where market demand of these species is at maximum.

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EPILOGUE

As can be seen from the dates of publication of the four parts of the present paper, there is a history behind this publication, not least a learning history of the author. With all the contradictory experiences, trying to be as realistic as possible, without giving in to wishful thinking, this paper is not intended to be taken as a plea against aquaculture. However, more realism is needed. Perhaps it is more convincing to quote a letter that I just wrote to a Norwegian colleague heavily involved in trying to prevent the consequences of rather early life stages of cod spawning in net cages:

"Dear T., I certainly wish you success, although wishful thinking has often been disappointing in the end. Nevertheless, we (in this case: you) have to do our best. However, we also have to face the worst scenario. And the strongest "enemy" is the profit-seeking entrepreneur (and motor of development; addition by the author to avoid misunderstandings). *If you succeed, the better. But what about all those people that have no mind to listen to reason? The super-rich in the far east above all (but not only there). Success with your trip and with all your endeavour! M. PS: Let me insist, once more – shouldn't there be possibilities to find inhibitors of maturation to be added to the feed?"*