

26 Aquaculture, the Next Wave of Domestication

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Aquaculture, the fastest growing sector of global food production, accounts for nearly 40% of aquatic production and will soon surpass capture fisheries, forecast to collapse by mid-century. While “animals are not essential” (Harlan, 1995), fish and shellfish make up a substantial portion of human diet, supplying protein and nutrients essential for human development and health. Aquaculture relies largely on natural reproduction or hatchery propagation of wild stocks and boasts few domesticated species (common carp, rainbow trout, Atlantic salmon). There are enormous challenges in conserving while utilizing the planet’s imperiled aquatic biodiversity. Overfishing, introduction of nonnative species, adverse interaction of wild and farmed stocks, and ocean warming and acidification are risks to aquatic genetic resources. The high fecundity of marine fish and shellfish, in particular, creates the risk that release or escape of large, hatchery-propagated families will dilute the genetic diversity of wild populations. Research on developing and improving domesticated stocks for aquaculture should have high priority alongside research on reducing or eliminating interactions with wild populations. There is an opportunity that Jack Harlan would have relished, to document the domestication process in aquaculture, though its course in the human-dominated world is likely to differ markedly from that of plant and animal domestication.

1

Aquaculture

How inappropriate to call this planet Earth, when clearly it is Ocean. (Arthur C. Clarke)

Both Harlan Symposia have naturally focused on the terrestrial species, whose domestication irrevocably changed the course of human history and evolution. Humans have domesticated a remarkably small number of plants and animals for food and fiber, many more plants than animals, although corn, wheat, and rice provide half of the protein consumed by humans. A similarly narrow diversity of animals is the basis of livestock production, and Diamond (1997) has argued that,

owing to the complex suite of characteristics required, all animals capable of domestication have been domesticated. Certainly, no terrestrial animal is likely to replace the cow, pig, sheep, or chicken. Yet it would be wrong to conclude that domestication is now a matter of history, for a new wave of plant and animal cultivation and domestication is building on planet Ocean.

Globally, per capita annual consumption of fish is 16.4 kg, about 7.8% of total protein consumption, although this ranges by region or country from less than 1 kg to more than 100 kg per person (FAO 2007). While “animals are not essential; plants supply over 90% of the food consumed by humans” (Harlan 1995:240), humans do obtain, in addition to protein, many beneficial nutrients, such as omega-3 fatty acids, from aquatic plants and animals. Until very recently, much of the supply of aquatic living resources came from capture fisheries, which a century ago seemed limitless. Thomas Huxley, the pre-eminent Victorian naturalist, famously stated (Huxley 1883): “I believe, then, that the cod fishery, the herring fishery, the pilchard fishery, the mackerel fishery, and probably all the great sea fisheries are inexhaustible; that is to say, that nothing we do seriously affects the number of the fish. And any attempt to regulate these fisheries seems consequently, from the nature of the case, to be useless.”

Of course, fishing methods became much more efficient than Huxley could have anticipated, under a variety of technological advances (the steam and diesel engines, radar, sonar, and global positioning systems) and government subsidies that permitted humans to exploit fully and beyond sustainable limits a third of world fisheries by the year 2000 (FAO 2007). According to statistics of the Food and Agriculture Organization (FAO), production from capture fisheries reached a plateau of just over 90 million metric tons (mmt) per year in the 1980s, a figure close to Ryther’s (1969) prediction of 100 mmt based on calculations of global marine primary productivity. The apparent stability in global average production from capture fisheries belies alarming signals of over-exploitation, fisheries collapses, and increasing exploitation of species at lower trophic levels. Indeed, Worm *et al.* (2006) predict the demise of global capture fisheries by 2050. Although debate continues about the status of fisheries, the causes of fisheries collapses, and the path to sustainability (Pauly *et al.* 1998, Myers and Worm 2003, Worm *et al.* 2006, Sibert *et al.* 2006, 2007, Hilborn 2007), capture fisheries, even if managed for sustainable harvests, clearly cannot meet the demand of the 9 billion humans projected for the mid-twenty-first century.

World fisheries supplies have steadily increased – to 155 mmt in 2006, the latest year for which data are available – despite the plateau in capture fisheries production, because of a rapid increase, since the early 1970s, of aquaculture, the farming of aquatic plants and animals (Figure 26.1). Aquaculture now supplies over 40% of all fisheries products and, growing at about 9% per year, will surpass capture fisheries as the dominant source of aquatic food within a few years. The inherent efficiency of producing protein from endothermic organisms in a three-dimensional aquatic environment, compared with traditional livestock species, was pointed out long ago by Bardach *et al.* (1972). Aquaculture can also provide protein with less

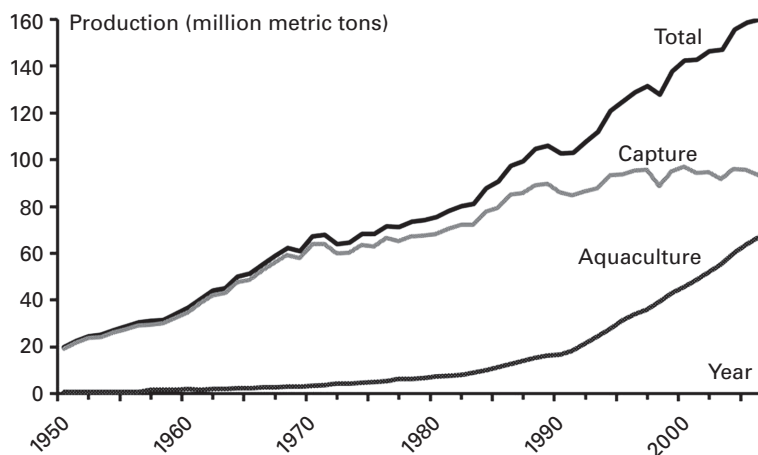


Figure 26.1. World production from capture fisheries and aquaculture (data from FAO 2007). Increases in world supplies since the 1980s have all come from aquaculture.

emission of greenhouse gases and less use of water resources than terrestrial systems; the Los Angeles Times reports, for example, that a six-ounce portion of beef results in the emission of 7,166 CO₂ equivalents, whereas the same amount of steamed mussels produces only 65 CO₂ equivalents (Wiess 2008). Although the negative environmental impacts of salmon and shrimp aquaculture have received attention (e.g., Naylor *et al.* 2000), environmental concerns are being addressed through the development of new technologies, alternative feeds, better management practices, standards for sustainability, and third-party verification. Aquaculture can be done with no more and possibly much less environmental impact than traditional agriculture or poorly managed capture fisheries. Carp aquaculture in central and eastern Europe has been sustainable for about eight centuries; indeed, Balon (2004) provides a remarkable example of sustainability. “Rožemberg pond, which was built in the 16th century and covers 711 ha. . . still operates on the 2 to 3 year cycle of common carp production (Kourzil & Guziur 2004).” Farming the sea and the domestication of new species for aquaculture are inevitable (Marra 2005).

Aquaculture is generally classified as extensive or intensive, according to the extent of control over environmental factors and input of feed. Extensive aquaculture of herbivorous or omnivorous fish and filter-feeding shellfish accounts for more than 80% of global aquaculture production (Figure 26.2). Stock enhancement, the practice of rearing early life stages in a hatchery and then releasing them into the wild to enhance capture fisheries, might also be viewed as an extensive, albeit inefficient, form of aquaculture.

The phylogenetic diversity of cultivated aquatic species is much broader than that in terrestrial agriculture, comprising fish, sea urchins, mollusks, crustaceans, and red, brown, and green algae (Figure 26.3). Given the diversity of species and culture methods world-wide (reviewed elsewhere: Bardach *et al.* 1972,

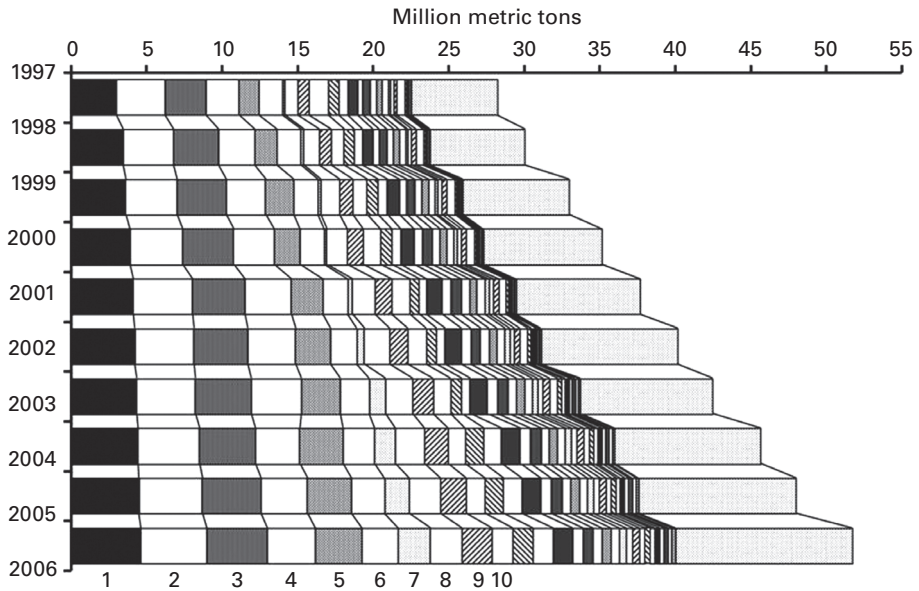


Figure 26.2. Aquaculture production, by species (data from FAO 2007). The upper ranks are dominated by filter-feeding molluscs or herbivorous or omnivorous fishes; production of carnivorous species, which has received much criticism, comprises a small fraction of total aquaculture production. The top ten species are: (1) Pacific oyster, (2) Silver carp, (3) Grass carp, (4) Common carp, (5) Manila clam, (6) Bighead carp, (7) Whiteleg shrimp, (8) Crucian carp, (9) Tilapia, (10) Japanese scallop.

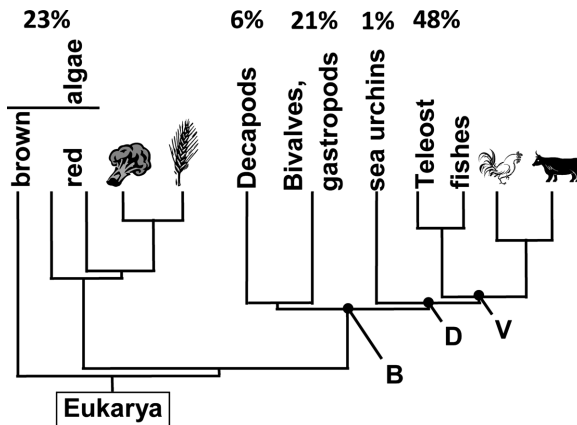


Figure 26.3. Phyletic diversity of aquacultural vs. agricultural species. Percentages above aquacultural species are contributions to global production. Nodes showing the separation of the bilaterian, deuterostome, and vertebrate animal clades are marked B, D, and V, respectively.

Stickney 1986, FAO 2007), a complete review of domestication and conservation of biodiversity in aquaculture is beyond the scope of this short chapter. Rather, the purpose of this chapter is to delineate main issues, primary challenges, and opportunities in aquaculture domestication and conservation of aquatic biodiversity, illustrating these, by necessity, with examples from the limited perspective of personal experience.

2 Domestication of aquatic species

If one takes domestication to mean profoundly changed from wild progenitors, less than a handful of aquatic species have been domesticated: goldfish, common carp, and perhaps two aquarium fishes, guppies and neon tetras (Balon 1995, 2004). These few aquatic domestications, moreover, are quite recent. While fish and shellfish culture trace back to Roman times (e.g., Günther 1897), Balon (2004) dates the domestication of the common carp, in Europe, and the goldfish, in China, both to the twelfth century. Other food species, such as rainbow trout, Atlantic salmon, Pacific salmon, tilapia, channel catfish, and several Asian carp species, as well as aquarium species, such as swordtails, platies, zebra fish, and discus, are regarded by Balon (2004) as in transition to domesticated status. Recently, Duarte *et al.* (2007) called attention to rapid domestication of aquatic species, but their liberal definition of domestication – “breeding, care, and feeding of organisms are controlled by humans” – leaves species unchanged from their wild progenitors, a key criterion in most definitions of domestication. For the most part, aquaculture is in the proto-domestication phase (Harris and Hilman 1989), in which the fish and shellfish are no more than exploited captives (Clutton-Brock 1981). The trend documented by Duarte *et al.* (2007) simply reflects the growth of aquaculture globally. The history of aquatic domestication will be written, perhaps, after another century.

Genetic improvements of domesticated species are well known and widely appreciated. Physiological and morphological changes in aquatic species will likely be just as profound and perhaps more dramatic for their rapidity, since the principles of breeding are now well developed, widespread, and aided by modern molecular and genomic approaches. More importantly, substantial levels of genetic diversity still exist in extant natural populations, from which most aquaculture species continue to be derived. Improvements in yield of c.10%–15% per generation have been obtained in Atlantic salmon, rainbow trout, tilapia, and the Pacific oyster (Bentsen *et al.* 1998, Gjedrem 2000, Langdon *et al.* 2003). The controversy over interaction of farmed and wild Atlantic salmon (see below) testifies to the extent of genetic change in that species and makes a case for considering Atlantic salmon an emerging domesticated species. Insofar as domestication and genetic improvement of aquatic species will increase the efficiency and sustainability of aquaculture, research towards these ends must be encouraged.



Figure 26.4. Growth heterosis (hybrid vigor), evident in the contrast of inbred and hybrid Pacific oysters produced by a factorial cross of two partially inbred lines, suggests that aquaculture yields could be improved several-fold.

Most of the initial improvement in production characteristics of aquatic species, such as the Atlantic salmon, has been based on additive genetic variance and realized by standard methods of individual or family selection. Nonadditive variance is relatively more important in breeding of common carp, perhaps because additive genetic variance has already been fixed during the longer history of carp domestication (Wohlfarth 1993). Nonadditive variance may also be relatively more important in marine species than fresh water species. The Pacific oyster, for example, shows hybrid vigor (heterosis) for yield (Figure 26.4) that is as dramatic as that in maize (Shull 1908, Crow 1998), particularly since it emerges, not from crosses among major landraces, but from crosses among partly inbred lines derived from a single wild population (Hedgcock and Davis 2007). Dramatic heterosis for yield in oysters is associated with equally dramatic levels of inbreeding depression (Evans *et al.* 2004) and mutational load (Bierne *et al.* 1998, Launey and Hedgcock 2001), which is consistent with the dominance explanation of heterosis (Crow 1998) and was predicted by G. C. Williams' (1975) Elm-Oyster model for the advantages of sexual reproduction in species with high fecundity and high early mortality. Since high fecundity and high early mortality are the dominant life history among marine fish (Winemiller and Rose 1992) and invertebrates (Thorson 1950), we might expect considerable scope for genetic improvement and domestication to come from crossbreeding.

3

Conservation

Conservation of genetic resources for agriculture employs strategies and approaches that are often distinct from those employed in conservation of natural biodiversity (seed banks versus protected reserves, for example). Conservation of genetic

resources for aquaculture, on the other hand, is tantamount to conserving natural aquatic biodiversity, since aquaculture is largely exploiting captives from the wild. Thus, the strategies and approaches employed to conserve wild and cultured aquatic species may be similar. The challenges in conserving, while utilizing, the planet's imperiled aquatic biodiversity are enormous and global in nature (Dulvy *et al.* 2003, Jackson 2008). It might be argued that the biodiversity of planet Ocean is more at risk in a human-dominated world with a global economy than was the terrestrial biodiversity of planet Earth at the time of crop and livestock domestication.

The global problem of overfishing has already been mentioned. Jackson *et al.* (2001) argue that overfishing preceded a host of contemporary problems causing disturbance and extinctions in coastal ecosystems. Now, "Synergistic effects of habitat destruction, overfishing, introduced species, warming, acidification, toxins, and massive runoff of nutrients are transforming once complex ecosystems like coral reefs and kelp forests into monotonous level bottoms, transforming clear and productive coastal seas into anoxic dead zones, and transforming complex food webs topped by big animals into simplified, microbially dominated ecosystems with boom and bust cycles of toxic dinoflagellate blooms, jellyfish, and disease" (Jackson 2008).

Coastal ecosystems are characterized as heavily invaded by nonindigenous species (Grosholz 2002); most biological invasions are attributable to shipping via the transport and exchange of ballast water (Ruiz *et al.* 2000), although purposeful, accidental, or inadvertent introductions of nonnative species, owing to aquaculture or the aquarium trade, for example, have also caused profound changes in coastal ecosystems. Purposeful introductions can be curtailed, in principle, with regulations and enforcement, but often these are lacking or insufficient to prevent some intentional or accidental introductions (NRC 2004).

A suite of life-history traits that characterizes the majority of marine fish and shellfish – relatively late maturation, high fecundity, small eggs, long-lasting and widely dispersing plankton-feeding larvae, and broad geographic ranges (Thorson 1950, Winemiller and Rose 1992, Palumbi and Hedgecock 2005) – makes these marine populations more vulnerable to loss of variation and extinction than one might suspect, based on their sheer abundance. These life-history traits appear to be adaptations to a biphasic life cycle, in which larvae disperse to planktonic habitats, far from potentially cannibalistic adults, but face tremendously high, though variable, early mortality. Conservation of such species depends, therefore, not only on protection of adult forms but also on the preservation of a vast, poorly delimited and understood planktonic environment. Conservation of planktonic larval forms has no counterpart in terrestrial conservation.

High fecundity, on the order of a million or more eggs per female per spawning event, and early mortality, typically in the range of 10%–20% per day, makes possible a high variance among spawning individuals in reproductive success, which is defined as the number of offspring contributed to the next generation.

Successful reproduction for most marine animals requires a complex chain of events, from the reproductive maturation and spawning of adults to external fertilization of gametes, development, growth and survival of the larval forms, metamorphosis and recruitment into the adult habitat, and survival and growth of juveniles to maturity. Reproductive activity, though often tuned to the annual seasonal cycle, must still match highly variable local conditions for this chain of events to be complete. The chances of successful reproduction can thus vary dramatically for individuals, perhaps even among individuals adjacent to one another in space but spawning at slightly different times. Consequently, reproductive success in marine organisms might, at times, resemble a sweepstakes lottery, in which there are a few big winners and many losers (Hedgecock 1994).

The hypothesis of Sweepstakes Reproductive Success, which makes testable predictions about temporal genetic change in populations and variance in the genetic composition of new recruits, has received a measure of support from both empirical (e.g., Li and Hedgecock 1998, Hauser *et al.* 2002, Turner *et al.* 2002, Hedgecock *et al.* 2007, Lee and Boulding 2007) and theoretical studies (Waples 2002, Hedrick 2005, Eldon and Wakeley 2006). The implication of this hypothesis for conservation is that these seemingly inexhaustible living marine resources may have effective population sizes that are orders of magnitude smaller than census sizes and, thus, rates of genetic drift and inbreeding that may erode biodiversity on ecological time scales.

Adverse interactions of wild and hatchery-propagated stocks are likely growing with the global expansion of aquaculture (McGinnity *et al.* 2003, Hindar *et al.* 2006) and stock enhancement programs (Born *et al.* 2004). High fecundity creates the risk that release or escape of large, hatchery-propagated families will dilute the genetic diversity of wild populations. Ryman and Laikre (1991) first called attention to this problem, using a simple mixing equation to determine the effective size of a fish population comprising both naturally (wild) and artificially (hatchery or captive) propagated components, $\frac{1}{N_e} = \frac{x^2}{N_c} + \frac{(1-x)^2}{N_w}$, where N_e is the effective population size of the mixed population, N_c is the effective size of the captive or hatchery population, N_w is the effective size of the wild component, and x is the proportion of the spawning population of hatchery origin. In the marine realm, where fecundities are higher than for fresh water species, the risk that an enhancement program might dilute genetic diversity of a wild population is great but manageable with appropriate data and care (Hedgecock and Coykendall 2007).

One way to eliminate much of the risk of interaction between wild and hatchery stocks is to render farmed stocks sterile. Triploidy can be induced in bivalve mollusks and even some fish; triploid animals tend to be effectively sterile and can be cultured in the wild with little risk that they will spawn and release planktonic and highly dispersing offspring into the coastal environment. The ability to culture triploids thus frees aquaculture to pursue the benefits of domestication while minimizing or preventing the interactions of farmed and wild stocks.

4 Conclusions

Research on developing and improving domesticated stocks for aquaculture, together with research on reducing or eliminating interactions between wild and farmed populations (e.g., by inducing triploidy in hatchery-propagated stocks) should have high priority.

There is an opportunity that Jack Harlan would have relished, to document the domestication process in aquaculture, though its course in the human-dominated world is likely to differ markedly from that of plant and animal domestication.

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