ECOLOGY

Rapid Domestication of Marine Species

Domestication has had higher success rates in the sea relative to those seen in the long history of land species' domestication. The rise of aquaculture has global consequences.

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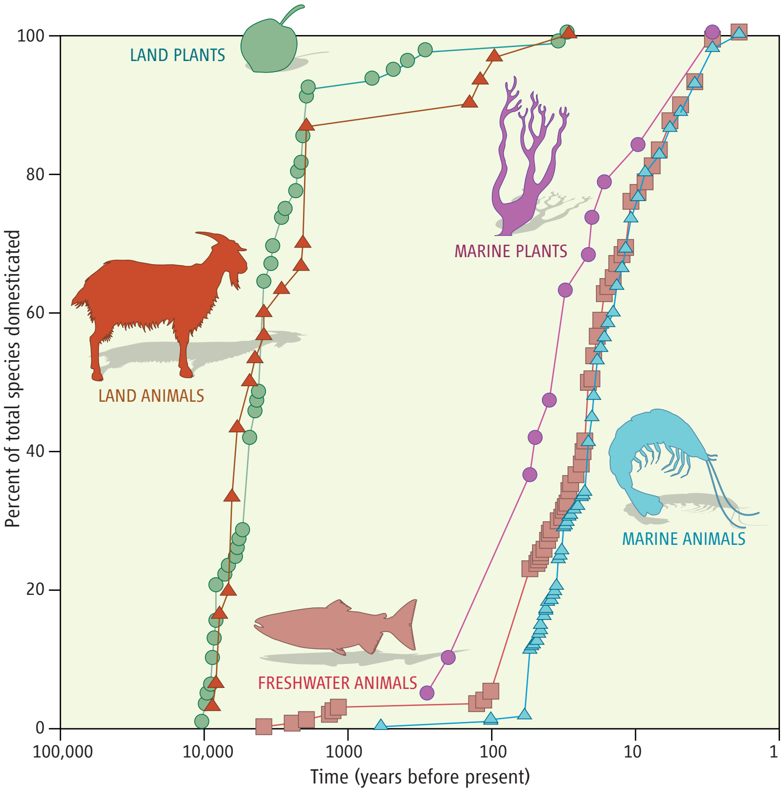
About 11,000 years ago, humans began to domesticate plants and animals (*1*–*3*). In the next 9000 years, hundreds of land species and a few aquatic species were domesticated. Since then, however, few land species have been domesticated. In contrast, the domestication of aquatic—particularly marine—species has grown exponentially. Aquaculture is emerging as a revolution in agriculture of global importance to humankind.

Domestication of wild species to produce food means that the breeding, care, and feeding of organisms are controlled by humans (*4*). By 2000 years ago, an estimated 90% of the species presently cultivated on land had been domesticated. Since the industrial revolution, the increase in the numbers of domesticated land plant and animal species has been modest (~3%) (see the figure).



Land versus water. Most land species were domesticated earlier than aquatic species, but in the past 100 years, many more aquatic species than land species have been domesticated (*6*).

In contrast, the rise of aquaculture is a contemporary phenomenon (*5*). 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) (*6*). The number of aquatic species domesticated is still rising rapidly (see the figure) (*6*). Even allowing that the rates for early domesticates are estimates, aquatic domestication rates are ~100 times as fast as the rates of domestication of plant and animal species on land over the period when domestication was fastest (see the table) (*6*). Despite a vastly longer history, the domestication of land species has been less successful than that of marine species (*7*), particularly for animals: 0.08% of known land plant species and 0.0002% of known land animal species have been domesticated (*7*), compared with 0.17% of known marine plant species and 0.13% of known marine animal species. Effective genetic improvement programs for many aquaculture species (*8*) should be facilitated by their huge reproductive output and short generation times compared to those of domesticated land animals.

There are several reasons for this contrast between the success in the domestication of land and marine animal species. First, land domestication has drawn largely from mammals and birds, with few invertebrates (such as bees and snails) domesticated. In contrast, a diverse array of marine taxa—including mollusks, crustaceans, vertebrates, echinoderms, jellyfish, and worms—have been domesticated (*9*, *10*). Many more wild marine species are used as food [more than 3000 marine species compared to fewer than 200 land species (*9*, *11*, *12*)], providing further scope for future domestication.

Second, the greater diversity of life forms in the ocean compared to those on land provides a broader range of opportunities for domestication. The limited success in domesticating land animal species has been attributed to the paucity of suitable species: Many land plants are poisonous or toxic to humans, and many land animal species have slow growth and long life cycles, specialized diets, or adverse behavioral traits (*3*).

Third, aided by the rapid spread of technical and scientific knowledge, domestication of aquatic species is developing globally, whereas land species were domesticated in just a few regions (*1*–*3*). A similar global effort to domesticate additional land animal species is precluded by the paucity of candidate species and the lack of market demand.

The domestication of an aquatic species typically involves about a decade of scientific research (*13*). Current success in the domestication of aquatic species results from the 20th-century rise of knowledge on the basic biology of aquatic species and the lessons learned from past success and failure. The domestication of aquatic species also involves fewer risks than that of land animals, which took a large toll in human lives through diseases transferred from herds (*3*); no human pathogens of comparable virulence have yet emerged from aquaculture.

The stagnation in the world's fisheries and overexploitation of 20 to 30% of marine fish species (*11*) have provided additional impetus to domesticate marine species, just as overexploitation of land animals provided the impetus for the early domestication of land species (*2*). Aquaculture production has been growing at rates of ~7 to 8% per year (*5*), compensating

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for the stagnation of fisheries, and is likely to become the main source of marine food for humans as demands continue to grow.

The broad range of domesticated marine species helps to integrate the production across trophic levels, thereby maximizing output while decreasing environmental impact (*14*). It also increases the range of marine habitats where aquaculture can be conducted, and diversifies food sources and generates a wide range of market prices for aquaculture products. However, aquaculture development also has negative consequences for the environment and biodiversity, including deterioration of coastal ecosystems by aquaculture effluents and impacts on wild species used as feed (*15*). The continuity of present rates of domestication and the capacity of aquaculture to meet the rising demands for seafood of a growing human population require that, by minimizing environmental impact, a sustainable model be achieved. Domestication should aim at closed production cycles, where feed is produced in the farm and the target organisms reproduce and grow from egg to adult in culture, reducing pressures on wild stocks.

The increase in aquaculture has global consequences, both as a food source and in terms of environmental implications. The development of aquaculture is bound to replace fisheries as animal husbandry replaced hunting on land. This should help release pressure on increasingly scarce freshwater resources used to produce food on land, and stimulate technological developments. These changes will modify employment and livelihood patterns of those involved in this industry. The growth in the domestication of marine biodiversity thus represents a fundamental change in the way humans relate to the oceans.

Global pace of species domestication

Species group	Number of species domesticated	Time since domestication (years before present)		Specific growth in the number of domesticated species (% year^{-1})
		50% species domesticated	90% species domesticated	
Land plants	250	4000	2000	0.026 (76)
Land animals	44	5000	146	0.014 (30)
Freshwater animals	180	22	4	3.4 (180)
Marine animals	250	19	4	3.3 (250)
Marine plants	19	32	<10	2.5 (19)

Rates of change. The numbers of presently domesticated species, the times by which 50% or 90% were domesticated, and the rates of domestication differ widely between land and aquatic species. In the last column, the specific growth in the number of domesticated species is defined as the percent increase in the number of species domesticated per year over the period of fastest domestication rates (*6*); the number of species for which domestication dates were available is given in parentheses.

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16. Supported by the projects SAMI and MarBEF Network of Excellence, funded by the European Commission. We are indebted to Y. Olsen and D. Soto for insights and comments that have greatly improved this work, J. Guieu for help in compiling data, and S. Agustí and S. Zanuy for helpful suggestions.

Supporting Online Material
Materials and Methods
Table S1
References

10.1126/science.1138042

EVOLUTION

Aging and Sexual Conflict

Aging of male organisms and of their sperm reduces fertility and embryo viability, leading to evolutionary conflict between the sexes.

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In many human societies, men are becoming fathers increasingly late in life, and it is estimated that fertility problems experienced by one-third of couples can be attributed to male factors, including aging (*1*). Aging can affect male reproductive success through two processes, each with distinct evolutionary implications: the age of the male and the age of his sperm. Recent empirical studies demonstrate that both male aging and sperm aging may have a dramatic impact on fertility, embryo viability, and ultimately on the evolutionary conflict between sexual partners, known as sexual conflict.

Male fertilizing efficiency is especially important in species where females mate with multiple males and the ejaculates of different males compete for fertilization, a process called sperm competition. One recent study of the hide beetle (*Dermestes maculates*) (*2*) reveals that male aging may be an important determinant of the outcome of sperm competition. The study analyzed fertilization success in two scenarios: when the ejaculates of two males were inseminated into a female (sperm competition), and when the ejaculate of only one male was inseminated (absence of sperm competition). The study demonstrates that the fertilizing ability of an ejaculate peaks at an intermediate male age. Most young males copulated with females but only 36% of them had developed mature sperm, indicating that most young males were not sexually mature. Similarly, although all old males produced mature sperm, some of them failed to transfer sperm during mating (aspermic copulation). Males in their prime (intermediate age), on the other hand, never failed to inseminate a female. Moreover, in sperm competition, their ejaculates outcompeted those of old and young males in fertilizing the eggs of a female. These results confirm earlier work on this species showing that a female incurs

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