Bivalve Life History & Genetics

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http://halfshell.usc.edu/index.html

Native vs. Nonnative?

Shellfish Farmed on the Pacific Coast

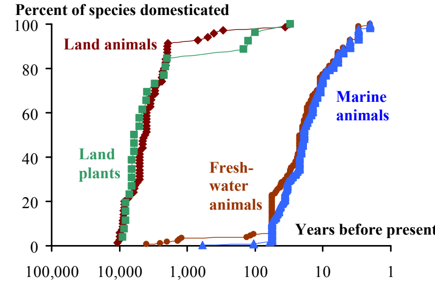
Native	Nonnative
Geoduck	Pacific oyster
Olympia oyster	Manila clam
Giant rock scallop	Mediterranean mussel
Western Blue mussel	Kumamoto oyster
Littleneck clam	Eastern Blue mussel
Nuttall's cockle	Eastern oyster
Red abalone	Japanese scallop
Spiny & pink scallops	European flat oyster
Green sea urchins	Varnish clam
Weathervane scallop	

Shellfish aquaculture in the Pacific NW is based largely on naturalized non-native species. Geoduck is a notable exception. Most agriculture and horticulture is based on non-native species. Regulations are extremely strict on international and interstate transport of shellfish. Aquaculture is not currently a vector of introductions. To import new Kumamoto oyster stock from Japan, for example, we are rearing to maturity, in quarantine, a first generation bred from wild parents, which will eventually produce seed that can be planting in West Coast waters, provided they pass disease testing.

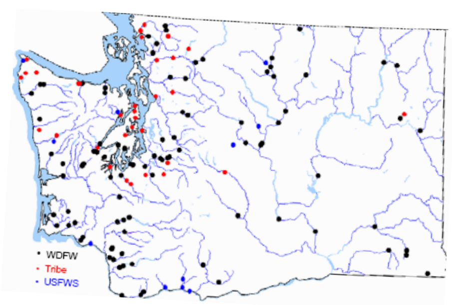
Washington's top 12 agricultural commodities, their absolute and relative values, and origins

Rank	Item	Value (millions)	Percent of WA $	Percent of U.S. $	Origin
1	Apples	942	16.2	59.2	Central Asia
2	Dairy products	832	14.3	3.1	Middle East
3	Cattle and calves	685	11.8	1.4	Middle East
4	Wheat	484	8.3	7.1	Middle East
5	Potatoes	431	7.4	18.1	S. America
6	Greenhouse/nursery	376	6.5	2.3	various
7	Cherries	338	5.8	61.7	Western Asia
8	Hay	262	4.5	5.5	Asia
9	Grapes	142	2.4	4.1	Middle East
10	Pears	138	2.4	46.7	Western China
11	Onions	133	2.3	12.9	Pakistan
12	Aquaculture	94	1.6	11.0	Japan, N. America

Wild vs. Domesticated? A Walk on the Wild Side

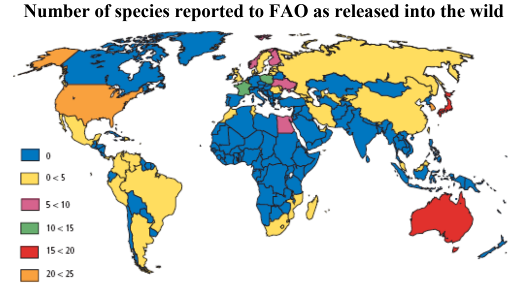


Humans have been domesticating species for over 10,000 years. Duarte *et al.* (2007) claim that aquatic species are being rapidly domesticated at present (figure, right). Yet, in defining domestication as any form of husbandry rather than profound genetic divergence from a wild progenitor, these authors merely describe the surging interest in aquaculture. Actually, very few marine or freshwater species have been domesticated in the true sense; common carp, rainbow trout, and more recently Atlantic salmon are reasonable candidates for domesticated status. Aquaculture is quite different from agriculture with respect to reliance on wild stocks. Although oysters have been cultivated for 1000s of years, mostly from naturally set seed, no bivalve molluscs have been domesticated. The Pacific oyster is probably the farthest along the path to domestication, as a result of the Molluscan Broodstock Program, a series of projects supported by the Western Regional Aquaculture Center, and commercial breeding programs.

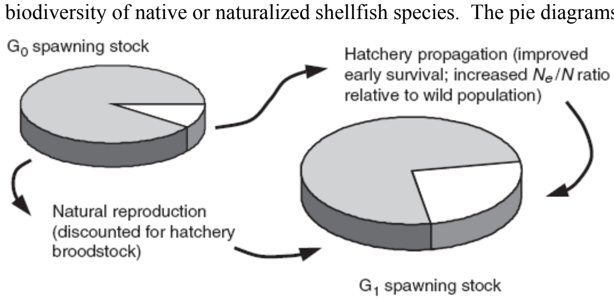


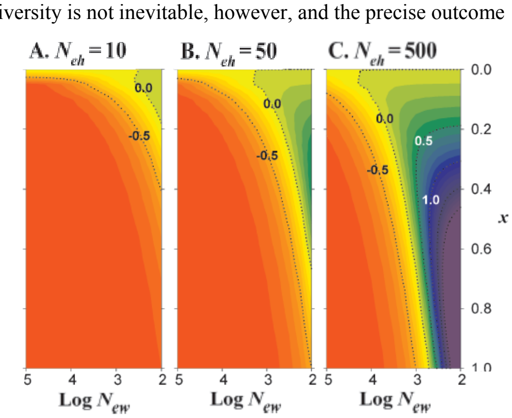
In a human-dominated world, what is wild? Many fished species are supplemented or enhanced by artificial propagation. In WA, there are more than 100 federal, state, and tribal salmon hatcheries, for example (map, left; http://www.lltk.org/HRP.html); a staggering 75% of the catch in Puget Sound is hatchery-bred. The impact of hatchery enhancement on natural stocks is being scrutinized globally (Born *et al.* 2004). The genetic impact of such activity on wild populations has been considered (*e.g.* Hedgecock & Coykendall 2007), but data are needed on a case-by-case basis.

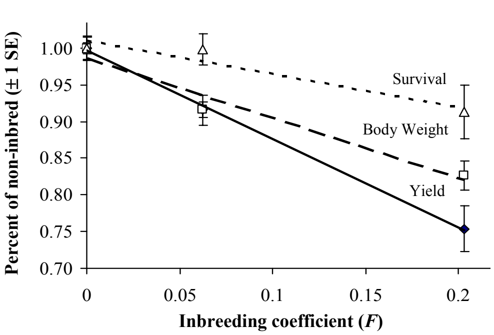
Number of species reported to FAO as released into the wild



High fecundity of bivalves – females typically spawn tens of millions of eggs – increases the risk that hatchery propagation of farmed species could erode the biodiversity of native or naturalized shellfish species. The pie diagrams (left) illustrate how the diversity of a natural population might be diluted by hatchery supplementation. Reduction of diversity is not inevitable, however, and the precise outcome depends, even in the simplest model (The Ryman-Laikre Model), on a complex interplay of three variables, the effective sizes of hatchery and wild populations (N_{eh} and N_{ew}, respectively) and the proportion of the total breeding population coming from the hatchery (x). The risk can be managed by (1) increasing the effective size of the hatchery stock (note [graph, lright] the increasing areas of positive impact on biodiversity [cooler colors], going from N_{eh} of 10 to N_{eh} of 500 and (2) decreasing x. The outcome depends critically on N_{ew}, which is poorly known but may be only a small fraction of the spawning population, which successfully leaves offspring (Hedgecock 1994). "Sweepstakes Reproductive Success" likely decreases genetic diversity and increases the range of relatedness in both natural and especially hatchery-propagated populations.





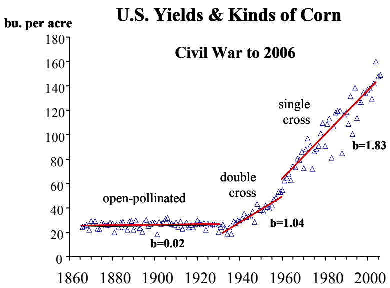


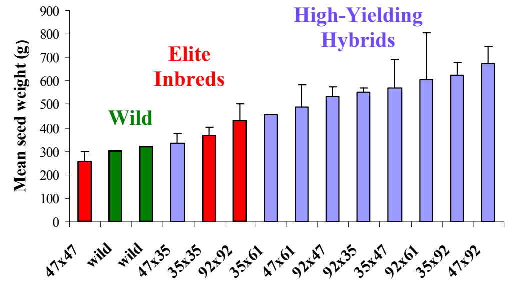
High fecundity also brings a large load of harmful recessive mutations. Upon inbreeding, recessive mutations cause a decrease in fitness, called "inbreeding depression" (*e.g.* graph, left, shows declines in survival, size, and yield with increased inbreeding; from Evans *et al.* 2004). The mutational load in shellfish populations increases the risk of negative impacts from hatchery enhancement (Launey & Hedgecock 2001).

Use of wild stock in aquaculture increases risks of detrimental hatchery *vs.* wild interaction and is a more variable and less efficient food production system than would be possible using improved domesticated stocks.

Wild vs. Domesticated? Down on the Farm

We have increased agricultural yields through domestication and improvement (see example of U.S. corn production, left, below), thereby reducing famine. Why not do the same in aquaculture, thereby meeting growing demand for seafood? The Pacific oyster shows hybrid vigor, *i.e.* offspring from crosses of inbred parent lines grow faster and survive better than those parent lines (middle, below, a cross of lines *6* and *7*). Note that these inbred lines were derived from Dabob Bay oysters and show natural variation; no Genetically Modified Organisms are being considered in shellfish aquaculture, nor are they needed, owing to an abundance of natural variation. Crossbreeding elite inbred lines could easily double the current yield of oysters (right panel, below), which is mainly based on the farming of wild stock.





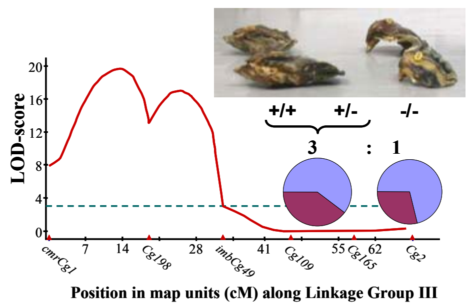
Other traits of importance in shellfish aquaculture, which can only be improved by means of domestication and breeding, are resistance to naturally occurring or introduced diseases (table, below, left; summer mortality of "susceptible" and "resistant" families of Pacific oysters in France) and shell shape and color (graphs, below, middle and right; mutations affecting the symmetry of the major growth axis and shell pigmentation have been mapped in the Pacific oyster). Knowledge of the genetic basis of complex traits is being aided by advances in genomics, functional genomics, and proteomics (Hedgecock et al. 2005; Hedgecock et al. 2007)

Mean mortality of six selected oyster families in three sites

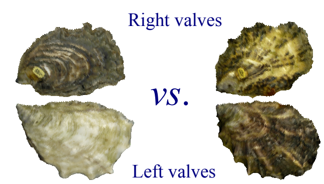
Group	Families	Baies des Veys	Rivière d'Auray	Ronce	All sites
"susceptible"	F7-25	19.6	56.0	57.6	44.4
"susceptible"	F7-26	8.7	38.1	28.7	25.2
"susceptible"	F7-27	6.9	31.3	28.9	22.4
Mean		**11.8**	**41.8**	**38.4**	**30.6**
"resistant"	F9-34	3.6	10.3	4.2	6.0
"resistant"	F9-35	4.1	9.0	4.0	5.7
"resistant"	F9-36	2.5	6.2	3.1	3.9
Mean		**3.4**	**8.5**	**3.8**	**5.2**

From Lambert et al. (2007) Aquaculture 270:276.

A mutation causing "hook hinge" maps to linkage group III in the oyster (LOD measures significance)



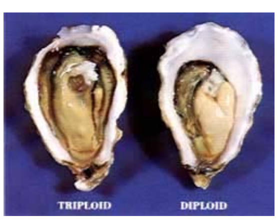
A gene affecting valve pigmentation maps to linkage group VIII



***Advantages of using improved domesticated stock*:**
Improved traits
Increased production efficiency
Reduced environmental and energy footprints

***Disadvantage of using domesticated stock*:**
Potentially increased risk of negative interaction between wild and genetically divergent farmed stocks
Decreased diversity & relative fitness?

If an elite F_1 hybrid stock were to spawn in the field, it might reduce the diversity of the local wild population because $N_{eh} = 2$ (see Ryman-Laikre model, last section, previous page). On the other hand, the F_2 hybrid generation would almost certainly show reduced performance, a phenomenon called *hybrid breakdown*. Hybrid reproduction might be self-limiting, since a large proportion of F_2 hybrids die (Launey & Hedgecock 2001); lethal mutations in a dozen independent genes would theoretically kill ~97% $[1-(0.75)^{12}]$ of an F_2 population. Also, fast growing hybrids might be harvested before spawning. Risk factors can and should be evaluated.



Shellfish aquaculture already has a potent tool to prevent interaction of wild and farmed stocks: the farming of sterile, triploid seed. Triploids, which have three sets of chromosomes rather than the normal two sets inherited from father plus mother, are generally sterile (*e.g.* bananas, seedless watermelons and grapes); this has been demonstrated for a number of shellfish species. Farming triploid shellfish thus greatly reduces the risk of interaction with wild populations. Presently, however, triploid Pacific oysters are made by fertilizing eggs from diploid females (1n) with sperm from tetraploid males (2n). Tetraploid oysters are fertile and could escape. Although experience suggests that tetraploids are weak competitors, research on their fitness and containment is needed.

Development of domesticated shellfish stocks, coupled with reduction in their interaction with wild stocks, is highly desirable.

Research Needs for Sustainable Aquaculture:

- Molecular markers and other genetic and genomic tools to study wild & farmed bivalve stocks and their interactions
- More data on basic reproductive and population biology of wild and farmed bivalves for models
- Much more regionally coordinated research on domestication and improvement of farmed bivalves
- Research on bivalve bio-security: sterility of triploids; fitness of tetraploids & their containment

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