ANNOTATED BIBLIOGRAPHY OF THE GENETICS OF BIVALVE MOLLUSKS

by

Dan Moore
Jim Seeb

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Alaska Department of Fish and Game
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ABSTRACT

Growth in the mariculture industry has lead to increased requests and inquiries to transport mollusks from various locations around the state to permitted and potential farm sites. A mollusk genetics policy is being developed and to better facilitate this process a search was conducted for the current literature in the industry. This is a preliminary literature search to help identify genetics issues related to stock transfer, and new citations continue to be added.

INTRODUCTION

This bibliography was prepared to support the deliberations of a policy review team tasked with developing guidelines, based upon genetic considerations, to regulate transport of mollusks in the state of Alaska. Transporting mollusks may put natural genetic resources at risk if hybridizations with discrete and locally adapted wild stocks erode natural production. Growth in the mariculture industry has lead to increased requests to transport mollusks from various seed locations around the state to existing and potential farm sites. The policy review team needs to balance the responsibility of helping to facilitate development of the emerging industry while protecting the genetic integrity of the wild populations that support commercial, subsistence, and sport fisheries (Appendix A).

The modern mariculture industry began developing in Alaska in 1988 when the Aquatic Farm Act was signed into law (AS 16.40.100 – 16.40.199). While the initial emphasis was on the culture of imported oyster spat from the Pacific Northwest (RaLonde 1993), the industry wanted to develop culture other species of mollusks. The State of Alaska built a shellfish hatchery in Seward which opened in 1997 and is currently operated by a private organization. Multiple species, including oysters, littleneck clams, geoducks, rock scallops, and cockles, could be cultured in the hatchery. A potential transfer of hatchery stocks of these species to remote farm sites further exacerbates genetic concerns.

Conclusive information on the boundaries of discrete stocks would help to provide an unambiguous framework within which to regulate mollusk transport. In the absence of conclusive information, Alaska adopted an informal policy permitting transport of stocks within but not among Commercial Fishery Regions I, II, and IV in the Gulf of Alaska (Southeast, Southcentral, Kodiak/Aleutians). This guideline incorporated the expectation of RaLonde (1993) that these three areas generally delimit discrete zones of larval drift (Appendix B). Some scientific studies suggest that some species subdivide into genetically discrete populations on a much finer scale.

This bibliography was generated cross-referencing species with issues. Searches were first made within the files and library of the State of Alaska Gene Conservation Laboratory. The majority of the literature search was conducted using the Alaska Resources Library and Information Services (ARLIS) librarian. Topics of the search included scallop genetics, Science Citation Index searches on particular authors, stock transfer and introduction, triploid/sterile shellfish development, broodstock design, development and protocols, and Alaskan rock scallop and geoduck range and distribution. The citations received were reviewed for relevancy and compiled in alphabetical order by main author.

SALIENT ISSUES

During development of the bibliography four issues emerged that are particularly relevant to the development of a genetic policy in Alaska:

1. No reports of research into the genetics and population boundaries of mollusks in Alaska were found in any of the searches. How might state and federal agencies, universities, Alaska Sea Grant, or other institutions provide research to aid in the promotion of wild stock conservation in the presence of mariculture?

2. For each species: what is the appropriate geographic scale to restrict transfer? Are there species-specific life history and population genetic differences that would warrant special consideration? We found a clear lack of consensus on the geographic limits of stock boundaries and the implications of stock transfer.

   Geographical subdivision of species into genetically discrete stocks was often observed (e.g., Adamkewicz 1988, Fevolden 1992, Beaumont 2000). Significant, very small-scale population differences are indicated in some studies of some species (Hilbish 1985 documents genetic differences between inshore and outer-coast populations of mussels separated by less than 30 km). In these cases, stock transfer resulting in interpopulation hybridization would likely erode local adaptations, depressing these discrete native stocks (Adamkewicz 1988, Hilbish 1985, Koehn 1976, Koehn 1984).

   Alternatively, in some cases, genetic homogeneity was observed for some species over large geographical areas (Grady et al. 1989, Dolganov and Pudovkin 1997).

   In some cases of transplantation, genetically discrete mollusks failed to thrive in the new environment; authors speculate that stock transfer would have limited impact on wild stocks (Krause 1989, Metznerroop 1994).

   At what scale should stock transfers be limited? What factors (such as demography, larval drift, salinity, current, substrate, competitors/predators, turbidity, depth, temperature—see Brand 1991) should the policy team consider when regulating stock transfer?

3. What hatchery guidelines are important to ensure maintenance of within-population genetic variability in hatchery stocks? The relatively high fecundity of mollusk species may easily lead to inbreeding in a hatchery (Benzie and

Williams 1996). The stocking of inbred mollusks may negatively impact adjacent wild stocks of the same species.

4. Some states are promoting the use of sterile hatchery stocks to reduce the potential genetic impact of mariculture. Sterile shellfish cannot hybridize with wild stocks. Sterile hatchery stocks can be made through the production of interspecies hybrids or triploids (three sets of chromosomes; see review in Thorgaard and Allen 1988). Recent findings suggest that triploid sterility is not always permanent (Allen and Guo 1997). In what circumstances should the State of Alaska permit or promote the use of sterile hatchery stocks?

BIBLIOGRAPHY

Adamkewicz, L., Taub, S.R. and Wall, J.R. 1984. Genetics of the clam *Mercenaria mercenaria*. 2. Size and genotype. Malacologia. 25(2):525-533.

- Wild clams of known genotype individually induced to spawn and all gametes mixed
- Strong evidence that some alleles at the *Lap* locus have selective advantage

Adamkewicz, L. 1988. Geographical effects on growth rate in the hard clam *Mercenaria mercenaria.* Journal of Shellfish Research. 7(1):146.

- Conference abstract
- Test if *Mercenaria mercenaria* might be genetically adapted to local conditions
- Factorial cross of 3 geographically separated natural populations on east coast (USA)
- Strong/significant effect of parental origin on shell length
- Effect of parental origin shows a clear pattern

Allen, S. Jr., P.Gagnon and H. Hidu. 1982. Induced triploidy in the soft-shell clam. Journal of Heredity. 73:421-428.

- Methods and results of producing triploid clams to enhance commercially important species
- Cytochalasin B used to induce polyploidy

Allen, S. Jr., H. Hidu and J. Stanley. 1986. Abnormal gametogenesis and sex ratio in triploid soft-shell clams (*Mya arenaris*). Biological Bulletin. 170:198-210.

- Triploids did not mature and most had undeveloped gonads

Allen, S. Jr. and S. Downing. 1986. Performance of triploid Pacific oysters, *Crassostrea gigas,* Survival, growth, glycogen content, and sexual maturation in yearlings. Journal of Experimental Marine Biology and Ecology. 102:197-208.

- Triploids created with cytochalasin B
- Triploid males half as much gonad as diploid
- Triploid females quarter as much gonad as diploid
- Triploids higher survival than diploids

Allen, S. Jr. and S. Downing. 1990. Performance of triploid Pacific oysters, *Crassostrea gigas*: Gametogenesis. Canadian Journal of Fisheries and Aquatic Sciences. 47:1213-1222.

- Cytochalasin B used to induce polyploidy
- Gametogenesis retarded but not absent; some triploids fertile

Allen, S. Jr. and D. Bushek. 1992. Large-scale production of triploid oysters, *Crassostrea virginica* (Gmelin), using "stripped" gametes. Aquaculture. 103:241-251.

- Several factors examined to increase survival and yield of triploids

Allen S.K., P.M. Gaffney, J. Scarpa and D. Bushek. 1993. Inviable hybrids of *Crassostrea virginica* (Gmelin) with *C rivularis* (Gould) and *C -gigas* (Thunberg). Aquaculture. 113(4):269-289.

- Factorial crosses of three species of oysters
- Diploid and triploid hybrids were inviable
- Offspring can be produced but are inviable after 8-10 days, with little growth
- Introduction of *C. gigas* to the range of *C. virginica* will not have direct genetic impact because of lack of hybridization

Allen, S.K. Jr. and X. Guo. 1997. Can we have our oyster and eat it too? A case for aquaculture parks using non-native species. Journal of Shellfish Research. 16(1):257.

- Conference abstract
- Potential ecological value as grazers and value to industry
- Potential ecological harm if they supersede native species
- Use of triploids may alleviate concerns
- Triploid production by manipulation of meiosis of normal diploid oocytes not 100%, individuals all need to be screened
- "Certified" triploids also seem to have instability of chromosome content
- Tetraploid oysters crossed with diploids produce 100% (statistically) triploids
- Crosses appear to have stable chromosome content
- Use of triploids from tetraploid/diploid crosses may be promising for enhancement

Allen, S.K. 1998. Aquaculture genetics and breeding technology center at the Virginia Institute of Marine Science: finally, a long-term opportunity? Journal of Shellfish Research. 17(1):317.

- Conference abstract
- Describes goals of the VIMS facility

Allen, S.K. Jr. 1998. Commercial applications of bivalve genetics: Not a solo effort. World Aquaculture. 29(1):38-43.

- Article outlines role of genetics in bivalve culture to date and describes a view of the future for bivalve genetics, particularly as it pertains to commercial application
- Development and transfer of genetically improved stocks to industry must be a team effort

Allen, S. Jr., S. Downing and K. Chew. 1998. Hatchery manual for producing triploid oysters. University of Washington. Sea Grant Program. University of Washington Press. Seattle. 27p.

- Outlines methods for producing and verifying triploids

Beaumont, A.R. 1982. Geographic variation in allele frequencies at three loci in *Chlamys opercularis* from Norway to the Brittany coast. Journal of the Marine Biological Association of the United Kingdom. 2(2):243-261.

- Four relatively genetically isolated populations of scallops around the British Isles based on frequency differences at three loci in nine populations
- Both random genetic drift and selection may be reason

Beaumont, A.R. and M.D. Budd. 1983. Effects of self-fertilization and other factors on the early development of the scallop *Pecten maximus*. Marine Biology. 76(3):285-289.

- A 2 x 5 factorial mating involving self- and cross-fertilization and the use of stripped spermatozoa
- Underlying genetic variation was evident at all stages

Beaumont, A.R. and C.M. Beveridge,. 1984. Electrophoretic survey of genetic variation in *Pecten maximus, Chlamys opercularis, C. varia* and *C. distorta* from the Irish Sea. Marine Biology. 81(3):299.

- Genetic variation was investigated using starch gel electrophoresis
- Number of polymorphic loci ranged from 50% to 73%
- Results similar to those observed for several oyster species, but higher rates of polymorphism than reported for mussels and other scallops

Beaumont, A.R. 1986. Genetic aspects of hatchery rearing of the scallop, *Pecten maximus* (L.). Aquaculture. 57(1-4):99-110.

- Existing hatchery culture data reviewed and new data on the induction of triploidy presented
- Scallops shown to be genetically very variable - natural variation valuable feature for hatchery broodstock
- Genetic and environmental causes of development variations

Beaumont, A.R. 1991. Allozyme data and scallop stock identification. Journal du Conseil, Conseil International pour l'Exploration de la Mer. 47(3):333-338.

- Significant differences between populations suggest little gene flow
- Differences between east and west coast of Ireland not maintained by strong selection but most likely restricted gene flow
- Unable to detect differences in local areas
- Within a normally isolated stock there may be occasional recruitment from an unusual source to due hydrographic conditions

Beaumont, A.R. and J.E. Fairbrother. 1991. Ploidy manipulation in molluscan shellfish: A review. Journal of Shellfish Research. 10(1):1-17.

- Paper explains details for ploidy manipulation

Beaumont, A.R., C. Morvan, S. Huelvan, A. Lucas and A.D. Ansell. 1993. Genetics of indigenous and transplanted populations of *Pecten maximus*: No evidence for the existence of separate stocks. Journal of Experimental Marine Biology and Ecology. 169(1):77-88.

- 13 populations of scallop from Scotland, UK and Brittany, France examined
- Deficiency of heterozygotes observed
- Little post-transplant selection
- High genetic similarity among all the populations surveyed and no overall differences between the Scottish and Brittany samples
- Authors conclude that Scottish and Brittany scallop populations are, nevertheless, genetically distinct

Beaumont, A.R. 1999. Genetic aspects to the transfer or introductions of scallop species. Book of Abstracts: 12th International Pectinid Workshop. School of Ocean Sciences, University of Wales-Bangor, Menai Bridge, Gwynedd, LL59 4EY, UK Conference Title: 12. Int. Pectinid Workshop.

- Little attention has been given to the genetic consequences of stock transfers
- Transfers between populations within the range of a species are most common
- Main genetic concern for introductions is the possibility of hybridization
- May be reproductive barriers to hybridization
- With transfers, the genetic consequences will be related to (a) the genetic differences between the populations, b) the relative sizes of the source and recipient populations, c) the source of the transferred population (hatchery or wild), and (d) the length of time since the transfer took place
- Risk of breakdown of co-adapted gene complexes following mixing and reproduction if populations are genetically very distinct
- Small numbers of individuals (particularly hatchery produced) transferred into a larger population do not carry the full genetic variability of the source population, but are likely to have little overall genetic effect.
- Mixed populations would be expected to achieve, over time and by natural selection, a maximum fitness but this may be different than the host or introduced population

Beaumont, A.R. 2000. Genetic considerations in transfers and introductions of scallops. Aquaculture International. 8(6):493-512.

- Main concerns about transfers usually ecological (i.e., interactions between long established plants and animals)
- Populations may be sub-structured by hydrographic forces such as a self recruiting circulating gyre
- Some populations never self recruit but are seeded from upstream
- Self-recruiting population will change genetically over time: mutation, recombination, and independent segregation of chromosomes at meiosis
- Changes from generation to generation by chance alone, random genetic drift
- Random genetic drift slow in large and fast in small populations
- Limited exchange of larvae between populations will tend to override random genetic drift
- Larvae settling away from source population may be under different selection pressures than parents, thus when differences are detected, it could be a result of random genetic drift, selection, or both
- Detectable population sub-structure continually broken down by intermixing from transfers. Unique genetic signature can be lost due to stocking
- American oyster in eastern Atlantic and Mexican Gulf homogeneous at allozyme loci but distinct in mtDNA and nDNA analysis (not always true with scallops)
- Hatchery progeny usually derived from few parents so represent small fraction of total variability of the source population. Number of individuals contributing to spawn may be much smaller than total adults available (in hatchery), due to sperm competition, high variability in fecundity, and early larval success

Benzie, J.A.H. 1994. Genetics of black-lipped pearl oyster (*Pinctada margarifera*). Journal of Shellfish Research. 13(1):331.

- Conference abstract
- High levels of genetic variation within populations and high levels of gene flow between populations widely separated geographically
- Early work emphasized the lack of geographic differentiation but recent surveys show significant genetic differences
- Differences were found between widely separated populations as well as geographically adjacent populations in island groups

Benzie, J.A.H. and S.T. Williams. 1996. Limitations in the genetic variation of hatchery produced batches of the giant clam, *Tridacna gigas.* Aquaculture. 139(3-4):225-241.

- Hatchery production methods can result in differences between hatchery seed and wild stocks
- Relatively small effective population size can lead to reduced genetic diversity in hatchery stocks
- More adults and multiple stockings from variety of spawnings may reduce problem
- Number of individuals contributing to spawn may be less than broodstock held because some individuals more successful than others at contributing to spawn
- No genetic differences within regions but highly significant differences between hatchery batches

Beveridge, C.M., M.D. Budd and G.M. Burnell. 1985. Studies on heterozygosity and size in the scallop, *Pecten maximus*. *In* Proceedings of the nineteenth European marine biology symposium: Plymouth, Devon, U.K., 16-21 September 1984. Beaumont, A R; Gosling, E M; NERC Unit, Marine Science Laboratory, Menai Bridge, Anglesey LL59 5EH, UK. 443-454.

- Samples taken in three consecutive years and scored a 6 loci
- No significant differences in allele frequencies between year classes except *Lap*
- Significant deficiency of heterozygotes in *Lap*-I locus in two of the year classes

Blake, S.G. 1994. Mitochondrial DNA variation in the bay scallop, *Argopecten irradians*, and the calico scallop, *Argopecten gibbus*. Journal of Shellfish Research. 13(1):277.

- Conference abstract
- Significant degree of overlap in shell morphology characters but no clear geographic boundaries delineating the ranges of the subspecies
- Variation in the mtDNA of four geographically separate populations studied

Brake, J.W., J. Davidson and J. Davis. 1999. Triploid production of *Mytilus edulis* in Prince Edward Island - an industrial initiative. Journal of Shellfish Research. 18(1):302.

- Conference abstract
- Developing triploids to increase harvest yield
- Discussion of various methods to produce triploids

Brand, E. Von and A. Kijima. 1990. Comparison of genetic markers between the Chilean scallop *Argopecten purpuratus* and the Japanese scallop *Patinopecten yessoensis*. Tohoku Journal of Agricultural Research. 41(1-2):25-35.

- Electrophoresis was carried out to determine the number of useful genetic markers in the population

Brand, A.R. 1991. Scallop ecology: Distributions and behaviour. *In* S. E. Shumway, editor. Scallops: Biology, ecology and aquaculture. 517-584.

- Factors effecting local distribution: salinity, current, substrate type, competitors/predators, turbidity, depth, temperature
- Each scallop species has geographically and bathymetrically desirable range
- Major scallop beds usually widely separated and thus very different, producing differences in population parameters
- Differences in population and age structure may be from differing rates of recruitment
- Major population centers often found in areas with gyres or two-layer circulation patterns which could provide mechanisms for larval retention
- Four relatively genetically isolated populations of one species of scallop, however discovery of rare allele in a year class suggests occasional recruitment from elsewhere
- Different beds within scallop grounds may be isolated due to hydrographic factors

Bricelj, V.M. and M.K. Krause. 1992. Resource allocation and population genetics of the bay scallop, *Argopecten irradians irradians*: Effects of age and allozyme heterozygosity on reproductive output. Marine Biology. 113(2):253-261.

- Electrophoretic analyses revealed a relatively low proportion of polymorphic loci and low level of heterozygote deficiency
- High degree of temporal stability within and among cohorts based on allele frequency distributions

Bushek, D. and S.K. Allen. 1989. Effective population size for shellfish broodstock management: Conflicts between theory and practice. Journal of Shellfish Research. 8(2):446-447.

- Conference abstract
- Loss of genetic diversity is inversely related to effective population size (N)
- Sex ratio and family size can be used to maximize N
- Practical culture methods being developed

Calvo, G.W. and M.W. Luckenbach. 1998. Non-native oysters survive and grow in Virginia: evaluating the performance of *Crassostrea gigas* against *Crassostrea virginica*, in relation to salinity, in Chesapeake Bay and Atlantic coast waters. Journal of Shellfish Research. 17(1):320-321.

- Conference abstract
- Field testing of non-native oysters, triploids and diploids

Carlton, J.T. 1992. Introduced marine and estuarine mollusks of North America: an end-of-the-20th-century perspective. Journal of Shellfish Research. 11(2):489-505.

- 36 non-indigenous bivalves and gastropods transplanted to coasts of North America, some intentional, some unintentional
- With a few exceptions, there is little experimental elucidation of the ecological impact of the introductions
- Some introductions (periwinkle) have altered indigenous environment

Carriker, M.R. 1992. Introductions and transfers of molluscs: risk considerations and implications. Journal of Shellfish Research. 11(2):507-510.

- Genetic consequences of introductions and transfers examined on how readily they hybridize
- Consequence of uncontrolled invasion could include ecosystem alteration by invaders and descendents
- Estuarine species rarely invade open water habitat and vice versa

Castagna, M. and J.J. Manzi. 1989. Clam Culture in North America: Hatchery Production of Nursery Stock Clams. *In* J. Manzi and M. Castagna, editors. Clam Mariculture in North America. Developments in Aquaculture and Fisheries Science, 19. Elsevier. New York, NY. 111-126.

- Over 100 species of clams have been cultured in North America.
- Less than 10 species of clams are cultured in commercial facilities in North America
- Occurrence of large numbers of wild seed is not dependable
- Discussion of hatchery procedures to produce seed

Chandler, W., A. Howe and S.K. Allen. 1999. Use of flow cytometry and histology to assess gametogenesis in triploid *Crassostrea ariakensis*. Journal of Shellfish Research. 18(1):327-328.

- Conference abstract
- Cytochalasin B used to induce triploidy
- Flow cytometry used to verify triploidy
- Good tool to detect hermaphrodites

Choromanski, J., S. Stiles, C. Cooper, E. Bedan, S.W. Lonergan and P.J. Trupp. 1999. Growth and survival of juvenile bay scallops from genetic lines at different densities and depths: Collaborative study between the National Marine Fisheries Service and the Bridgeport Aquaculture School. Journal of Shellfish Research. 18(1):263.

- Hatchery-reared juvenile scallops field tested to evaluate growth and survival of genetic lines

Cochard, J.C., F. Delaunay, B. Fauconneau and F. Takashima. 1991. What about growth variability for *Pecten maximus* production? Oceanis. 18(1):49-66.

- Large production variability in rearing observed under standard hatchery conditions
- Improvement in reliability important to industry
- Sources of variability include food source, water quality and genetic source of parents

Cochard, J.C. and N. Devauchelle. 1993. Spawning, fecundity and larval survival and growth in relation to controlled conditioning in native and transplanted populations of *Pecten maximus* (L.): Evidence for the existence of separate stocks. Journal of Experimental Marine Biology and Ecology. 169(1):41-56.

- Differences in reproductive behavior suggest genetically-determined reproductive strategies between stocks

Cruz, P., C. Rodriguez-Jaramillo and A.M. Ibarra. 2000. Environment and population origin effects on first sexual maturity of catarina scallop, *Argopecten ventricosus* (Sowerby II, 1842). Journal of Shellfish Research. 19(1):89-93.

- Experimental groups of hatchery scallops evaluated for age at first sexual maturity at different sites
- Differences suggest environmental conditions have a significant role in maturation processes

Dame, R.F. 1996. Ecology of Marine Bivalves: an Ecosystem Approach. CRC Press. Boca Raton, FL. 254p.

- Larval stage is planktonic and subject to very high mortality
- Planktonic stage is important for the dispersal of the species
- Juvenile-adult stage is important for reproduction
- For organisms with great potential for dispersal (e.g., bivalve plankton) large geographic areas and single closed population is difficult to define
- Physical factors that limit populations: temperature, aerial exposure, salinity, oxygen, siltation and waves

Debrosse, G.A. and S.K. Allen. 1996. The suitability of land-based evaluations of C*rassostrea gigas* (Thunberg, 1793) as an indicator of performance in the field. Journal of Shellfish Research. 15(2):291-295.

- Introduction of non-native species to the mid-Atlantic requires prior knowledge of their likely ecological response
- Not attainable without experimental introduction
- Will land based experiments work? Tests indicate no

Dolganov, S.M. 1995. Allozyme Markers In Scallop *Mizuhopecten-Yessoensis* Jay. Genetika. 31(6):825-832.

- Gene markers developed, adductor muscle used

Dolganov, S.M. and A.I. Pudovkin. 1997. Genetic diversity of the scallop *Mizuhopecten (Patinopecten) yessoensis* Jay, 1856 from Primorye. Genetika. 33(10): 1387-1394.

- 19 natural settlements studied along 1300 km coast and found to be genetically homogenous
- Settlement located furthest south differed significantly from the others assumed to belong to another scallop population
- Age groups did not differ significantly in allele frequencies
- Findings based on limited available data

Dolganov, S.M. and A.I. Pudovkin. 1998. Population-genetic structure of the Japanese scallop *Mizuhopecten (Patinopecten) yessoensis* from Sakhalin Island and the southern Kuril Islands. Genetika. (Language: Russian). 34(10):1411-1419.

- Authors observed several populations of genetically different Japanese scallops
- Large genetically homogeneous populations along 1300 km coastline
- Interpretation of the genetic structure based on limited available data

Fevolden, S.E. 1987. Genetic variation within and between populations of Iceland scallops (C*hlamys islandica*) Ices Council Meeting 1987 (Collected Papers). Publisher: Ices, Copenhagen (Denmark) Report Number: ICES-CM-1987/K: 499p.

- Investigate genetic variation and of thirty enzymes; glucosephosphate isomerase (*GPI*) and phosphoglucomutase (*PGM*) are the most variable
- Within sample heterozygosity = 80%
- Extreme variability at the *GPI* locus does not support hypotheses suggesting that more stable environments regulate more monomorphic species

Fevolden, S.E. 1992. Allozymic variability in the Iceland scallop *Chlamys islandica*: Geographic variation and lack of growth-heterozygosity correlations. Marine Ecology Progress Series. 85(3):259-268.

- Populations were investigated for allelic variation at 6 polymorphic gene loci
- Substantiated earlier findings of exceptionally high polymorphism
- Allele frequencies varied between populations
- Partial geographic isolation between stocks

Freeman, K. 1988. Ecology and aquaculture: Shall the twain meet? Biology Bulletin of the Aquaculture Association of Canada. 88-2:82-87.

- Growing industry in Canada raises questions of potential impact to environment

Frischer, M.E., J.M. Danforth, L.C. Tyner, J.R. Leverone, D.C. Marelli, W.S. Arnold and N.J. Blake. 1999. A genetic probe for bay scallop larvae. Book of Abstracts: 12th International Pectinid Workshop. Skidaway Institute of Oceanography, Savannah, GA 31411, USA, Conference Title: 2. Int. Pectinid Workshop.

- Genetic marker developed to track larvae in water column to areas of settlement

Fujio, Y. and E. Von Brand. 1991. Differences in degree of homozygosity between seed and sown populations of the Japanese scallop *Patinopecten yessoensis*. Dep. Fish. Sci., Fac. Agric., Tohoku Univ., Sendai, Miyagi 981, Japan. Nippon Suisan Gakkaishi/ Bulletin of the Japanese Society of Scientific Fisheries. 57(1):45-50.

- Starch gel electrophoresis to estimate level of genetic variation in seed and sown populations
- Observed heterozygosity lower than expected in the seed population, indicating an excess of homozygosity
- Not observed in the samples of the sown population
- Homozygote excess lower in large size than in the small size animals
- Decrease of homozygosity during growth may depend on differentiated survival rate between homozygotes and heterozygotes

Fuller, K.M. and E. Zouros. 1988. Size variation in mitochondrial DNA *of Placopecten magellanicus*. Journal of Shellfish Research. 7(1):158.

- Differences in mitochondrial genome sizes may be useful as an indicator of population differences

Gaffney, P.M., T. M. Scott, R.K. Koehn and W.J. Diehl. 1990. Interrelationships of heterozygosity, growth-rate and heterozygote deficiencies in the coot clam, *Mulinia lateralis*. Genetics. 124(3): 687-699.

- Heterozygote deficiencies correlated between multiple locus heterozygosity and size or both
- Large sample size, 1906 individuals
- Significant heterozygote deficiencies at 13 of 15 loci
- Correlation between magnitude of heterozygote deficiency at a locus and effect of heterozygosity at that locus on shell length
- Distribution of multiocus heterozygosity deviates from that predicted by observed single locus heterozygosities

Gaffney, P.M., C.V. Davis and R.O. Hawes. 1992. Assessment of drift and selection in hatchery populations of oysters (*Crassostrea virginica).* Aquaculture*.* 105:1-20.

- Effective breeding numbers were significantly lower than the total number of adults in mass-spawned populations
- Discrepancy reduced by pooling the progeny of multiple small spawning groups

Gaffney, P.M. and S.K. Allen. 1992. Genetic aspects of introduction and transfer of molluscs. Journal of Shellfish Research. 11(2):535-538.

- Small transfers into large natural populations less of a genetic impact than large transfers
- Beneficial genes from even small transfers may have long term positive impact
- Immediate and long-term genetic effects of transfers range from negligible to positive
- Pacific oyster introduced repeatedly into east coast but has not become established

Gaffney, P.M. and S.K. Allen. 1993. Hybridization among C*rassostrea* species - a review. Aquaculture. 116(1):1-13.

- No unequivocal evidence for hybridization among C*rassostrea* species

Gaffney, P.M. and D. Bushek. 1996. Genetic-aspects of disease resistance in oysters. Journal of Shellfish Research. 15(1):135-140.

- Resistance to disease is generally subject to underlying genotypic variability
- Understanding of genetic influences on physiological and life history variation in *Crassostrea* reviewed
- Current view of population structure and how it may affect the evolution of disease resistance described
- Explore approaches to the development of disease-resistant oysters

Gaffney, P.M., V.P. Rubin, D. Hedgecock, D.A. Powers, G. Morris and L. Hereford. 1996. Genetic-effects of artificial propagation - signals from wild and hatchery populations of red abalone in California. Aquaculture. 143(3-4):257-266.

- Effective breeding numbers in hatchery less than total number of spawners available
- Localized variation may arise from post-settlement selection
- Hatchery stocks prone to bottlenecks from unequal spawning and nonrandom larval mortality
- Rare alleles lost in bottlenecks
- Reseeding projects can succeed but care must be taken to minimize production of large quantities of progeny from few parents

Gerard, A., C. Ledu, P. Phelipot and Y. Naciri Graven. 1999. The induction of MI and MII triploids in the Pacific oyster *Crassostrea gigas* with 60DMAP or CB. Aquaculture (Amsterdam). 174(3-4):229-242.

- Meiosis I triploids more difficult to induce than Meiosis II

Gilg, M.R. and T.J. Hilbish. 2000. The relationship between allele frequency and tidal height in a mussel hybrid zone: a test of the differential settlement hypothesis. Marine Biology. 137(3):371-378.

- Two species of blue mussels hybridize
- Nuclear alleles specific to one species increase in frequency with age and size
- Relationship changes with tidal height
- No evidence of differential settlement of mussels with different genotypes in connection with tidal height
- Newly settled larvae may be experiencing different selective pressures than adults
- Genetic structure of hybrid mussel populations with respect to tidal height is consequence of differences in selection intensity

Gjetvaj B., D. Cook and E. Zouros. 1992. Repeated sequences and large-scale size variation of mitochondrial-DNA - a common feature among scallops (*Bivalvia, Pectinidae*). Journal of Molecular Biology and Evolution. 9:106-124.

- Mitochondrial genomes of seven species of scallops examined for the presence of repeated sequences and within-species size variation

Gosling, E.M. 1982. Genetic variability in hatchery-produced Pacific oysters (*Crassostrea gigas* Thunberg). Aquaculture. 26(3-4):273-287.

- Bottlenecked hatchery production exhibit as much variation as natural populations

Goswami, U. 1991. Sperm density required for inducing gynogenetic haploidy in scallop *Chlamys nobilis*. Indian Journal of Marine Sciences. 20(4):255-258.

- Conducted experiments for standardizing sperm density for artificial insemination and induction of gynogenesis by ultra-violet rays irradiated sperm

Grady, J.M., T.M. Soniat and J.S. Rogers. 1989. Genetic variability and gene flow in populations of *Crassostrea virginica* (Gmelin, 1791) from the northern Gulf of Mexico. Journal of Shellfish Research. 8(1):227-232.

- Gene flow among populations was quite high
- Allelic frequency differences did not represent a discernible geographic pattern
- Homogeneous populations can occur when effective population size is large and there are few isolating mechanisms
- Differentiation can occur when there are local selective pressures

Guo, X. 1999. Superior growth as a general feature of triploid shellfish: Evidence and possible causes. Journal of Shellfish Research. 18(1):266.

- Interest in triploid shellfish so far has primarily focused on their sterility
- Superior growth, has been largely overlooked
- Review of recent data indicates that superior growth may be a general feature of triploid molluscs

Hadley, N.H. and Dillon, R.T., Jr. 1989. Use of offspring genotypes to determine "best" parents in a mass spawning of hard clams. Journal of Shellfish Research. 8(2):448.

- Conference abstract
- Gametes, from South Carolina wildstock clams, collected separately from each individual and then pooled
- Progeny segregated by size and approximately 60 of the largest and 60 of the smallest were subjected to electrophoresis
- Best parents selected to reduce size variation

Hadley, N.H., R.T. Dillon, Jr. and J.J. Manzi. 1991. Realized heritability of growth rate in the hard clam *Mercenaria mercenaria*. Aquaculture. 93(2):109-119.

- Directed breeding program
- Largest 10% of population, and an equal number of mean size clams, were segregated to become selected and control-line parents
- Mass selection appears to be a promising technique for improvement broodstocks

Hadley, N.H. 1993. Effects of hard clam hatchery management practices on productivity and on broodstock quality. World Aquaculture. 24(3):30-31.

- Performance of cohort improves with increasing number of parents
- Effective parental number is 20
- Gametes from under-conditioned clams have lower viability
- Mass-spawning in common containers disadvantageous (super spawner)

Hallerman, E., D. King and A. Kapuscinski. 1998. A computer software package for assessing and managing risks posed by experiments with genetically modified fish and shellfish. NAGA The ICLARM Quarterly. 21(1):12-17.

Harasewych, M.G. and S. Tillier. (Editors). 1994. The highly variable and high mutable mitochondrial DNA molecule of the deep sea scallop *Placopecten magellanicus*. Nautilus. 108(Suppl. 2):85-90.

- Because of its rapid turnover, mtDNA size polymorphisms, do not provide useful information for taxonomic studies

Heath D.D., P.D. Rawson and T.J. Hilbish. 1995. PCR-based nuclear markers identify alien blue mussel (M*ytilus* spp.) genotypes on the west coast of Canada. Canadian Journal of Fisheries and Aquatic Sciences. 52(12):2621-2627.

- Two markers are described to differentiate between mussel species

Heath, D.D., D.R. Hatcher and T.J. Hilbish. 1996. Ecological interaction between sympatric *Mytilus* species on the west coast of Canada investigated using PCR markers. Molecular Ecology. 5(3):443-447.

- One mussel species dominant on exposed coast and another dominant in sheltered waters
- Physically indistinguishable so markers were developed
- Outside mussels excluded from inside waters during early life stages while inside mussels excluded from outside waters by mortality later in life

Hedgecock, D., V. Chow and R.S. Waples. 1992. Effective population numbers of shellfish broodstocks estimated from temporal variance in allelic frequencies. Aquaculture. 108(3-4):215-232.

- Few estimates of effective population size in hatchery stocks have been made
- Small (N_e) can result from inadequate number of breeders, poor sex ratios, "super spawners"
- High fecundities and variable spawning success results in hatchery seed from few parents
- Effective population only a fraction of available spawners
- Genetic drift controlled by development of pedigreed broodstock

Hedgecock, D. 1993. Human impacts on the biological diversity of sessile marine invertebrate populations: Introductions, invasions, and artificial propagation. *In:* Human Impact on Self-Recruiting Populations. 125-150

- Commercial shellfish hatcheries generally ineffective in safeguarding genetic resources
- Variation in recruitment appears to be caused chiefly by climate
- Sweepstakes survival scenario: Match spawn with correct current, climate, food, etc.
- Random genetic drift in finite populations erodes genetic diversity

Hedgecock, D. 1995. Triennial meeting of fish culture section of American Fisheries Society World Aquaculture Society and National Shellfisheries Association. Journal of Shellfish Research. 14(1):268.

- Conference abstract
- Paper refers to management of broodstock for the purposes of maintaining genetic diversity
- Studies of aquatic hatchery broodstock have revealed substantial genetic drift likely due to inadequate numbers of broodstock and large individual variance

Hedgecock, D. 1995. The cupped oyster and the Pacific oyster. Conservation of Fish and Shellfish Resources: Managing Diversity. Academic Press, London. 115-137.

- Different segments of natural population ripening and spawning at different times
- Risks to wild stocks due to over harvesting and replacement by hatchery stock
- Random genetic drift in finite populations erodes genetic diversity
- Risks to genetic conservation: habitat destruction, over harvesting and over planting, hatchery propagation

Heipel, D.A., J.D.D. Bishop, A.R. Brand and J.P. Thorpe. 1998. Population genetic differentiation of the great scallop *Pecten maximus* in western Britain investigated by randomly amplified polymorphic DNA. Marine Ecology Progress Series. (162):163-171.

- DNA (RAPD) banding patterns compared between samples of the same year class
- The RAPD data indicates population genetic structuring in exploited open water stocks
- Previous allozyme studies indicated genetic uniformity
- Differentiation of the Mulroy Bay population from open-water stocks has been demonstrated previously in a study of mtDNA polymorphisms

Heipel, D.A., J.D.D. Bishop, and A.R. Brand. 1999. Mitochondrial DNA variations among open-sea and enclosed populations of the scallop *Pecten maximus* in western Britain. Journal of the Marine Biological Association of the United Kingdom. 79(4):687-695.

- Genetic differentiation between locations can provide important indirect evidence reflecting the pattern and scale of effective larval dispersal
- Dynamic hydrographic conditions may generally ensure extensive mixing of the planktonic larvae

Herbinger, C.M., B.M. Vercaemer, B. Gjetvaj and R.K. O'Dor. 1998. Absence of genetic differentiation among geographically close sea scallop (*Placopecten magellanicus* G.) beds with cDNA and microsatellite markers. Journal of Shellfish Research. 17(1):117-122.

- Studied extent of genetic differentiation between two geographically close beds (shallow and deep)
- No genetic differences were found between the shallow and deep scallops
- Physiological differences observed in situ appear to be mainly related to environmental conditions and not genetic differentiation
- The use of genetic markers allowed us to clarify the level of differentiation between physiologically distinct but proximate beds of sea scallops
- Variety of approaches can be used to address population differences: oceanographic modeling, ecology, physiology, and genetics

Hilbish, T.J. 1985. Demographic and temporal structure of an allele frequency cline in the mussel *Mytilus edulis*. Marine Biology. 86:163-71.

- Steep allele-frequency cline at the *Lap* locus in eastern Long Island Sound over a distance of 30 km
- Large temporal and demographic variation in frequency
- Recruitment composed of larvae originating from oceanic populations
- Selection is directed against the Lap^{94} allele
- Larger size classes seem to be relatively immune to selective forces

Hilbish, T.J., and R.K. Koehn. 1985. The physiological basis of natural selection at the *Lap* locus. Evolution. 39:1302-1317.

- Describes research program to evaluate the contribution of genetic variation at the *Lap* locus to variation in physiological traits under natural conditions

Hilbish, T.J., B.L. Bayne and A. Day. 1994. Genetics of physiological differentiation within the marine mussel genus *Mytilus*. Evolution. 48(2):267-286.

- Two divergent taxa largely isolated geographically and routinely exposed to different thermal environments are physiologically differentiated
- Differentiation between these taxa may be controlled by a few genes

Hilbish, T.J. 1996. Population-genetics of marine species - the interaction of natural-selection and historically differentiated populations Journal of Experimental Marine Biology and Ecology. 200(1-2):67-83.

- High gene flow usually viewed as sufficient to limit geographic isolation
- Cases of divergence have been observed and natural selection has usually been used to explain geographic divergence
- Study provides evidence that selection may be the predominant force that determines genetic divergence in marine systems
- Growing evidence that marine species with high larval dispersal rates may lead to distinct populations

Humphrey, C. and J. Crenshaw. 1989. Clam Genetics. *In* J. Manzi and M. Castagna, editors. Clam Mariculture in North America. Developments in Aquaculture and Fisheries Science, 19. Elsevier. New York, NY. 323-356

- Generally, little genetic work has been done on clams
- Citation for one study of genetic relationships of east coast clam that demonstrated little or no gene flow between the Atlantic coast and Gulf of Mexico
- Discussion about use of genetic selection to improve broodstock

Igland, O.T. and G. Naevdal. 1995. Genetic differentiation between samples of scallops, *Pecten maximus*, from two areas in Norway: Hordaland and Troendelag. Department Fisheries Marine Biology, University of Bergen, N-5008 Bergen, Norway Univ. Bergen, Bergen (Norway) Sent. Miljoe Ressursstud. Rapp 18, 15p.

- Two Norwegian populations studied showed no genetic differences
- Significant differences between populations from UK and France

Insua, A., M.J. Lopez-Pinon and J. Mendez. 1999. Cytogenetic analysis of the pectinid *Chlamys distorta.* Book of Abstracts: 12th International Pectinid Workshop. Conference Title: 12. Int. Pectinid Workshop.

- 400 known species of scallops
- Work presents cytogenetic data of *Chlamys distorta*

International introductions of inland aquatic species. 1988. Fisheries Resource Environmental Division, Fisheries. Department, FAO, 00100 Rome, Italy FAO, Rome (Italy) 294. 318p.

- 1,354 introductions of 237 species into 140 countries are analyzed
- Introductions carry risks such as degradation of environment, disruption of the host community, genetic degradation of the indigenous stock, introduction of diseases and socio-economic effects

Jamieson, G.S. and D.A. Armstrong. 1991. Spatial and temporal recruitment patterns of Dungeness crab in the northeast Pacific. Memoirs of the Queensland Museum 31:365-381

- Increasing evidence that "inland sea" side of Vancouver Island may be distinct from stock on outer coast

Johnson, M.S. and R. Black. 1982. Chaotic genetic patchiness in an intertidal limpet, *Siphonaria* sp. Marine Biology. 70:157-164.

- Significant genetic differences were found among sites along 50 m of shore, between high and low portions of the shore within sites, between adults and recruits, and between recruits
- Genetic heterogeneity chaotic, no discernable pattern
- May result from temporal variation of numbers and genotypes of recruits
- Planktonic dispersal can create fine scale genetic patchiness and still cause uniformity on a large scale

Karl, S.A. 1997. Geographic scale and molecular stock assessment. Journal of Shellfish Research. 16 (1):324-325.

- Conference abstract
- Use of politics and geography to define boundaries can be misleading

Kenchington, E., C.J. Bird and E. Zouros. 1999. Genetic variation in *Placopecten magellanicus* with implications for fisheries management. Journal of Shellfish Research. 18(1):313.

- Conference abstract
- Significant differences between the scallop beds
- Significant year class effect observed

Kijima, A., K. Mori and Y. Fujio. 1984. Population differences in gene frequency of Japanese scallop *Patinopecten yessoesis* on Okhotsk Sea coast of Hokkaido. Bulletin of the Japanese Society of Science and Fisheries/Nissoishi 50(2):241-248.

- Genetic variability studied in ten collections of native and sown populations
- Analysis indicates an independent breeding structure
- Genetic distance larger in native versus sown populations
- Results suggest population has a structure capable of being split into a number of local subpopulations

Kittel, M.T. 1988. Comparative analysis of Tasmanian Pacific oysters, *Crassostrea gigas,* after growout in Washington State. Journal of Shellfish Research. 17(1):329.

- Conference abstract
- Imported (Tasmania) *C. gigas,* transferred to Washington state and compared with local (control) *C. gigas*
- Study shows that the imported F_1 generation had significantly lower mortalities at one location and significantly greater length, weight, and volume than control oysters at both locations

Knaub, R.S., A.G. Eversole and J.J. Manzi. 1988. Reproductive development in three *Mercenaria mercenaria* stocks grown in South Carolina waters. Journal of Shellfish Research. 7(1):122-123.

- Conference abstract
- Crosses made between two stocks
- Original stocks had distinct and separate spawning periods and spawn timing of the hybrid progeny fell between the two

Koehn, R.K., R. Milkman, and J.B. Mitton. 1976. Population genetics of marine pelecypods. IV. Selection, migration, and genetic differentiation in the Blue Mussel *Mytilus edulis.* Evolution. 30:2-32.

- 25,000 individuals from 150 sites from Virginia to Iceland analyzed at six loci
- Homogeneity in allele frequencies, in some loci, over large distances while other loci exhibited differences over very small, medium and large distances
- Variation consistence with selection against some genotypes
- Populations exposed to reduced salinity had reduced allele most common to marine coastal animals

Koehn, R.K., B.L. Bayne, M.N. Moore and J.F. Siebenauer. 1980a. Salinity related physiological and genetic differences between populations of *MytiIus edulis*. Biological Journal of the Linnean Society. 14:319-334.

- Allele frequencies differ between populations according to environmental salinities
- Salinity changes can be measured on the biochemical, physiological, and population genetic levels

Koehn, R.K. and S.E. Shumway.1982. A genetic physiological explanation for differential growth-rate among individuals of the American oyster, *Crassostrea virginica* Marine Biology Letters. 3(1):35-42.

- Studies the correlation between the degree of individual heterozygosity and growth rate as related to oxygen consumption rates

Koehn, R.K. and P.M. Gaffney. 1984. Genetic heterozygosity and growth rate in *MytiIus edulis.* Marine Biology. 82:1-7.

- Growth rate positively correlated with individual heterozygosity

Koehn, R.K., J.G. Hall, D.J. Innes and A.J. Zera. 1984. Genetic differentiation of *Mytilus-edulis* in eastern north America. Marine Biology. 79(2):117-126.

- Significant differentiation at five polymorphic loci among certain geographical areas
- Three population groups identified
- No evidence for interbreeding among genetically distinct individuals
- May be distinct species

Koehn, R.K. and T.J. Hilbish. 1987. The adaptive importance of genetic variation. American Scientist. 75:134-141.

- Long Island Sound mussels
- One study confirms that gene flow is extensive among populations
- Another study shows genetic differentiation over small distances (few meters to several kilometers) "which implies a high degree of differential mortality among genotypes in a species with enormous fecundity"

Koehn, R.K. 1991. The genetics and taxonomy of species in the genus *Mytilus*. Aquaculture. 94(2-3):125-145.

- Study of *Mytilus* genetics after a 15-year hiatus
- Substantial genetic differentiation thought to occur between adjacent populations in early work
- Populations relatively homogeneous, over vast geographical distances
- Differences between adjacent populations represent taxonomic differences, not population differences

Krause, M.K. 1989. Genetics of transplanted bay scallops in Long Island waters: Evidence for selective mortality. Journal of Shellfish Research. 8(2):449.

- Conference abstract
- Hatchery produced seed were transplanted into Long Island waters
- Differences in allele frequencies between transplanted and native populations
- Transplanted scallops shifted allele frequencies towards wild populations after one year (selective mortality)

Krause, M.K. 1992. Use of genetic markers to evaluate the success of transplanted bay scallops. Journal of Shellfish Research. 11(1):199.

- Conference abstract
- Hatchery produced seed transplanted into Long Island waters
- Significant allele frequency differences among indigenous and transplanted scallops
- Differences not sufficient to separate the stocks using discriminate analysis
- Maximum likelihood estimation of stock composition more reliable

Krause, M.K., W.S. Arnold and W.G. Ambrose. 1994. Morphological variation and genetic variation among 3 populations of calico scallops, *Argopecten gibbus*. Journal of Shellfish Research. 13(2):529-537.

- Analyses of electrophoretic loci showed significant allele frequency heterogeneity among sites for one of seven polymorphic loci
- Gene flow estimates between populations suggest relatively frequent migration, sufficient for panmixia
- Oceanographic processes play a critical role in larvae transport between populations

Krause, M.K. 1999. Molecular evolution of the GPI locus in bay scallops, *Argopecten irradians*. Journal of Shellfish Research. 18(1):294.

- Presents initial results from a molecular evolutionary study of nucleotide variation at the *Gpi* locus

Laing, I. and S.D. Utting. 1994. The physiology and biochemistry of diploid and triploid Manila clam (*Tapes philippinarum* Adams & Reeve) larvae and juveniles. Journal of Experimental Marine Biology and Ecology. 184(2):159-169.

- Methods and results of producing triploids

Lakra, W.S. and P. Das. 1998. Genetic engineering in aquaculture. Indian Journal of Animal Sciences. 68(8):873-879.

- Discusses progress made in genetic manipulations including induced polyploidy

Landau, B. and X. Guo. 1999. Growth characteristics in triploid Pacific oysters. Journal of Shellfish Research. 18(1):270-271.

- Conference abstract
- Triploids grow faster and heavier than diploids

Levinton, J.S. and R.K. Koehn. 1976. Population genetics of mussels. *In* Marine Mussels: Their Ecology and Physiology, B. L. Bayne, editor. Cambridge University Press. 357-384.

- Geographic variation on east and west coast
- Micro-geographic variation by distance (less than one meter) and size
- Differential selective mortality of setting mussels
- Environmental factors in intertidal zone can influence variation: exposure time, water retention, heat transfer

Lewis, R.I. and J.P. Thorpe. 1994. Temporal stability of gene-frequencies within genetically heterogeneous populations of the queen scallop *Aequipecten (Chlamys) opercularis*. Marine Biology. 121(1):117-126.

- Hydrographic data suggest that the particular population studied is self-recruiting, even though the larvae stage lasts several weeks

Manzi, J.J., N.H. Hadley and R.T. Dillon. 1988. Applied breeding of the hard clam *Mercenaria*: Growth of outbred lines from crosses of selected commercial hatchery stocks. Journal of Shellfish Research. 7(1):168-169.

- Discusses and analyzes breeding strategies to "improve" clam stocks

Manzi, J.J., N.H. Hadley and R.T. Dillon. 1988. Improved stocks of hard clams (*Mercenaria* spp.) through genetic manipulation. Journal of Shellfish Research. 7(1):125.

- Discusses and analyzes breeding strategies to "improve" clam stocks

McDonald, J.H. and R.K. Koehn. 1988. The mussels *Mytilus galloprovincialis* and *M. trossulus* on the Pacific coast of North America. Marine Biology. 99:111-118.

- Southern California mussels similar to Mediterranean species, apparently due to introductions

McDonald, J.H. and J.F. Siebenaller. 1989. Similar geographic variation at the *Lap* locus in the mussels *Mytilus trossulus* and *M. edulis.* Evolution. 43:228-231.

- Differences between estuary and coastal samples, possibly due to selection
- Environmental differences include salinity, temperature, food quantity and type

McDonald, J.H., R. Seed and R.K. Koehn. 1991. Allozyme and morphometric characteristics of three species of *Mytilus* in the Northern and Southern hemisphere. Marine Biology. 111:1313-1335.

- Northern and southern hemisphere populations may be similar because of transfers

McLean, D.C., Jr. 1988. Variations in allelic frequencies in juveniles of the hard clam, *M. mercenaria*. World Aquaculture. 19(3):66-67.

- Long Island sound *M. edulis* have different allele frequencies at *Lap* locus due to differences in selection pressures
- Natural selection acts on the *Lap* locus

McLean, D.C., Jr., R.T. Dillon, Jr. and J.J. Manzi. 1988. Variations in allelic frequencies in juveniles of the hard clam, *Mercenaria mercenaria*. Journal of Shellfish Research. 7(1):203.

- Mendelian cross at the *Lap* locus made to study differential survival rates

Metznerroop, K.L. 1994. The effect of aquaculture on the genetics of natural-populations of the hard-clam, *Mercenaria mercenaria* (L.). Journal of Shellfish Research. 13(2):487-491.

- Hatchery clams with unique alleles transplanted to wild areas
- Three years after last transplant, wild areas surveyed
- Effect of aquaculture on genetics of wild population negligible

Milkman, R. and R.K. Koehn. 1977. Temporal variation in the relationship between size, numbers, and an allele-frequency in a population of *Mytilus edulis*. Evolution. 31:103-115.

- Differences in allele frequencies over short distances observed
- Influences from several sources, differing over time
- Genetic composition of the studied population does not result directly from self-seeding

Moore, M.N., R.K. Koehn and B.L. Bayne. 1980. Leucine aminopeptidase (aminopeptidase-I), N-acetyl-β-hexosamidase and lysosomes in the mussel, *Mytilus edulis* L., in salinity changes. Journal of Experimental Zoology. 214:239-249.

- Study of various enzymes in the mussel

Myrand B. and J. Gaudreault. 1995. Summer mortality of blue mussels (*Mytilus-edulis linneaus*, 1758) in the Magdalen Islands (southern Gulf of St. Lawrence, Canada). Journal of Shellfish Research. 14(2):395-404.

- Survival is influenced by genetic rather than environmental factors

Myrand, B., R. Tremblay and J.M. Sevigny. 1999. Impact of culture practices on the heterozygosity of suspension-cultured blue mussels. Journal of Shellfish Research. 18(1):294.

- Conference abstract
- Changes in heterozygosity in cultured mussels
- May be rectified with changes in culture methods

Nikiforov, S.M. and S.M. Dolganov. 1982. Genetic variability of the Yezo scallop in the Vostok Bay of the Sea of Japan. Biologija Morya. (2):46-51.

- Description of polymorphic protein systems likely to serve as gene markers

Oniwa, K., A. Kijima and Y. Fujio. 1994. Relationship between genetic variability and quantitative traits in the Japanese scallop, *Patinopecten yessoensis*. Fac. Agricult., Tohoku Univ., Sendai 981, Japan. Tohoku Journal of Agricultural Research. 45(1-2):1-10.

- Positive correlations observed between body weight (whole and soft parts) and heterozygosity
- Genetic variation in the quantitative traits is hypothesized from the positive correlation between quantitative traits and genetic variability

Patwary, M.U., E.L. Kenchington, C.J. Bird and E. Zouros. 1994. The use of random amplified polymorphic DNA markers in genetic studies of the sea scallop *Placopecten magellanicus* (Gmelin, 1791). Journal of Shellfish Research. 13(2):547-553.

- First published application of the random Amplified polymorphic DNA (RAPD) technique to bivalve DNA
- Genetic similarities based on allele frequencies can be estimated and used as an additional tool for understanding the genetic structure of sea scallop populations

Patwary, M.U., M. Reith and E.L. Kenchington. 1996. Isolation and characterization of a cDNA encoding an actin gene from sea scallop (*Placopecten magellanicus*). Journal of Shellfish Research. 15(2):265-270.

- Description and results from analysis of specific scallop gene

Perez, J.E. and C. Alfonsi. 1999. Selection and realized heritability for growth in the scallop, *Euvola ziczac* (L.). Aquaculture Research. 30(3):211-214.

- Selection experiment
- Largest 10% of population, and an equal number of mean size scallops were segregated to become selected and control-line parents

Perez, J.E., O. Nusetti, N. Ramirez and C. Alfonsi. 2000. Allozyme and biochemical variation at the octopine dehydrogenase locus in the scallop *Euvola ziczac.* Journal of Shellfish Research. 19(1):85-88.

- Study of the octopine dehydrogenase (Odh) locus in the adductor muscle

Picozza, E., J. Crivello, M.V. Brown, L. Strausbaugh and S. Stiles. 2000. Status report for the characterization of the bay scallop, *Argopecten irradians*, genome. Journal of Shellfish Research. 19(1):578-579.

- Describes creation of genomic library and potential uses

RaLonde, R. 1993. Shellfish aquaculture in Alaska and the potential of interaction with wild species. Proceeding of the twenty-second U.S.- Japan aquaculture panel symposium. Homer, Alaska, August 21-22, 1993. 27-39.

- Discussion of potential larval drift zones is Alaska

Rigaa A., D. Cellos and M. Monnerot. 1997. Mitochondrial DNA from the scallop *Pecten maximus*: An unusual polymorphism detected by restriction fragment length polymorphism analysis. Heredity. 79(4):380-387.

- Analysis of mitochondrial DNA diversity presented

Rios, C., J. Canales and J.B. Pena. 1996. Genotype-dependent spawning: Evidence from a wild population of *Pecten jacobaeus* (L.) (Bivalvia: Pectinidae). Journal of Shellfish Research. 15(3):645-651.

- Study of genetic basis for spawning asynchrony
- Genotype dependent spawning time for the genetic structure of the population discussed

Robinson, S.M.C. 1999. An overview of aquaculture research in Atlantic Canada. Journal of Shellfish Research. 18(1):276.

- Conference abstract
- 1989-1999 shellfish industry growth rate 10% and finfish industry 28%
- Mostly Atlantic salmon research
- Four main areas of shellfish research: broodstock, health, grow out and environment

Rodriguez-Juiz, A.M., M. Torrado and J. Mendez. 1996. Genome-size variation in bivalve molluscs determined by flow cytometry. Marine Biology. 126(3):489-497.

- The nuclear DNA content in 10 species studied using flow cytometry
- Distribution of DNA values among all species continuous and overlapping

Shaklee, J.B. and P. Bentzen 1998. Genetic identification of stocks of marine fish and shellfish. Bulletin of Marine Science. 62(2):589-621.

- Describes utility of using genetic markers for stock identification
- Differences in allozyme and DNA techniques with regards to resolution and tissue collection
- Methods for restriction enzyme analysis of mtDNA and length polymorphism analysis of nuclear mini- and microsatellites are being refined
- Genetic analyses revealing existence of multiple species where only one was thought to exist

Stiles, S, T. Robinson and J. Choromanski. 2000. Observations on growth and survival of juvenile bay scallops (*Argopecten irradians*) from genetic lines under different density and holding conditions. Journal of Shellfish Research. 19(1):582-583.

- Genetic selection for hatchery line of scallops
- Held in various types of rearing units
- Performance equal among all lines

Thorgaard, G.H. and S.K. Allen Jr. 1988. Environmental impacts of inbred, hybrid, and polyploid aquatic species. Journal of Shellfish Research. 7(3):556.

- Conference abstract
- Using hybrids and inbred animals for aquaculture transplants has led to concern for environment (competition, interbreeding or replacement)
- Sterile animals are least likely to have negative impacts
- Caution as sterile hybrids or triploids may interfere with reproduction of natural stocks in non-genetic ways
- Fertile hybrids should not be used outside closed systems
- Fertile hybrids provide opportunity for introducing beneficial genes into domesticated stocks

Tweed, S.M. and X. Guo. 1999. Preliminary evaluation of triploid American oysters, *Crassostrea virginica*, on a mid-Atlantic oyster farm. Journal of Shellfish Research. 18(1):335.

- Conference abstract
- Select stock triploids and diploids growth compared

Vadopalas, B.A. and J.P. Davis. 1998. Induction of triploidy in the geoduck clam, *Panope abrupta*. Journal of Shellfish Research. 17(4):1285.

- Conference abstract
- Concerns about genetic risks in cultured stocks
- No definitive results in diversity of Puget Sound stocks
- Temperature and chemical methods for triploidy induction studied

Vercaemer, B. and R.K. O'Dor. 1993. Filtration rate variations in scallops: Environmental and/or genetic control? Proceedings of the 10th Annual Meeting of the Aquaculture Association of Canada. Bulletin of the Aquaculture Association of Canada. (93-4):128-131.

- Physiological differences between close populations appeared to be related to environmental conditions but distant populations may be genetically different

Volckaert, F. and E. Zouros. 1989. Allozyme and physiological variation in the scallop *Placopecten magellanicus* and a general model for the effects of heterozygosity on fitness in marine molluscs. Marine Biology. 103(1):51-61.

- Heterozygosity and growth rate have been correlated in many molluscs
- Heterozygote deficiency was small in six samples collected and decreased with age
- No correlation observed between genotype and growth rate

Wada, K.T. 1998. The present status of genetic conservation of cultured aquatic species in Japan: Action before extinction. *In* World Fisheries Trust. 202-505 Fisgard St. 225-231.

- Government support to promote genetic diversity in aquaculture stocks
- Description of status and effectiveness programs

Wang, Z., R. Wang, R.Yu and C. Tian. 1998. Biological characteristics of polyploid shellfish. Journal of Ocean University of Qingdao. 28(3):399-404.

- Production and culture of polyploid shellfish reviewed
- Reduced survival at larval stage but similar to diploids at adult stage
- Triploids not 100% sterile

Wilbur, A.E. and P.M. Gaffney. 1993. The effect of parental relatedness on progeny growth and viability in the bay scallop, *Argopecten irradians*. Journal of Shellfish Research. 12(1):151-152.

- Inbreeding depression can affect progeny fitness
- Outbreeding depression may also reduce offspring fitness

Wilbur, A.E., and P.M. Gaffney. 1997. Mitochondrial DNA variation and population structure of the bay scallop, *Argopecten irradians*. Journal of Shellfish Research. 16(1):329-330.

- Conference abstract
- Geographic variation in morphology and physiology has led to the recognition of three subspecies
- Test hypothesis of restricted gene flow among subspecies
- Results from mtDNA analysis suggested significant variation among populations
- Pattern of divergence among populations was inconsistent with expectations based on geographic proximity

Wilbur A.E., E.A. Orbacz, J.R. Wakefield and P.M. Gaffney. 1997. Mitochondrial genotype variation in a Siberian population of the Japanese scallop, *Patinopecten yessoensis* (*Jay*). Journal of Shellfish Research. 16(2):541-545.

- Genetic variation evaluated with restriction fragment-length polymorphisms

Wilbur, A.E., W.S. Arnold and T.M. Bert. 1999. Evaluating bay scallop stock enhancement efforts with molecular genetic markers. Journal of Shellfish Research. 18(1):315-316.

- Conference abstract
- Collapsing Florida population of bay scallops not halted by management efforts
- Enhancement taken place with genetic evaluation to determine impact from hatchery infusions
- Genetic markers used for evaluation

Wilding, C.S., J.W. Latchford and A.R. Beaumont. 1998. An investigation of possible stock structure in *Pecten maximus* (L.) using multivariate morphometrics, allozyme electrophoresis and mitochondrial DNA polymerase chain reaction-restriction fragment length polymorphism. Journal of Shellfish Research. 17(1):131-139.

- Total concordance not found across methodologies: morphology, allozymes and mtDNA
- Trends suggestive of morphological distinctness of a population or populations were difficult to uncover

Wilhelm, R. and T.J. Hilbish. 1998. Assessment of natural selection in a hybrid population of mussels: Evaluation of exogenous vs. endogenous selection models. Marine Biology. 131(3):505-514.

- Frequency of hybrid genotypes among age classes evaluated
- Strong viability selection occurs among hybrid genotypes
- Recombinant hybrid genotypes intermediate in fitness

Xiang, Jian-Hai, R.R. Desrosiers and F. Dube. 1993. Studies on the chromosomes of the giant scallop *Placopecten magellanicus* (Gmelin) and the surf clam *Spisula solidissima* (*Dillwyn*). International Journal of Cytology. 58(2):125-132.

- Increased desire to enhance declining stocks
- Use of polyploids considered
- Paper identifies karyotypes of diploids and triploids.

Zouros, E., G.H. Pogson, D.I. Cook and M.J. Dadswell. 1992. Apparent selective neutrality of mitochondrial DNA size variation: A test in the deep-sea scallop *Placopecten magellanicus*. Evolution. 46(5):1466-1476.

- Individual shell lengths compared with different copy numbers of a large mtDNA repeated sequence

Appendix A

Selected Fish and Game Laws, Regulations and Guidelines Related to Shellfish Transport and Aquaculture

Commercial Fisheries Mission Statement.

The mission of the Division of Commercial Fisheries is to manage, protect, rehabilitate, enhance, and develop fisheries and aquatic plant resources in the interest of the economy and general well-being of the state, **consistent with the sustained yield principle** and subject to allocations established through public regulatory processes. The division is responsible for management of the state's commercial, subsistence, and personal use fisheries; the rehabilitation and enhancement of existing fishery resources; and the development of new fisheries. Technical support is provided to the private sector mariculture and salmon ranching industries. The division also plays a major role in the management of fisheries in the 200-mile Exclusive Economic Zone and participates in international fisheries negotiations.

5 AAC 41.070. Prohibitions on Importation and Release of Live Fish.

(a) Except as provided in (b), (c), and (d) of this section, no person may import any live fish into the state for purposes of stocking or rearing in the waters of the state.

(b) Live oysters native to and originating from the Pacific Coast of North America may be imported for aquaculture purposes, under a permit required by this chapter, and may be released into the waters of the state only of the

(1) broodstock is derived from oysters commercially cultured on the Pacific Coast of North America through three or more generations; and

(2) disease history or an inspection indicates no incidence of disease that is not indigenous to Alaska.

(c)Ornamental fish not raised for human consumption…..

(d) Weathervane scallops originating from wild stocks or cultured stocks in the Southeastern Alaska and Yakutat Areas may be imported for aquaculture purposes and may be released only in the Southeastern and Yakutat Areas……

Sec. 16.05.251. Regulations of the Board of Fisheries.

(a) The Board of Fisheries may adopt regulations it considers advisable in accordance with AS 44.62 (Administrative Procedures Act) for

(1) setting apart fish reserve areas, refuges, and sanctuaries in the waters of the state over which it has jurisdiction, subject to the approval of the legislature;

(2) establishing open and closed seasons and areas for the taking of fish; if consistent with **resource conservation and development goals**, the board may adopt regulations establishing restricted seasons and areas necessary for persons 60 years of age and older to participate in sport, personal use, or subsistence fishing;

(12) regulating commercial, sport, guided sport, subsistence, and personal use fishing as needed for the **conservation**, development, and utilization of fisheries;

(d) Regulations adopted under (a) of this section must, **consistent with sustained yield** and the provisions of AS 16.05.258, provide a fair and reasonable opportunity for the taking of fishery resources by personal use, sport, and commercial fishermen.

(h) The Board of Fisheries shall adopt by regulation a policy for the management of mixed stock fisheries. The policy shall provide for the management of mixed stock fisheries in a manner that is consistent with **sustained yield of wild fish stocks.**

Sec. 16.40.100. Aquatic farm and hatchery permits.

(c) The commissioner may attach conditions to a permit issued under this section that are necessary to **protect natural fish and wildlife resources**.

Sec. 16.40.105. Criteria for issuance of permits.

The commissioner shall issue permits under AS 16.40.100 on the basis of the following criteria:

(2) the proposed farm or hatchery **may not require significant alterations in traditional fisheries** or other existing uses of fish and wildlife resources;

(3) the proposed farm or hatchery **may not significantly affect fisheries, wildlife, or their habitats in an adverse manner**;

Sec. 16.40.120. Aquatic stock acquisition permits.

(d) **The commissioner shall deny or restrict a permit under this section upon finding that the proposed harvest will impair sustained yield of the species** or will unreasonably disrupt established uses of the resources by commercial, sport, personal use, or subsistence users. The commissioner shall inform the Board of Fisheries of any action taken on permit applications for species that support commercial fisheries subject to limited entry under AS 16.43 and of any permits denied because of unreasonable disruption of an established use. A denial of the permit by the commissioner must contain the factual basis for the findings.

Policy and Requirements for Fish Resource Permits.

Permit Issuance, Denial, or Revocation The commissioner will deny a fish resource permit if it is determined that the proposed activities will adversely affect the **continued health and perpetuation** of native, wild, or propagated stocks of fish, shellfish, aquatic plants, or their habitat. The commissioner will also deny a fish resource permit if the proposed activities will adversely disrupt traditional common property fisheries.

Alaska Constitution
Article 08
Natural Resources

Section 8.1 - Statement of Policy.

It is the policy of the State to encourage the settlement of its land and the development of its resources by making them available for maximum use consistent with the public interest.

Section 8.3 - Common Use.

Wherever occurring in their natural state, fish, wildlife, and waters are reserved to the people for common use.

Section 8.4 - Sustained Yield.

Fish, forests, wildlife, grasslands, and all other replenishable resources belonging to the State shall be utilized, developed, and maintained on the **sustained yield principle**, subject to preferences among beneficial uses.

Section 8.15 - No Exclusive Right of Fishery.

No exclusive right or special privilege of fishery shall be created or authorized in the natural waters of the State. This section does not restrict the power of the State to limit entry into any fishery for purposes of resource conservation, to prevent economic distress among fishermen and those dependent upon them for a livelihood and to **promote the efficient development of aquaculture in the State.**

Appendix B

(Transcribed copy from original Rosier letter)

April 29, 1994

Mr. Jeff Hetrick
President, ASGA
P.O. BOX 7
Moose Pass, AK

Dear Jeff:

Thank you for taking the time to bring your thoughts regarding the proposed shellfish genetics policy to my attention. I appreciate that you would like to see the policy developed rapidly. You must understand, however, that the little knowledge there is available upon which to base such a policy is incomplete and complex (in contrast with information available on Pacific salmon, for example).

My staff has virtually no data on the population genetics of bivalves, in Alaska. In addition, the published data on bivalves from other areas is in disagreement. Many studies do suggest that unique stocks of shellfish subdivide along short sections of beach. If a genetics policy was written to protect wild stocks without gaining more knowledge of the structure of Alaskan stocks, then that policy would likely end up being very restrictive. We are faced with a tough-to-reconcile dichotomy: We want to restrict transfers in order to protect wild stocks, yet we want to promote a policy, that will facilitate the development of mariculture.

Superimposed over this dichotomy is the fact that I have limited staff assigned to genetics policy issues. As important as the finfish and shellfish genetics policies are, I am not willing to redirect them on the three-month schedule you suggest in your letter.

Let me relay the progress we have made and the direction I see the shellfish portion of the policy going. I fully understand the frustrations you and the industry must feel in not knowing what the final, policy will be.

First, after one meeting that you had with Mr. Jim Cochran and Dr. Jim Seeb last year, we did bring the University of Alaska Fairbanks(UAF) Marine Advisory Program into genetics policy discussions. Staff has spoken with and met with Mr. Ray RaLonde a number of times. Dr. Seeb met with Mr. RaLonde and reviewed his theories on larval drift which were presented to an international panel of mari ulturists in Homer last August. Mr. RaLonde's paper, *Shellfish Aquaculture in Alaska and the Potential of Interaction with Wild Species*, was well received, and he has recently submitted a final draft for review through the Sea Grant process.

We are enthused about this document because, depending on the reviews, it appears to offer important insight upon which to base a meaningful genetics policy. I encourage you to ask Mr. RaLonde for a copy.

Based upon this preliminary information, staff believe it will be possible to divide the state into three regions, corresponding to our management regions, I (Southeast), II (Prince William Sound to Cook Inlet), III (Kodiak and the Aleutians), for genetics and mariculture purposes using Mr. RaLonde's larval drift model. Transports between regions for purpose of release will be prohibited. Transports within a region will be approved on a case-by-case basis following appropriate staff review. Transports within regions, like the one you describe in paragraph two of your letter, will be approved within the guidelines of hatchery quarantine, though two transport permits will still be required. One permit allows acquisition and transport of a stock to the hatchery. The second allows transport of a given number of progeny from that stock to a specific location. This second permit covers a new generation and allows the department to review specific management, pathology, and genetic concerns after the species has been through the hatchery phase.

The point is that we are using the above guidelines for shellfish transport recommendations right now, and you can see where your projects fit within the framework the department is constructing. We are waiting for the peer review of Mr. RaLonde's paper, and if that is acceptable, plan to use it for the basis of a shellfish genetics policy. An operational Mariculture Technical Center is still years away with possible operation in 1996. Whereas the process. for developing a shellfish policy seems arduous, I believe such a completed policy will be in place when needed by the industry.

If you have additional questions or concerns please contact Mr. RaLonde about his paper and Dr, Seeb for his interpretation of this paper. Dr. Seeb can be reached at the department's Anchorage Office at 333 Raspberry Road, or at 267-2385,. Please let me know if I can be of further assistance.

Carl L. Rosier

Commissioner

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Amendment of Additional Citations

Bowen, B.W. 1998. What is wrong with ESUs?: The gap between evolutionary theory and conservation principles. Journal of shellfish Research. 17(5):1355-1358.

- Discussion of evolutionary significant units (ESUs), management units (MUs) and geminate evolutionary units (GEUs)

Mulvey, M., H. Liu and K.L. Kandl. 1998. Application of molecular genetic markers to conservation of freshwater bivalves. Journal of Shellfish Research. 17(5):1395-1405.

- Review of molecular genetic techniques and their application to freshwater bivalves
- Law enforcement
- Hatchery stock management
- Genetic data provides valuable insight for management
- Genetic data must be coupled with life history, geography and ecological data

Nammack, M. 1998. National marine fisheries service and the evolutionarily significant unit:implications for management of freshwater mussels. Journal of Shellfish Research. 17(5):1415-1418.

- Endangered Species Act limits consideration only to vertebrates
- Freshwater mussel populations tend to be locally adapted as they become reproductively isolated from other populations
- Host fish important factor in delineating populations

Villella, R.F., T.L. King and C.E. Stariper. 1998. Ecological and evolutionary congress in freshwater bivalve relocation programs. Journal of Shellfish Research. 17(5):1407-1413.

- Relocation efforts designed around effect population size, measuring impact of introduction on entire bivalve community
- Items to consider in any relocation effort: define goals of effort, ecology and genetics of any existing population, complexity of species life cycle and relationship between donor stock and receiving populations
- Minimize effects of gene drift and inbreeding depression by using large effective population sizes
- Avoid mixing different evolutionary lineages