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The Role of Hybridization in the Distribution, Conservation and Management of Aquatic Species

Symposium review

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> *"The view generally entertained by naturalists is that species, when intercrossed, have been specially endowed with the quality of sterility, in order to prevent the confusion of all organic forms"*
>
> Charles Darwin, 1859

This issue of *Reviews in Fish Biology and Fisheries* contains six papers addressing several critical aspects of hybridization in fishes and aquatic organisms. Hybridization is a phenomenon long recognized in fishes (Hubbs, 1920, 1955; Schwarz, 1981), as well as in other plant and vertebrate taxa, despite some rather dogmatic proclamations to the contrary, e.g., comments made by David Starr Jordan at the beginning of the 20th century that the species "line" is rarely crossed in fishes (Clark Hubbs, personal communication). Since that time, interspecific genetic introgression has been well documented in many fish genera and species: *Barbus* (Berrebi and Cattaneo-Berrebi, 1993); *Cyprinodon* (Echelle and Connor, 1989; Dowling and DeMarais, 1993); *Gambusia* (Hubbs, 1959; Scribner and Avise, 1994); *Esox* (Wahl and Stein, 1993); *Lepomis* (Avise et al., 1984); *Luxilus* (Duvernell and Aspinwall, 1995); *Morone* (Harrell et al., 1993); *Notropis* (Dowling et al., 1989; Dowling and Hoeh, 1991); *Oncorhynchus* (Busack and Gall, 1981; Campton and Utter, 1985; Loudenslager et al., 1986; Leary et al., 1987; Forbes and Allendorf, 1991; Dowling and Childs, 1992); *Salmo* (Nyman, 1970; Wilkins et al., 1993; Giuffra et al., 1996; Hartley, 1996; Perez et al., 1999); *Salvalinus* (Hammar et al., 1991; Bernatchez et al., 1995; Baxter et al., 1997; Glemet et al., 1998; Wilson and Bernatchez, 1998); *Sebastes* (Seeb, 1988); *Stizostedion* (Billington et al., 1988). See also reviews in Campton (1987), Verspoor and Hammar (1991), Smith (1992), and Scribner et al. (2000). More recently, a number of investigations have documented not only first generation hybrids, but also subsequent generation introgressant hybrids (Bartley et al., 1990; Verspoor and Hammar, 1991). As a result, our views about species typology and hybrids continue to change.

Hybridization between recognized taxa has proven to be somewhat of a conundrum, in part because of how we view speciation as a diversifying process incorporating reproductive isolation, selective and random phylogenetic divergence, and descent with modification, but also because of how species, as naturally cohesive biological units, are defined. Therefore, hybridization among divergent taxa is generally viewed as a destructive process because it:

1) Contradicts the basic principle of dichotomous divergence (Mayr, 1970; Smith, 1992).
2) Leads to sterile or nonviable dead ends due to the lower reproductive fitness of hybrid offspring and the wastage of reproductive investment (Dowling and Moore, 1985; Ferguson, 1986; Leary et al., 1985; Hawkins and Foote, 1998).
3) Contributes to the loss of unique genetic diversity and the breakdown of adaptive multi-gene complexes (Barton and Hewitt, 1989; Taylor and Hebert, 1993; Leary et al., 1995).

Although this may appear to be true, we should recognize that speciation, in most cases, is a temporal phenomenon occurring at different scales over an extended time frame (Avise and Walker, 2000) and hybridization, especially those cases leading to genomic introgression, may be an evolutionarily constructive process as well (Lewontin and Birch, 1966; Arnold, 1997; Dowling and Secor, 1997). In contrast to the negative points listed above we need to consider the following evolutionary evidence concerning hybridization as a constructive process:

1) Reproductive barriers, both pre- and post-zygotic, between described species appear incomplete among many fishes (Simon and Noble, 1968; Bartley et al., 1990; Rosenfield et al., 2000; Hendry et al., 2000).
2) Permanent transfer of genetic information apparently is possible even when hybrids and backcrosses are under negative selection (Arnold and Hodges, 1995; Arnold, 1997; Glemet, 1997; Epifanio and Philipp, 2001).
3) Genetic exchange through introgressive events may have significant effects on the genetic composition of a species, and thereby, actually contribute to diversity within taxa (Arnold, 1992; Dowling and DeMarais, 1993; Bernatchez et al., 1995; Dowling and Secor, 1997; Glemet et al., 1998).

Although the term hybridization is generally applied to the interbreeding of taxa at the species level (of taxonomic organization), recently recognized implications and concerns over interbreeding below the species level, especially of divergent and locally adapted populations further reinforces a need to understand the causes and consequences of gene flow among divergent groups at all levels of organization (see Nielsen, 1995 and papers therein). Because fishes occupy a unique stature in vertebrate evolution, direct observations and patterns in fishes will shape our views of processes and patterns of evolution in other vertebrate groups (Sydney Brenner, Molecular Sciences Institute, Berkeley, CA, personal communications). Finally, considerable controversy has erupted over the treatment of hybrids within the context of the US Endangered Species Act (16 United States Code, Sections 1531 to 1544; O'Brien and Mayr, 1991a and b). We are faced with the question of whether individuals or populations of recent polyphyletic origin warrant *de facto* inclusion in protected populations (Moritz, 1994; Bowen, 1998 and 1999; Stone, 2000). Ultimately, the widespread occurrence of hybridization in fishes suggests the need to revisit the phenomenon and explore its importance in fishes for both basic understanding of biological principles and for practical application of this understanding in living resource management and conservation (Crandall et al., 2000; Kark and Blackburn, 2000).

The following papers were solicited from a symposium held at the August, 1999 Annual Meeting of the American Fisheries Society in Charlotte, NC (USA) entitled, "The role of hybridization in the distribution, conservation, and management of aquatic species." Nineteen invited papers addressing the history, evolutionary theory, use, and management of hybrids and hybridization were presented over a two-day period. Clark Hubbs provided a keynote in which he reviewed the historical context of hybridization in fishes based on the works of his father, Carl Leavitt Hubbs, and himself (see also Hubbs, 1955). Looking backward to the beginning of the 1900s, it seems rather remarkable that hybridization in fishes was once viewed as fodder for mythology or at best a rare and accidental occurrence. The six papers contained within this issue span the range of topics presented and provide an update on several issues or topics surrounding hybridization in aquatic organisms. These papers also represent theoretical and empirical works that transcend taxonomic focus and geographic coverage.

Avise (2001) reviews the theory and support for using patterns of disequilibrium between cytoplasmic and nuclear genotypes as signatures for understanding ecological and evolutionary processes where reproductively interbreeding taxa co-occur. Here, six patterns of disequilibrium are discussed relative to the processes responsible for their occurrence. Moreover, several case studies are highlighted to demonstrate how examination of disequilibrium has led to our understanding of how hybridization operates (i.e. asymmetrical interbreeding, breakdown of reproductive isolation, and other mechanisms) in different settings. An important message emerges; hybridization is not a single process leading to a uniform outcome, but rather a suite of processes and outcomes shaped by ecological conditions and variations in life history.

Utter (2001) reviews the evidence of introgressive hybridization within species of two salmonid genera resulting from widespread translocations. The author observed that published accounts following introductions varied in terms of whether formerly isolated conspecific populations introgressed. Although there are well-documented examples of interspecific and intraspecific introgressions resulting from species translocations or sub-specific stock transfers, especially in inland freshwater taxa, anadromous populations appear more immune to introgression from distinct conspecific lineages, suggesting the importance of complex adaptation to local environments. Ultimately, however, the propensity and relative ease of introgressions within major conspecific anadromous lineages promotes an erosion of population genetic substructure. The collapse of such substructure (often cryptic or occurring at the threshold of detection with molecular markers) resulting from extensive translocation or straying can be an insidious process leading to a reduction of natural population productivity.

Poteaux et al. (2001) reports on a study of the dynamics and introgression of genomes from introduced brown trout into aboriginal gene pools occurring in the Sorgue River of southern France. This was a comparative study of the distribution and fate of introgressing hatchery-genes in disturbed and undisturbed populations of French Mediterranean trout using allozymes, mtDNA and microsatellite markers. The genetic pattern observed among drainage basins was found to be noticeably different for different markers with a lack of concordance among protein-coding and microsatellite loci. The authors suggest that protein-coding alleles of domestic origin may have been subject to selection due to the advantage of the wild phenotype over the hatchery phenotype when artificial stocking ceased. A reduction in population size was suggested as the cause of lower genetic variability in the undisturbed (upstream) areas of the Sorgue River.

Bartley et al. (2001) reviews worldwide application of interspecific hybrids in aquaculture production. From a commercial perspective, various hybrids are favored in situations where production can be enhanced, directed toward some desirable physical or physiological feature, or accelerated. In many cases, hybrids display a relatively high propensity for economically-important performance traits, provide a non-biotechnological method for the potential transfer of desirable traits, and provide a way to combine multiple desirable traits into a single product. Hybrids are sometimes sterile, lowering the genetic risks to local fauna from possible escapement and interbreeding. Unfortunately, accurate estimates of hybridization events and accounting for the use of hybrids in different countries have been hampered by the absence of systematic reporting or survey. Therefore, the actual benefits and costs of using hybrids from both the commodity and conservation perspectives are largely unknown.

Epifanio and Philipp (2001) explore the consequences of hybrid swarm formation on formerly isolated and divergent taxa. Using a heuristic model based on three variables (initial frequency of parental taxa, strength of fitness gradients between parental and hybrid lineages, and strength of assortative mating) they observed that even in face of a strong (but not absolute) fitness gradient favoring parental taxa, resulting populations composed almost entirely of hybrid lineages can emerge in fewer than 10 generations. Moreover, the time required (in generations) for the relative proportion of parental taxa in a hybrid-parental population mixture to drop below 5% is shaped by initial frequencies of the parentals and the strength of assortative mating favoring preferential mating among individuals within each of the parental lineages. These results support the contention that hybridization is a suite of processes leading to multiple outcomes depending on ecological conditions and evolutionary constraints.

Scribner et al. (2001) give a thorough overview of the literature concerning hybrid formation in natural populations and suggest that the array of genotypes found in hybrid zones may be useful in determining the selective forces separating taxa and the evolution of species differences. These authors also explore the rate and direction of evolutionary change in fishes relative to complex hybrid events. The authors describe how genetic markers can be used in a variety of ecological contexts and spatial scales to provide insight into the level and direction of hybridization, effects of assortative mating, and the type and intensity of selection in hybrid populations. Empirical evidence is presented from case studies using *Gambusia*. Here they use experimental field and laboratory studies to test hypotheses concerning mate choice, life history variation, and population characteristics in predicting the directionality of hybridization and the rate of evolutionary change. They observe, for example, that females of *G. holbrooki* were apparently more discriminating in choosing their own species with which to mate than were *G. affinis* or even reciprocal F1 hybrid females. Moreover, the patterns of selective advantage and life history trait variation suggest *G. holbrooki*-mediated gene flow has historically proceeded north and west into the *G. affinis* historical range.

Clearly these topics do not address the entirety of evolutionary, conservation, or management interests in hybrids, but merely serve as updates on specific issues, tools, and knowledge encountered by scientists interested in hybridization in fishes. Following the technical sessions, a forum was opened to speakers, and other interested parties, to address some of the special concerns and challenges associated with interspecific and intraspecific hybridization in fishes. This follow-up discussion identified several other issues that need refinement. Three overarching issues that should be vital to fish biologists and other fisheries professionals were also illuminated. These discussions focused on the biological importance of hybridization and accurate identification of hybrids, resource management and conservation concerns associated with hybrids and hybridization, and the continued legal or policy challenges associated with gene flow. Within each of these general topics more specific questions were identified for future scientific inquiry and professional debate.

Issues of identification, measurement, and the consequences of hybridization in fishes

Identification of hybrids and their impact on aboriginal phyletic architecture

- Are modern molecular tools alone sufficient for identifying the extent of hybridization between taxa?
- What are the appropriate methods for identification of hybrids in terms of accuracy, precision, and error risks?
- Is there taxonomic substructure, undetected by current molecular markers and approaches, that can be affected by hybridization?
- What are the special considerations for identifying and monitoring cytoplasmic genomic introgression (vs. nuclear genomic introgression)?

The ecological and evolutionary role of hybrids in aquatic communities

- How do we perceive and define hybrids and how do they function within an ecosystem?
- Are the compositions and functions of hybrid zones well understood?

Terminology

- Does terminology carry a negative/positive connotation (*sensu* Mayden and Wood, 1995)?
- Are the commonly applied terms “pure” and “purity” appropriately value-neutral or do they carry an aura of eugenics?

Management and conservation concerns associated with hybridization

- What is the relative importance of natural sources of hybridization in fishes vs. artificial sources of hybridization?
- In what *contexts* are hybrids good, bad, or an idle curiosity?
- Can we distinguish between recent and human-caused vs. ancient and natural hybridization?
- Is there a fundamental difference between hybridization among native sympatric taxa and introduced (secondary contact) taxa?
- What are the demographic and population-level concerns of which we need to be aware?
- How do hybrids fit in with “stock transfer” concerns?
- What is the relationship between hybrid fertility (of hybrids used or resulting from management or aquaculture) and risks to related taxa?
- What is the “appropriate” role of hybrids in fisheries management?
- What are the ecological (rather than direct genetic) risks from hybrids?
- Are sterile hybrids an appropriate tool to diminish genetic risks from aquaculture escapement (i.e., can we balance genetic and ecological risks)?

Legal and policy challenges associated with hybridization

- What are the important differences in legal vs. biological views of hybridization?
- What level of polyphyletic origin is “permissible” for recovery (e.g., under ESA)?

The management and conservation issues associated with hybridization and introgression in aquatic species are experiencing a renewed interest based in part on scholarly treatments of the subject (e.g., Arnold, 1997) and in part because of controversies and difficulties associated with legal mandates such as the Endangered Species Act. In the half century since Hubbs’ (1955) seminal synthesis on his work with interspecific hybrids, our view of hybridization has drifted away from doctrines that considered it a rare “mistake” toward a more evolutionary perspective that considers it a more common and occasionally constructive process. We hope these papers serve as a springboard toward more scientific endeavors to understand hybridization as an evolutionarily important phenomenon and an important living resource management issue, rather than an idle curiosity in nature.

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References

Arnold M.L. (1992) Natural hybridization as an evolutionary process. *Annu. Rev. Ecol. Syst.* **23**, 237–261.

Arnold M.L. (1997) *Natural Hybridization and Evolution*. Oxford University Press, New York.

Arnold M.L. and Hodges, S.A. (1995) Are natural hybrids fit or unfit relative to their parents? *Trends Ecol. Evol*. **10**, 67–71.

Avise J.C. (2001) Cytonuclear genetic signatures of hybridization phenomena: Rationale, utility, and empirical examples from fishes and other aquatic animals. *Reviews in Fish Biology and Fisheries* **10**, 253–263.

Avise J.C. and Walker D. (2000) Abandon all species concepts? A response. *Cons. Gene*. **1**, 77–80.

Avise J.C., Bermingham E., Kessler L.G. and Saunders N.C. (1984) Characterization of mitochondrial DNA viability in a hybrid swarm between subspecies of bluegill sunfish (*Lepomis macrochirus*). *Evolution* **38**, 931–941.

Bartley D.M., Gall G.A.E. and Bentley B. (1990) Biochemical genetic detection of natural and artificial hybridization of chinook and coho salmon in northern California. *Trans. Am. Fish. Soc.* **119**, 431–437.

Bartley D.M., Rana K. and Immink A.J. (2001) The use of interspecific hybrids in aquaculture and fisheries. *Reviews in Fish Biology and Fisheries* **10**, 325–337.

Barton N.H. and Hewitt G.M. (1989) Adaptation, speciation, and hybrid zones. *Nature* **341**, 497–503.

Baxter J.S., Taylor E.B., Devlin R.H., Hagen J. and McPhail J.D. (1997) Evidence for natural hybridization between Dolly Varden (*Salvelinus malma*) and bull trout (*Salvelinus confluentus*) in a north central British Columbia watershed. *Can. J. Fish. Aquat. Sci*. **54**, 421–429.

Bernatchez L., Glemet H., Wilson C.C. and Danzmann R.G. (1995) Introgression and fixation of Arctic char (*Salvelinus alpinus*) mitochondrial genome in an allopatric population of brook trout (*Salvelinus fontinalis*). *Can. J. Fish. Aquat. Sci*. **52**, 179–185.

Berrebi P. and Cattaneo-Berrebi G. (1993) Natural hybridization of two species of tetraploid barbells: *Barbus meridionalis* and *Barbus barbus* (*Osteichtyes*, Cyprinidae) in southern France. *Biol. J. Linn. Soc*. **48**, 319–333.

Billington N., Hebert P.D.N. and Ward R.D. (1988) Evidence of introgressive hybridization in the genus *Stizostedion*: interspecific transfer of mitochondrial DNA between sauger and walleye. *Can. J. Fish. Aquat. Sci*. **45**, 2035–2041.

Bowen B.W. (1998) What is wrong with ESUs?: the gap between evolutionary theory and conservation principles. *J. Shellf. Res*. **17**(5), 1355–1358.

Bowen B.W. (1999) Opinion: Preserving genes, species, or ecosystems? Healing the fractured foundations of conservation policy. *Mol. Ecol*. **8**, S5–S10.

Busack C.A. and Gall G.A.E. (1981) Introgressive hybridization in populations of Paiute cutthroat trout (*Salmo clarki seleniris*). *Can. J. Fish. Aquat. Sci*. **38**, 939–951.

Campton D.E. (1987) Natural hybridization and introgression in fishes. *In*: Ryman N. and Utter F. (eds.), *Population Genetics and Fisheries Management*. University Washington Press, Seattle, pp 161–192.

Campton D.E. and Utter F.M. (1985) Natural hybridization between steelhead trout (*Salmo gairdneri*) and coastal cutthroat trout (*Salmo clarki clarki*) in two Puget Sound streams. Can. *J. Fish. Aquat. Sci*. **42**, 110–119.

Crandall K.A., Bininda-Emonds O.R.P., Mace G.M. and Wayne R.K. (2000) Considering evolutionary processes in conservation biology. *Trends Ecol. Evol*. **15**, 290–295.

Darwin C. (1859) The *Origin of Species by Means of Natural Selection; or the Preservation of Favored Races and the Struggle for Life.* Penguin Books, New York.

Dowling T.E. and Childs M.R. (1992) Impact of hybridization on a threatened trout of the southwestern United States. *Cons. Biol*. **6**, 355–364.

Dowling T.E. and DeMarais B.D. (1993) Evolutionary significance of introgressive hybridization in cyprinid fishes. *Nature* **362**, 444–446.

Dowling T.E. and Hoeh W.R. (1991) The extent of introgression outside the contact zone between *Notropis cornutus* and *Notropis chrysocephalus* (Teleostei: Cyprinidae). *Evolution* **45**, 944–956.

Dowling T.E. and Moore W.S. (1985) Evidence for selection against hybrids in the family Cyprinidae (genus *Notropis*). *Evolution* **43**, 620–634.

Dowling T.E. and Secor C.L. (1997) The role of hybridization and introgression in the diversification of animals. *Ann. Rev. Ecol. Syst.* **28**, 593–619.

Dowling T.E., Smith G.R. and Brown W.M. (1989) Reproductive isolation and introgression between *Notropis cornutus* and *Notropis chysocephalus* (family Cyprinidae): Comparison of morphology, allozymes, and mitochondrial DNA. *Evolution* **43**, 620–634.

Duvernell D.D. and Aspinwall N. (1995) Introgression of *Luxilus cornutus* mtDNA into allopatric populations of *Luxilus chrysocephalus* (Teleostei: Cyprinidae) in Missouri and Arkansas. *Mol. Ecol*. **4**, 173–181.

Echelle A.A. and Conner P.J. (1989) Rapid geographically extensive genetic introgression after secondary contact between two pupfish species (*Cyprinodon*, Cyprinodontidae). *Evolution* **43**, 717–727.

Epifanio J.M. and Philipp D.P. (2001) Simulating the extinction of parental lineages from introgressive hybridization: the effects of fitness, initial proportions of parental taxa, and mate choice. *Reviews in Fish Biology and Fisheries* **10**, 339–354.

Ferguson M.M. (1986) developmental stability of rainbow trout hybrids: genomic coadaptation or heterozygosity? *Evolution* **40**, 323–330.

Forbes S.H. and Allendorf F.W. (1991) Associations between mitochondrial and nuclear genotypes in cutthroat trout hybrid swarms. *Evolution* **45**, 1332–1349.

Giuffra E., Guyomard R. and Forneris G. (1996) Phylogenetic relationships and introgression patterns between incipient parapatric species of Italian brown trout (*Salmo trutta* L. complex). *Mol. Ecol*. **5**, 207–220.

Glemet H. (1997) Mitochondrial DNA introgression in brook charr, *Salvelinus fontinalis*, from eastern Quebec: characterization, geographical distribution and evolutionary significance. PhD. Dissertation. University of Quebec (INRS-Eau).

Glemet H., Blier P. and Bernatchez L. (1998) Geographical extent of Arctic char (*Salvelinus alpinus*) mtDNA introgression in brook char populations (*S. fontinalis*) from eastern Quebec, Canada. *Mol. Ecol.* **5**, 207–220.

Hammar J., Dempson J.B. and Vespoor E. (1991) Natural hybridization between Arctic char (*Salvelinus alpinus*) and brook trout (*S. fontinalis*): evidence from northern Labador. *Can. J. Fish. Aquat. Sci.* **48**, 1437–1445.

Harrell R.M., Lan X. and Ely B. (1993) Evidence of introgressive hybridization in Chesapeake Bay *Morone*. *Mol. Mar. Biol. Biotech*. **2**, 291–299.

Hartley S.E. (1996) High incidence of Atlantic salmon x brown trout hybrids in a Lake District stream. *J. Fish. Biol*. **48**, 151–154.

Hawkins D.K. and Foote C.J. (1998) Early survival and development of coastal cutthroat trout (*Oncorhynchus clarki clarki*), steelhead (*Oncorhynchus mykiss*), and reciprocal hybrids. Can. *J. Fish. Aquat. Sci*. **55**, 2097–2104.

Hendry A.P., Vamosi S.M., Latham S.J., Heibuth J.C. and Day T. (2000) Questioning species realities. *Cons. Gene*. **1**, 67–76.

Hubbs C.L. (1920) Notes of hybrid sunfishes. *Aquatic Life* **5**, 101–103.

Hubbs C.L. (1955) Hybridization among fishes in nature. *System. Zool.* **4**, 1–20.

Hubbs C. (1959) Population analysis of a hybrid swarm between *Gambusia affinis* and *G. heterochir. Evolution* **13**, 236–246.

Kark S. and Blackburn T.M. (2000) The future of evolution. *Trends Ecol. Evol*. **15**(8) 307–308.

Leary R.F., Allendorf F.W. and Knudsen K.L. (1985) Developmental instability and high meristic counts in interspecific hybrids of salmonid fishes. *Evolution* **39**, 1318–1326.

Leary R.F., Allendorf F.W., Phelps S.R. and Knudsen K.L. (1987) Genetic divergence among seven subspecies of cutthroat trout and rainbow trout. *Trans. Am. Fish. Soc*. **116**, 580–587.

Leary R.F., Allendorf F.W. and Sage G.K. (1995) Hybridization and introgression between introduced and native fish. American Fisheries Society Symposium **15**, 91–101.

Lewontin R.C. and Birch L.C. (1966) Hybridization as a source of variation for adaptation to new environments. *Evolution* **20**, 315–336.

Loudenslager E.J., Rinne J.N., Gall G.A.E. and David R.E. (1986) Biochemical genetic studies of native Arizona and New Mexico trout. *Southwest Nat.* **31**, 221–234.

Mayden R.L. and Wood R.M. (1995) Systematics, species concepts, and the evolutionarily significant unit in biodiversity and conservation biology. *In*: Nielsen J.L. (ed.), *Evolution and the Aquatic Ecosystem: Defining Unique Units in Population Conservation. Am. Fish. Soc. Symp. 17*. American Fisheries Society, Bethesda.

Mayr E. (1970) *Populations, Species and Evolution.* Harvard University Press, Cambridge, MA.

Moritz C. (1994) Defining "evolutionary significant units" for conservation. *Trends Ecol. Evol.* **9**, 373–375.

Nielsen J.L. (1995) *Evolution and the Aquatic Ecosystem: Defining Unique Units in Population Conservation*. *Am. Fish. Soc. Symp. 17*. American Fisheries Society, Bethesda.

Nyman O.L. (1970) Electrophoretic analysis of hybrids between salmon (*Salmo salar* L.) and trout (*Salmo trutta* L.) *Trans. Amer. Fish. Soc*. **99**, 229–236.

O'Brien S.J. and Mayr E. (1991a) Bureaucratic mischief: recognizing endangered species and subspecies. *Science* **251**, 1187–1188.

O'Brien S.J. and Mayr, E. (1991b) Species, hybridization, and protection of endangered animals. *Science* **253**, 251–253.

Perez J., Martinez J.L., Moran P., Beall E. and Garcia Vazquez E. (1999) Identification of Atlantic salmon x brown trout hybrids with a nuclear marker useful for evolutionary studies. *J. Fish Biol*. **54**, 460–464.

Poteaux C., Berrebi P. and Bonhomme F. (2001) Allozymes, mtDNA, and microsatellites study introgression in a stocked trout population in France. *Reviews in Fish Biology and Fisheries* **10**, 281–292.

Rosenfield J.A., Todd T. and Greil R. (2000) Asymmetric hybridization and introgression between pink and chinook salmon in the Laurentian Great Lakes. *Trans. Am. Fish. Soc*. **129**, 670–679.

Schwartz F.J. (1981) World literature to fish hybrids, with an analysis by family, species, and hybrid: supplement No. 1. NOAA Technical Report NMFS SSRF-750. U.S. Department of Commerce. Washington.

Scribner K.T. and Avise J.C. (1994) Population cage experiments with a vertebrate: the temporal demography and cytonuclear genetics of hybridization in *Gambusia* species. *Evolution* **48**, 155–171.

Scribner K.T., Page K. and Bartron M. (2001) Hybridization in freshwater fishes: a review of case studies and cytonuclear methods of biological inference. *Reviews in Fish Biology and Fisheries* **10**, 293–323.

Seeb L.W. (1988) Gene flow and introgression within and among three species of rockfishes, *Sebastes auriculatus*, *S. caurinus* and *S. maliger*. *J. Hered*. **89**, 393–403.

Simon R.C. and Noble R.E. (1968) Hybridization in *Oncorhynchus* (salmonidea). I. Viability and inheritance in artificial crosses of chum and pink salmon. *Trans. Am. Fish. Soc*. **97**, 109–118.

Smith G.R. (1992) Introgression in fishes: Significance for paleontology, cladistics, and evolutionary rates. *Syst. Biol*. **41**, 41–57.

Stone G. (2000) Phylogeography, hybridization and speciation. *Trends Ecol. Evol*. **15**(9), 354–355.

Taylor D.J. and Hebert P.D.N. (1993) Cryptic intercontinental hybridization in *Daphnia* (Crustacea): the ghost of introductions past. *Proc. R. Soc. Lond. B* **254**, 163–168.

Utter F.M. (2001) Patterns of subspecific anthropogenic introgression in two salmonid genera. *Reviews in Fish Biology and Fisheries* **10**, 265–279.

Verspoor E. and Hammar J. (1991) Introgressive hybridization in fishes: the biochemical evidence. *J. Fish Biol*. **39** (Supplement A), 309–334.

Wahl D.H. and Stein R.A. (1993) Comparative population characteristics of muskellunge (*Esox masquinongy*), northern pike (*E. lucius*, and their hybrid (*E. masquinongy* x *E. lucius*). *Can. J. Fish. Aquat. Sci*. **50**, 1961–1968.

Wilkins N.P., Courtney H.P. and Curatolo A. (1993) Recombinant genotypes in backcrosses of male Atlantic salmon x brown trout hybrids to female Atlantic salmon. *J. Fish. Biol*. **43**, 393–399.

Wilson C.C. and Bernatchez L. (1998) The ghost of hybrids past: fixation of arctic charr (*Salvelinus alpinus*) mitochondrial DNA in an introgressed population of lake trout (*S. namaycuch*). *Mol. Ecol*. **7**, 127–132.