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# Species pairs of north temperate freshwater fishes: Evolution, taxonomy, and conservation

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## Abstract

Many fish species contain morphologically, ecologically and genetically distinct populations that are sympatric during at least some portion of their life cycle. Such reproductively isolated populations act as distinct biological species, but are identified by a common Latin binomial. These ‘species pairs’ are particularly common in freshwater fish families such as Salmonidae, Gasterosteidae and Osmeridae and are typically associated with postglacial lakes in north temperate environments. The nature of the divergences between sympatric species, factors contributing to reproductive isolation, and modes of evolution are reviewed with particular emphasis on benthic and limnetic pairs of threespine sticklebacks, *Gasterosteus aculeatus*, and anadromous (sockeye salmon) and nonanadromous (kokanee) pairs of *Oncorhynchus nerka*. Phylogenetic analyses typically indicate that divergences between members of replicate pairs have occurred independently and, hence, particular phenotypes are not monophyletic. Consequently, taxonomic resolution of such ‘species complexes’ is a vexing problem for adherents to our traditional Linnaean classification system. Sympatric species pairs represent a significant component of the biodiversity of temperate freshwater ecosystems which may be underestimated because our system of formal taxonomy tends to obscure diversity encompassed by species pairs. Conservation of such systems should be recognized as a priority without formal taxonomic designation of members of species pairs because taxonomic resolution will likely continue to prove extremely difficult when employing traditional hierarchies and procedures.

*Key words: Gasterosteus*, *Oncorhynchus*, reproductive isolation, sympatric populations, speciation, species concepts

## Introduction

> Like – but oh, how different (Wordsworth)

The nature and origin of species (‘speciation’) are central issues in evolutionary biology (Mayr, 1963; Otte and Endler, 1989; Ayala and Fitch, 1997; Claridge et al., 1997; Howard and Berlocher, 1998). Such focus stems from the desire for taxonomic categorization of living things and because the ‘species’ – rather than family, order, or genus – represents the taxonomic unit with the most tangible connection to populations and individuals, which are the fundamental units of biodiversity. The nature of species has also been of great importance because the definition of what constitutes a species allows taxonomists to assemble higher units of evolutionary diversity (Levin, 1979). As well, a framework for the nature of species establishes relationships between and within groups while defining the limits of what constitutes a species (and higher and lower units of diversity). Such interrelationships and their boundaries, therefore, influence how we think about and study them. The nature (e.g. mode and tempo of speciation) of species has received renewed interest because formal taxonomic recognition gives more weight in biodiversity conservation issues (Avise, 1989). Understanding how species arise can assist in measures to preserve biodiversity and the evolutionary potential of species. The intense interest in the nature of species, however, has certainly not resulted in a consensus on what constitutes a species or how most species arise. Mayr (1982, p. 251) argued that no other concept in biology has remained “so consistently controversial as the species concept.” Seventeen years after Mayr made this statement, a unified concept of species remains elusive (Mallet, 1995; Ayala and Fitch, 1997; Claridge et al., 1997; Howard and Berlocher, 1998).

Evolutionary and taxonomic studies of fishes have contributed significantly to research on the nature of species and speciation, including studies of: the evolution of reproductive isolation (Hubbs, 1940; Nelson, 1968a; Aspinwall and McPhail, 1995), hybridization (Hubbs, 1955; Dowling and Moore, 1985), unisexuality (Vrijenhoek, 1994), the geography of speciation (Svärdson, 1961; Meyer et al., 1990), ecological speciation (Schluter, 1996), and various species concepts (e.g. Mayr, 1963; Mayden and Wood, 1995).

One aspect of research on species that has received considerable attention in fishes is the concept of ‘sibling species’, i.e. sympatric populations that are morphologically very similar (if not indistinguishable), but which are nonetheless “reproductively isolated” (Mayr, 1963). Although the idea of sibling species appears to have arisen from the biological species concept (Mayr, 1963), sibling species are morphologically similar populations that are valid species under a number of alternative concepts (e.g. phylogenetic species, evolutionary species – see below).

The occurrence of sibling species in fishes was detailed by Mayr (1963) and the origins of selected sibling fish species was treated by Svärdson (1961). Typically, sibling species were recognized (despite their morphological similarity) by differences in ecology or life history (e.g. spawning at different times or places in the same lake, different sizes at maturity) from which genetic differentiation and reproductive isolation were inferred (Behnke, 1972). Most examples came from north temperate freshwater fishes such as whitefishes, smelt, and trout (Svärdson, 1961; Mayr, 1963). With the development of more sophisticated morphological analyses (e.g. multivariate analysis), most of these ‘sibling species’ could be demonstrated to exhibit at least some morphological divergence. Subsequent development of biochemical and molecular assays have corroborated genetic isolation inferred from morphology and behaviour of forms residing sympatrically (e.g. compare Larson, 1976 with McPhail, 1992). These developments have led to the identification of several cases of so-called sympatric ‘species pairs’ of fishes, i.e. populations of fishes that are to a large extent reproductively isolated in sympatry, but which are identified by a common Latin binomial. These species pairs are also typically distinguished from each other by differences in ecology, behaviour, and/or morphology, traits which themselves may be the basis for genetic distinctiveness between sympatric species.

Sympatric species pairs are part of a continuum of diversity that extends from phenotypic plasticity within single randomly-mating populations to flocks of species numbering in the hundreds within single lakes. Species pairs, however, represent an association between ecological and reproductive isolation and thus fulfil the principal criteria of biological species, yet their status as species is unrecognized taxonomically. Hence, the occurrence of sympatric pairs has led to concern that biodiversity in systems containing sympatric pairs may be underestimated (and perhaps undervalued) because each member of a pair shares the same scientific name (Behnke, 1972; Lindsey, 1988). Although taxonomic identity is not necessary for formal conservation protection in some jurisdictions (e.g. the distinct population segment clause of the US Endangered Species Act) it can help substantially (e.g. Avise, 1989). Given the common occurrence of species pairs and the concern that they ‘complicate’ issues of species conservation owing to their uncertain taxonomic status, it is important to ask: what evidence warrants the formal taxonomic recognition of sympatric species pairs with unique Latin binomials? The study of sympatric species pairs has also provided fresh insights into mechanisms of speciation particularly in terms of the tempo, mode and geography of speciation. Motivated by these concerns and new insights, the objectives of this paper are threefold: (1) to review the geographic and taxonomic distribution of species pairs of fishes, (2) to review the evidence from the best known cases that sympatric species pairs are indeed distinct species, and (3) to offer some recommendations concerning the conservation of biodiversity represented by species pairs.

## Species concepts and species pairs

What constitutes a species remains a contentious issue in biology. In fact, up to 22 species concepts have been offered as definitions (Mayden, 1997), but two seem to have the most widespread support as operational concepts: the biological species concept (BSC, Mayr, 1963) and the phylogenetic species concept (PSC, Cracraft, 1983). The BSC originally defined species as “groups of actually or potentially interbreeding natural populations which are reproductively isolated from other such groups” (Mayr, 1940). By reproductive isolation, I adopt the modified definition of Mayr (1982) that allows some hybridization between individuals of different species, but the populations to which they belong persist as distinct (nonrandomly intermating) gene pools. There are at least three versions of the PSC, but they all have in common the definition of species as “the smallest biological entities that are diagnosable and/or monophyletic” (Mayden, 1997). In this paper, I adopt the BSC when discussing sympatric species pairs of fishes because persistence in sympatry provides the ‘acid test’ of species status under the BSC (Avise, 1994). Further, species pairs appear to be very recently derived and members tend to be distinguished by distinct *frequencies* of character states rather than by fixed differences. Consequently, the PSC, owing to its reliance on monophyly and/or diagnosability, may be too insensitive to resolve recent speciation events. For instance, Neigel and Avise (1986) estimated that it would require at least $4N_e$ generations after lineage splitting for two recently formed species to achieve reciprocal monophyly for mitochondrial DNA via genetic drift and lineage sorting (and hence to be designated as valid phylogenetic species), where $N_e$ is the effective female population size. Times to reciprocal monophyly for nuclear loci or for morphological traits (which are typically controlled by expression of many nuclear genes) are even longer because of the fourfold larger effective population size for nuclear loci at equilibrium (Nei, 1987).

## Taxonomic and geographic distribution of species pairs

Sympatric species pairs have been most commonly described from freshwater ecosystems in the temperate regions of the Northern Hemisphere in several families of teleost fish, but principally in the Salmonidae (salmon, trout, charr, whitefish, and grayling), Gasterosteidae (sticklebacks), and Osmeridae (smelts) in postglacial lakes (Figure 1). Although such pairs are the focus of this review, there is evidence of a much wider taxonomic distribution of species pairs. For instance, Mayr (1963) discussed the work of Minamori (1956) who documented the existence of a species pair of loach (*Cobitis taenia*, Cobitidae) that are ecologically and genetically isolated in freshwater areas of western Honshu, Japan. In lampreys, derivatives of the most ancestral lineage of fish, several species include anadromous and nonanadromous populations (McPhail and Lindsey,

1970) although sympatric populations have not been reported. Further, an allozyme-based analysis of the western brook lamprey (*Lampetra richardsoni*, Petromyzontidae) and the river lamprey (*L. ayresi*, Petromyzontidae) suggested that each species was not monophyletic (Beamish and Withler, 1986). Multiple occurrences of nonanadromous/nonparasitic western brook lamprey may result from independent divergences from the anadromous/parasitic river lamprey. From an allozyme survey, Turner and Grosse (1980) described ecotypes of the goodeiid fish *Ilyodon*, Goodeidae, that were reproductively isolated at at least one site in Mexico. Recently, Ruzzante et al. (1998) described the existence of sympatric ecotypes in the fish *Percichthys trucha*, Percichthyidae, from six lakes in the Andean region of Argentina. Also, lake-resident and anadromous forms of the common smelt, *Retropinna retropinna*, Retropinnidae, have been described in New Zealand (Northcote and Ward, 1985). The mountain whitefish (*Prosopium williamsoni*, Salmonidae) exhibits two apparent ecotypes (normal and 'pinnochio' forms) that differ in rostral morphology, gill raker counts, and feeding behaviour (Troffe, 2000). Unlike most species pairs in salmonids, however, the pinnochio and normal forms of whitefish coexist in *riverine* environments in several watersheds in western Canada and the US (Troffe, 2000). It is also possible that the remarkable body form variation in fossil semionotid fishes in freshwater deposits dating as far back as the Triassic Period (McCune et al., 1984) may, in some cases, represent sympatric species pairs.

Finally, Jensen (1941; cited in Mayr, 1963), Okamoto (1989) and Planes and Doherty (1997) describe putative sympatric species pairs in the marine fish *Ammodytes*, Ammodytidae (sand lances) and *Acanthochromis polyacanthus*, Pomacentridae (damselfish), respectively, while Blouw and Hagen (1990) report a putative species pair for marine populations of threespine stickleback, *Gasterosteus aculeatus*, Gasterosteidae.

In cases such as the putative lamprey, percichthyid, New Zealand smelt, and sand lance species pairs, it is unclear to what extent the morphological and ecological differences between members of each pair are associated with distinct gene pools or whether phenotypic plasticity plays a role in the differentiation. These examples, however, do illustrate the possibility that sympatric species pairs of fish may exist in groups other than the well-studied salmonids, gasterosteids and osmerids. Further, these lesser-known fishes highlight the possibility that sympatric pairs may be found in a diversity of habitats, ranging from temperate lake ecosystems in the Northern Hemisphere to temperate and subtropical streams (*Prosopium, Ilyodon*) to lakes and streams of the southern temperate zone (*Percichthys* and *Retropinna*), to marine coral reef systems (*Acanthochromis*).

Within a particular taxon, sympatric species pairs tend to be geographically widespread. For instance, replicate sympatric pairs of anadromous (sockeye salmon) and nonanadromous (kokanee) *Oncorhynchus nerka*, Salmonidae, are found throughout the geographic distribution of *O. nerka*, which ranges from southern Kamchatka in the western North Pacific to the Columbia River in the eastern North Pacific (Nelson, 1968b; Taylor et al., 1996). Sympatric dwarf and normal lake whitefish (*Coregonus clupeaformis*, Salmonidae) are found throughout the range of whitefish in North America from Yukon Territory to northeastern North America (Fenderson, 1964; Lindsey et al., 1970; Bernatchez and Dodson, 1990; Bodaly et al., 1992). Although certain cases of sympatric pairs appear to be geographically localized (e.g. sympatric pygmy whitefish (*Prosopium coulteri*, Salmonidae) in coastal Alaskan lakes, McCart, 1970a), such 'endemism' may stem from limited sampling. One possible exception involves the 'benthic' and 'limnetic' species pairs of lake-resident threespine stickleback *G. aculeatus*. Despite a geographic range that involves marine, estuarine and coastal freshwater ecosystems throughout the Holarctic and reasonably extensive observations through this region, benthic and limnetic species pairs of *Gasterosteus* have only been recorded from six coastal lakes in the Strait of Georgia region of southwestern British Columbia, a minute portion of the range available for such divergences (McPhail, 1993).

Despite the widespread taxonomic and geographic occurrence of species pairs in north temperate fishes, two examples stand out as particularly instructive regarding their ecology and evolution: benthic and limnetic *Gasterosteus aculeatus*, and anadromous and nonanadromous forms of *Oncorhynchus nerka* (sockeye salmon and kokanee). I have chosen to focus on these species pairs because they are the most comprehensively studied in terms of divergence in morphology, behaviour, and general life history, often over extensive geographic areas, and because aspects of the genetics and origins of divergence, as well as factors contributing to reproductive isolation have

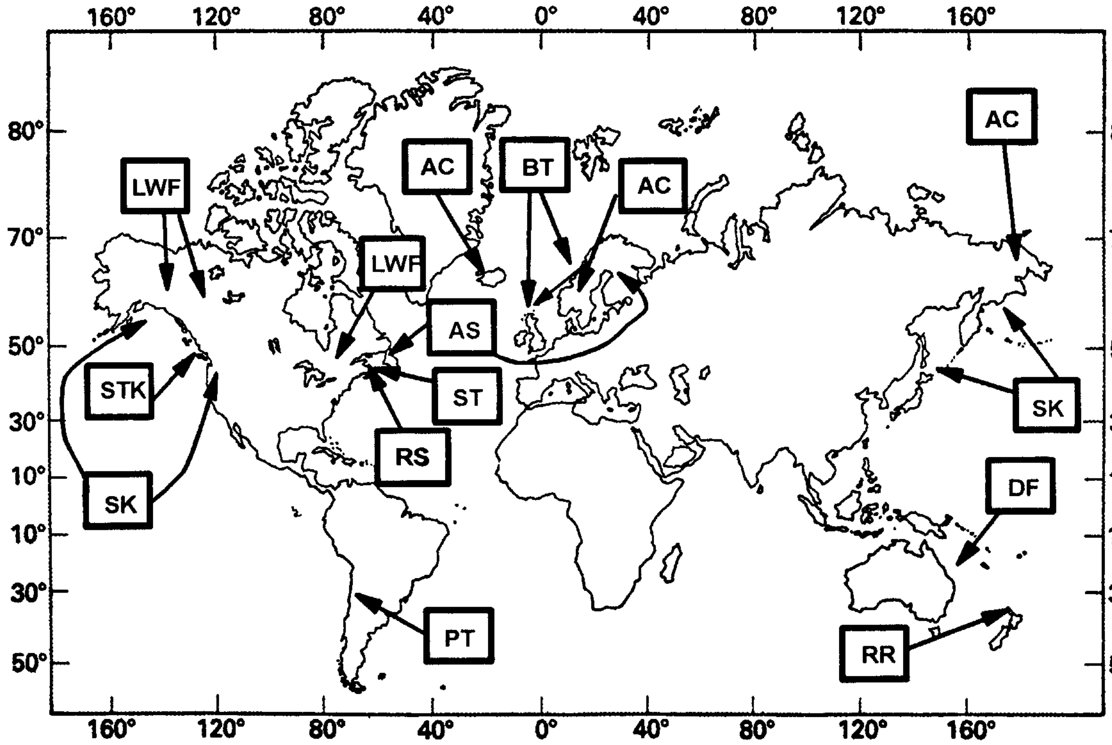

*Figure 1.* Geographic distribution of major species pair complexes. LWF, dwarf and normal lake whitefish (*Coregonus clupeaformis*); SK, sockeye salmon and kokanee (*Oncorhynchus nerka*); STK, limnetic and benthic threespine stickleback (*Gasterosteus aculeatus*); ST, white and normal colour reproductive ecotypes of *G. aculeatus*; AS, anadromous and nonanadromous Atlantic salmon (*Salmo salar*); AC, dwarf and normal, anadromous and nonanadromous, or trophic forms of Arctic charr (*Salvelinus alpinus*); RS, dwarf and normal rainbow smelt (*Osmerus mordax*); BT, trophic forms or anadromous and nonanadromous brown trout (*Salmo trutta*). Also shown are distributions of possible species pairs in Southern Hemisphere taxa: RR, anadromous and nonanadromous smelt (*Retropinna retropinna*); DF, colour forms of marine damselfish (*Acanthochromis polyancanthus*), and PT, trophic forms of perch (*Percichthys trucha*).

been investigated. Further, sticklebacks and sockeye salmon and kokanee have been studied for a reasonably long time frame (up to 50 years). Individual or combinations of these fundamental components have been explored in many other instances of sympatric species pairs, but information on other components is usually lacking. I will then draw generalizations from comparisons with other well-known, but less extensively studied, examples of species pairs.

## Benthic and limnetic sticklebacks: *Gasterosteus aculeatus*

### *Nature of the divergence*

The threespine stickleback is found in marine, estuarine, and coastal freshwater ecosystems throughout the Holarctic. The prevailing model of evolution within this "species complex" (Hagen and McPhail, 1970) posits repeated foundings of newly emerging postglacial freshwater habitats in coastal areas by ancestral anadromous and marine forms (Hagen and McPhail, 1970; Bell, 1976). Although there is a tremendous range of adaptive diversity in freshwater *G. aculeatus* throughout its distribution (Bell, 1984), the two trophic forms that coexist in each of six lakes located on three separate islands in the Strait of Georgia region of southwestern British Columbia have received special attention. The distribution and characteristics of each form have been thoroughly reviewed by McPhail (1984, 1992, 1994) and are only briefly summarized here. One species, the 'benthic' is deep bodied, with few (about 18) short gill rakers, a wide mouth, and a short broad snout. The other species, the 'limnetic', is slim bodied, with many (about 26) long gill rakers, a narrow mouth and a long slim snout (see Figure 3 in McPhail, 1984). Benthics and limnetics differ in habitat use and foraging ecology in each of the lakes; benthics are solitary littoral bottom browsers on large benthic invertebrates, whereas limnetics are schooling planktivores in open-water areas in each lake (Larson, 1976; Bentzen and McPhail, 1984; Schluter, 1993, 1995). The extent and patterns of morphological and ecological divergences between benthics and limnetics are remarkably similar among the five lakes in which they still co-occur (a pair in one lake has gone extinct through illegal introduction of an exotic catfish), but they are not identical. For instance, benthic sticklebacks in Paxton Lake have greatly reduced pelvic armour and dorsal spines relative to other benthics. Benthic males in Enos Lake have black nuptial coloration whereas those in other lakes show the ‘typical’ blue eyes, backs, and sides and red throat nuptial coloration (McPhail, 1994).

### *Evidence for distinct gene pools*

Distinct forms of sympatric sticklebacks could result from phenotypic plasticity, genetic polymorphism within a single randomly mating population or from the existence of two distinct gene pools. In two lakes that have been studied in detail (Paxton Lake on Texada Island and Enos Lake on Vancouver Island), two lines of evidence indicate that benthics and limnetics represent distinct gene pools in sympatry: breeding studies, and biochemical and molecular genetic assays. Detailed breeding experiments have demonstrated that the morphological differences between the species persist in laboratory-raised (e.g. common garden) populations (McPhail, 1984, 1992) and that $F_1$ hybrids are intermediate in morphology. It has been estimated that a minimum of eight loci contribute to the differences in gill raker architecture in the Paxton Lake species pair (Hatfield, 1997). Further, crosses between limnetics within each lake produce only limnetic offspring and crosses between benthics produce only benthics (McPhail, 1984, 1992).

A total of 25 allozyme loci have been examined in the Enos Lake and Paxton Lake pairs, of which five are polymorphic. In Enos Lake the species show highly significant allele frequency differences at two loci (McPhail, 1984). In Paxton Lake, benthics and limnetics are significantly divergent at four of five polymorphic loci, differences that have remained stable between sampling periods in 1969 and 1980 (McPhail, 1992). Taylor and McPhail (1999) demonstrated significant differences in mtDNA haplotype frequencies between benthics and limnetics in Enos, Priest, and Emily lakes (but not in Paxton Lake – see below). Further, in all lakes the species are genetically distinct at up to six microsatellite loci assayed; mean $F_{st}$ (i.e. the proportion of total genetic variance in allele frequencies attributable to differences between species) between pairs within lakes ranges from 0.18 to 0.33 across lakes (E. Taylor, unpublished data). Taken together, the quantitative and molecular genetic analysis of stickleback clearly demonstrate that the species pairs are distinct gene pools in each of the lakes where they coexist. Notwithstanding their high degree of genetic isolation, there is evidence of some level of current and past hybridization between species in at least two lakes. About 1–2% of adult sticklebacks appear to be benthic–limnetic $F_1$ hybrids as inferred from morphological analysis (McPhail, 1992, 1994). Furthermore, this level of hybridization appears to have been stable for at least 20 years in Paxton Lake (McPhail, 1992). In Enos Lake, despite evidence of hybridization, the benthics have remained fixed for the *MDH-3**100 allele while the limnetics have an 18% occurrence of the *55 allele. These data clearly indicate that the species pairs maintain their genetic independence despite some hybridization and hence there appears to be no gene flow currently between benthics and limnetics in sympatry. It is possible, however, that hybridization and gene flow between species was higher in the past. For instance, Paxton Lake benthics and limnetics share a common mtDNA haplotype at a frequency of about 90% in both species, and the level of divergence ($F_{st}$) is about 0.035 and nonsignificant (Taylor and McPhail, 1999). By contrast, in Priest Lake the pairs have highly distinct haplotype frequencies with an $F_{st}$ of 0.18 (Taylor and McPhail, 1999). Thus, members of individual pairs show genetic divergence between them within all lakes, but the exact pattern and extent of divergence are not identical among lakes.

### *Reproductive isolation*

McPhail (1994) summarized data for Enos and Paxton lakes’ sticklebacks that indicated that there are no intrinsic barriers to gene flow between species within lakes (see also Hatfield, 1997). Survival and fertility of $F_1$ and post-$F_1$ hybrids and backcrosses generally show no depressions from levels in pure species crosses although benthic backcrosses exhibit small reductions in hatching success and juvenile growth rate (Hatfield and Schluter, 1999). The lack of strong intrinsic barriers to gene flow between the species suggests that hybridization is limited by premating isolation or by selection against hybrid genotypes in nature before they reach sexual maturity or during mating. Premating isolation may be facilitated by nesting location because, although the species breed at the same time (April–June), benthic males build nests in dense cover while limnetic males nest in open areas of the littoral zone (McPhail, 1994). Consequently, nest location may provide females the means by which to differentiate benthic and limnetic males. Further, Ridgway and McPhail (1984) demonstated clear assortative mating by species in choice mating trials in the Enos Lake pair. Assortative mating by species has also been observed in the field in Paxton Lake (McPhail, 1994) and no-choice trials suggest strong assortative mating by species under laboratory settings for Paxton and Priest lakes' sticklebacks (Nagel and Schluter, 1998; Rundle and Schluter, 1998). Both body size and coloration likely play a role in assortative mating. In Enos Lake, benthic males are black whereas limnetic males have blue backs and sides and bright red throats and thus nuptial coloration provides a powerful visual mate recognition signal (McPhail, 1994). Benthics also tend to be larger than limnetics in all lakes and mating in sticklebacks tends to be size assortative (Borland, 1986; Nagel and Schluter, 1998). Although less well studied than differences in body size and color, benthics and limnetics tend to differ in subtle aspects of courtship behaviour that may combine with differences in microhabitat, coloration, and body size to provide powerful mechanisms of positive assortative mating between sympatric species (Nagel and Schluter, 1998).

Reproductive isolation between sympatric species pairs of *Gasterosteus* may also be maintained by natural or sexual selection against hybrid genotypes in nature. There is good evidence of morphologically based trade-offs in foraging performance in parental species and reduced foraging abilities of morphologically intermediate benthic–limnetic hybrids under laboratory conditions (Bentzen and McPhail, 1984; Schluter, 1993). Hatfield and Schluter (1999) found evidence of reduced foraging performance (assayed by differences in growth rate) between $F_1$ hybrids and parental species under more natural conditions in Paxton Lake. Hatfield and Schluter (1996) could not reject the hypothesis of equal mating success of $F_1$ hybrid males compared to benthic and limnetic males from Paxton Lake in the laboratory. Vamosi and Schluter (1999), however, showed that under more natural conditions in Paxton Lake, $F_1$ hybrid males obtained less than 20% of the matings of male limnetics in choice trials with limnetic females in the microhabitat favoured by all three. Hybrid disadvantage in nature may also be an important component of reproductive isolation when other aspects of juvenile ecology (e.g. overwinter survival, susceptibility to predators) or mating behaviour (e.g. nest-building ability, biases in encounter rates) are considered.

## Sockeye salmon and kokanee: *Oncorhynchus nerka*

### *Nature of the divergence*

Commonly, species of euryhaline freshwater fish include both anadromous (searun) and nonanadromous (freshwater-resident) ecotypes. In *Oncorhynchus nerka*, the anadromous form is known as sockeye salmon and the nonanadromous form is called kokanee (Ricker, 1940). Offspring of anadromous sockeye salmon that remain in fresh water throughout their life-span constitute a third form known as 'residuals' (Ricker, 1938). Sockeye salmon typically mature at 2–4 kg whereas kokanee usually mature at less than 1 kg although larger individuals are occasionally produced (Vernon, 1957; Burgner, 1991). Sockeye salmon spend 1–3 years feeding in lakes before migrating to the sea to spend an additional 1–3 years feeding before returning to fresh water to spawn. Kokanee, by contrast, grow to maturity over 2–4 years entirely in lakes (Ricker, 1940). Both sockeye salmon and kokanee are found in watersheds throughout the western and eastern North Pacific with kokanee often found in areas where access to the sea has been eliminated or is difficult (Nelson, 1968b; Wood, 1995). Although sockeye spend considerable portions of their life cycle in the sea and kokanee do not, there are numerous watersheds where sockeye and kokanee occur sympatrically, i.e. juveniles may be sympatric while feeding in the limnetic zone of nursery lakes for 1–3 years (Wood, 1995). There are fewer lake systems where sockeye and kokanee spawn sympatrically (McCart, 1970b; Foote and Larkin, 1988; Wood and Foote, 1996). As such, the major divergence between sockeye and kokanee is in terms of life history, migratory behaviour, and the habitat occupied prior to maturity. The most dramatic consequence of this ontogenetic habitat shift in sockeye is greater size at maturity owing, in large part, to the much greater productivity of marine habitats. Sockeye and kokanee, however, exhibit differences in several heritable traits linked to anadromous and nonanadromous life histories, respectively. Sockeye salmon have a higher size threshold for maturity than kokanee which may be an adaptation to the increased energetic demands of anadromous migration (Wood and Foote, 1996). Sockeye and kokanee usually differ in gill raker counts and length (Nelson, 1968c; Wood and Foote, 1996; Foote et al., 1999) which may reflect divergent selection for exploitation of different average particle sizes during their life cycles. In Takla Lake (Fraser River system) kokanee have markedly higher gill raker counts and longer gill rakers than sockeye, differences that are inherited and, in the case of gill raker counts, that have been stable for over 30 years (Nelson, 1968c; Foote et al., 1999). Similarly, Taylor and Foote (1991) demonstrated genetic differences in vertebral counts between sockeye and kokanee from Babine Lake (Skeena River system) that mirrored those first reported by McCart (1970b). Wood and Foote (1990) demonstrated differences in developmental rate that may compensate for differences in egg size between sympatric sockeye and kokanee. In the Shuswap River system, sockeye and kokanee overlap in spawning time and location (Wood and Foote, 1990). Kokanee alevins (larvae) are smaller, yet develop at the same rate as sockeye alevins, an unexpected result given that sockeye have larger eggs than kokanee (Wood and Foote, 1990). Such developmental compensation presumably reflects selection for optimal emergence timing to match seasonal zooplankton production in the nursery lake in which sympatric forms exploit the same food resources. Sockeye salmon show greater prolonged swimming performance, faster average growth rates, as well as less variation in growth rate than kokanee, differences that might be advantageous for sockeye juveniles and adults that must smolt and undergo spawning migrations (Taylor and Foote, 1991; Wood and Foote, 1990, 1996). Differences in circannual seawater adaptability and age at maturity between sockeye and kokanee have also been suggested to represent adaptations to anadromous and nonanadromous life cycles, respectively (Foote et al., 1992, 1994; Wood and Foote, 1996; Wood, 1995).

### *Evidence for distinct gene pools*

The best evidence for sympatric sockeye salmon and kokanee being distinct gene pools comes from allozyme and DNA assays. Foote et al. (1989) demonstrated allele frequency differences between sockeye salmon and kokanee spawning sympatrically in three independent watersheds in Takla, Shuswap and Babine lakes, British Columbia. These results were corroborated and extended by Taylor et al. (1996) who demonstrated significant allele frequency differences between sympatric sockeye and kokanee at two minisatellite DNA loci. Wood and Foote (1996) used variation at 15 loci to estimate the effective number of migrants between sockeye salmon and kokanee populations spawning sympatrically and allopatrically in tributaries of Takla Lake. The effective number of migrants between forms spawning sympatrically averaged about 1.2 migrants per generation compared with an average of up to 45 migrants within forms spawning in different tributaries of Takla Lake (i.e. among allopatric sockeye populations and among allopatric kokanee populations, Wood and Foote, 1996). Of the total gene diversity, approximately 18% was due to differences between sockeye and kokanee compared with 0.5% within forms among tributaries (Wood and Foote, 1996). Genetic differences between sympatric sockeye and kokanee in development and maturity schedules were also documented in Shuswap and Takla lakes (Wood and Foote, 1990, 1996) and in carotenoid utilization and color at maturity in Takla Lake (Craig, 1995).

Although these data clearly indicate that sockeye salmon and kokanee are distinct gene pools in sympatry, they do hybridize in nature. Kokanee males often act as ‘sneaks’ during spawning between male and female sockeye salmon (Hanson and Smith, 1967; Foote and Larkin, 1988) to successfully fertilize sockeye eggs. Experimental field tests show that kokanee males acting as sneaks sired an average of 20% of an individual female sockeye’s eggs in competition with male sockeye salmon (Foote et al., 1997). These is also some suspicion that so-called ‘residual’ sockeye salmon, originally thought only to represent offspring of sockeye salmon that mature in lakes without entering the ocean (Ricker, 1938), may in some cases represent hybrids between sockeye salmon and kokanee. Residual sockeye in Takla Lake tend to be intermediate between sockeye and kokanee in coloration, gill raker number, and allele frequency at some allozyme loci (C. Foote and C. Wood, pers. comm.; Craig, 1995).

### *Reproductive isolation*

How is reproductive isolation between sympatric sockeye salmon and kokanee facilitated and how do they remain as distinct gene pools in sympatry? There is some evidence that even where they spawn in sympatry (same streams at the same time), sockeye and kokanee often chose different spawning microhabitats (Wood and Foote, 1996). Behavioural aspects of mate choice, however, also contribute to reproductive isolation in sympatry. Foote (1988) and Foote and Larkin (1988) conducted a series of experiments on the spawning behaviour and mechanisms of mate choice in sockeye salmon and kokanee. Within a kokanee population that was polymorphic for male size at maturity, Foote (1988) showed that mating was strongly assortative by size; male mate choice was dependent on the *relative* size of females with a strong preference for females that were the same size as the male or larger. Foote and Larkin (1988) demonstrated that assortative mating between sockeye and kokanee in sympatry appeared to be largely the result of such assortative mating by size, but also that a 'form' component was involved; kokanee males preferred to mate with kokanee females even in the presence of larger and more fecund sockeye salmon females (Foote and Larkin, 1988). In addition, female sockeye rarely spawn with kokanee males even when no sockeye males are present (McCart, 1970b; Foote and Larkin, 1988). As such, reproductive isolation appears to be largely based on size differences between sockeye and kokanee. Because kokanee are smaller than sockeye, size-based differences in male and female mate choice may drive form-based assortative mating (Wood, 1995). Similarly, intrasexual competition also appears to act to limit gene flow between sockeye and kokanee. Kokanee males, owing to their smaller size, are unable to obtain dominant positions when in competition with sockeye males (and thus they are restricted to sneaking and reduced mating opportunity (Foote and Larkin, 1988)). Female kokanee also are generally unable to compete with sockeye females as preferred mates with male sockeye owing to their smaller size (Foote and Larkin, 1988).

As is evident from experimental matings between stickleback species pairs, there appear to be no intrinsic postmating barriers to gene flow between sockeye and kokanee. Wood and Foote (1990) conducted experimental reciprocal crosses between sockeye salmon and kokanee from the Shuswap River system in British Columbia and uncovered no evidence of reduced survival or fertility of $F_1$ hybrids raised in the laboratory. Furthermore, $F_2$ hybrids and backcrosses have been made with no evidence of reduced survivorship under laboratory development and growth environments (C.C. Wood and C.J. Foote, pers. comm.).

By contrast, there appear to be abundant opportunities for postmating isolation in the form of reduced survival of juvenile hybrids in nature. For instance, hybrid progeny likely sustain higher mortality because of inherited differences between sockeye and kokanee in growth, development, seawater adaptability, morphology and meristics, age at maturity and swimming performance (Wood and Foote, 1990, 1996; Taylor and Foote, 1991; Foote et al., 1992, 1999). These differences between sockeye and kokanee probably stem from divergent selection in *O. nerka* associated with specialization to an anadromous (sockeye) versus freshwater-resident (kokanee) life history (Ricker, 1940; Wood, 1995).

## Origins of species pairs in stickleback and salmon

### *Evolutionary mechanisms of divergence*

As exemplars of species pairs in freshwater fish, ideas on the mode and tempo of evolution of benthic and limnetic sticklebacks and sockeye salmon and kokanee have focused on: (1) the mechanisms involved in the divergences (e.g. natural or sexual selection versus drift or founder effect speciation); and (2) the geography of divergence (allopatric versus sympatric divergence). At least for sticklebacks and salmon, available biogeographic and phylogenetic data strongly implicate deterministic forces, i.e. natural and/or sexual selection, in driving the divergences. In *Gasterosteus*, both mtDNA and microsatellite-DNA-based analyses indicate that the divergences between benthics and limnetics have occurred independently in at least three of the six lakes containing sympatric pairs (Taylor et al., 1997a; Taylor and McPhail, 1999; Taylor, unpubl. data). Similarly, Taylor et al. (1996) used mtDNA and minisatellite DNA variation to argue that parallel divergences of kokanee from sockeye salmon had occurred throughout the range of *O. nerka*. These molecular phylogenetic analyses complemented earlier biogeographic and allozyme studies that suggested multiple origins for sympatric pairs in these fish (Nelson, 1968b; Foote et al., 1989; McPhail, 1993). Multiple origins inferred from phylogenetic analyses strongly implicate selection in driving the divergences because random forces such as drift are less likely to generate divergences along parallel ecological axes among replicate evolutionary lineages within a taxon (Bell and Andrews, 1997).

Schluter (1996) used the term ‘ecological speciation’ to describe the evolution of reproductive isolation as a consequence of divergent natural selection acting in a population exploiting distinct ecological niches. Divergent selection drives the evolution of premating reproductive isolation either indirectly via a pleiotropic effect of adaptation to alternative niches or directly by reinforcement (Dobzhansky, 1940), but both are based on the expectation that intermediate phenotypes have reduced fitness in specialized (alternative) niches within the environment (Schluter, 1996). Such processes appear to have been major instruments of divergence in intralacustrine divergences in fish, from species flocks of cichlid fishes (Liem, 1973; Strauss, 1984) to sympatric pairs of sticklebacks and salmon. For instance, sympatric pairs in sticklebacks and salmon are adapted to alternative niches and such adaptations result in marked phenotypic differences between pairs in body size, morphology, coloration and behaviour. There is also good evidence that selection may act against phenotypically intermediate individuals and hybrids (Schluter, 1994; Wood, 1995; Hatfield and Schluter, 1999). Such phenotypic differences, particularly body size, appear to be major determinants of assortative mating between pairs where they coexist (Foote and Larkin, 1988; Nagel and Schluter, 1998). Consequently, some or most reproductive isolation appears to have evolved as a pleiotropic effect of natural selection to alternative niches in both sticklebacks (benthic versus limnetic foraging niches) and salmon (lake-resident and sea-run life history). Premating isolation, however, may have become enhanced in sympatry via reinforcement (Rundle and Schluter, 1998).

In contrast to natural selection, the role of sexual selection in driving divergences in species pairs of sticklebacks and salmon has received comparatively little study. Dominey (1984), however, discussed situations in which sexual selection may promote the evolution of reproductive isolation. Among the factors he cited, two would appear to be common in species pair systems, specifically: (1) complex mate recognition systems; and (2) environments with opportunities for founder populations to develop in isolation. Both in sticklebacks and in salmon, elaborate morphological and behavioural signals that function in mate recognition and choice have been well described (reviews in Groot and Margolis, 1991; Foster, 1994) and most are thought to be heavily influenced by sexual selection, which itself is thought to be a strong feature of the mating systems of these animals. As well, at least for sticklebacks, one of the major hypotheses for the origin of species pairs involves repeated founding of lacustrine populations and a period of allopatry from postglacial marine colonists followed by secondary contact between forms (McPhail, 1993). Dominey’s (1984) conceptual model posits rapid genetic change in mate-recognition systems (in which intrapopulation variation is maintained by sexual selection) in small founder populations that drove the evolution of reproductive isolation expressed during secondary contact between founder and ancestral populations.

One of the predictions of Dominey’s model of sexual-selection-driven divergence is that such divergences should be characterized by differences related to courtship and mate choice while traits related to competition for shared resources (under an ecological speciation hypothesis) should be relatively minor or should at least appear later (Mayr, 1984). The pronounced differences in male nuptial coloration or in courtship behaviours between morphologically similar (sibling) species of cichlids and fruit flies (*Drosophila*, Drosophilidae) are consistent with model systems in which sexual selection is suspected of driving divergence (Dominey, 1984). For sticklebacks and salmon, however, differences between species pairs in morphological or behavioural components of courtship, while detectable (Foster et al., 1998), appear minor relative to pronounced differences in traits associated with adaptation to alternative foraging and migratory niches (see above). Although these observations argue for a greater role for natural than sexual selection in driving divergences between species pairs, the latter has not been well studied. In addition, the pronounced differences in nuptial coloration between benthic and limnetic male stickleback from Enos Lake (benthics are black) and between ‘white’ and normal sticklebacks from Nova Scotia, Canada (Blouw and Hagen, 1990) are notable exceptions to the general similarity between sympatric pairs in reproductive traits. Such variability deserves further study in terms of the role of sexual selection in driving the evolution of reproductive isolation.

### *Geography of divergence*

From the earliest detailed accounts of species pairs in freshwater fish, their origin has been considered in the context of the relative importance of models of sympatric and allopatric speciation (Mayr, 1963).

McPhail (1993) outlined distributional and geological information that suggested that benthic and limnetic stickleback evolved from ‘double invasions’ of marine ancestral sticklebacks into postglacial lakes during the last 10 000 years (cf. Svärdson (1961) for species pairs of Scandinavian fishes). McPhail (1993) also suggested that the alternative double invasion and sympatric speciation models might be testable at the molecular level. Such tests were conducted using mtDNA by Taylor et al. (1997a) and by Taylor and McPhail (1999). These data suggested that some species pairs may have arisen by sympatric speciation because within each of two lakes, benthics and limnetics were monophyletic. There is, however, some evidence for hybridization between sympatric stickleback species in nature (McPhail, 1984, 1992) and because mtDNA may cross species boundaries (Tegelström, 1987; Echelle and Conner, 1989) and may hence obscure phylogenetic resolution, the hypothesis of allopatric divergence (from double invasions) followed by mtDNA introgression from hybridization during secondary contact could not be discounted. Subsequently, Taylor (unpubl. data) assayed the same stickleback populations at six microsatellite (nDNA) loci and rejected within-lake monophyly for all but the one species pair lake where hybridization is suspected to have been most common (Paxton Lake). Further, various genetic distance measures indicated that limnetic sticklebacks were less divergent from the marine or anadromous sticklebacks than were benthics. This latter result is a prediction of McPhail’s (1993) double invasion hypothesis which posits that limnetic sticklebacks result from the more recent of two invasions of coastal lakes by marine or anadromous sticklebacks (benthics are thought to have arisen from an earlier invasion of the lakes by marine or anadromous sticklebacks). Limnetic sticklebacks are also more similar to anadromous or marine *Gasterosteus* in allozyme frequencies at three loci (McPhail, 1984, 1992; Wither and McPhail, 1985) and in salinity tolerance (Kassen et al., 1995). The microsatellite data, in combination with the geological, distributional, allozyme and physiological data, appear to favour the double-invasion (allopatric) model of stickleback species pair evolution. If this model does indeed hold, the mtDNA data imply that gene flow between the species was initially rather high during or after secondary contact (recall that the sympatric sticklebacks are monophyletic for mtDNA in two lakes). These results, therefore, suggest that divergence between benthic and limnetic sticklebacks has proceeded to the level of biological species *despite* gene flow when sympatry was reestablished during secondary contact.

Distributional and molecular phylogenetic data have also been considered in models of evolution for sympatric pairs of sockeye salmon and kokanee (Nelson, 1968b; Foote et al., 1989; Taylor et al., 1996). Ricker (1940) was the first to suggest that kokanee populations have been independently derived from sockeye salmon in postglacial times (Nelson, 1968b; Behnke, 1972). Foote et al. (1989) used allozyme data to suggest that sockeye and kokanee have diverged sympatrically in several lake systems where they now coexist. Wood and Foote (1996) provided a plausible mechanism for divergence-with-gene-flow based on assortative mating between forms as a correlated response to differences in body size between sockeye salmon and kokanee. Further analysis of sympatric sockeye salmon and kokanee using minisatellite DNA (Taylor et al., 1996) and allozymes (Winans et al., 1996), however, did not support monophyletic relationships between sockeye salmon and kokanee within single lakes that would provide the best phylogenetic evidence for sympatric divergence. Rather, both studies noted strong similarities in allele frequencies among kokanee populations in adjacent watersheds with a history of watershed interconnectedness. Both Taylor et al. (1996) and Winans et al. (1996) suggested that more rigorous analyses (e.g. character-state-based phylogenetic analysis across multiple loci) will be required to adequately test for monophyletic origins of sympatric sockeye and kokanee.

In both stickleback and salmon species pairs, the divergences have occurred multiple times independently. Although species pairs in sockeye salmon and kokanee and in sticklebacks may involve multiple postglacial colonizations of lakes, the different colonist populations do not appear to represent distinct phylogenetic groups that have diverged in allopatry over long time periods (e.g. $>$100 000 years in distinct glacial refugia) as has been proposed for other species pairs (Svärdson, 1961; Behnke, 1972; Bernatchez and Dodson, 1990; Hynes et al., 1996). Rather, stickleback and salmon species pairs have apparently evolved multiple times *within* major lineages (Figure 2). Sympatric pairs of *O. nerka* occur in large lake systems, several of which have been connected historically and there were probably numerous opportunities for microspatial isolation events during the recent glaciations. These features of lakes with sympatric

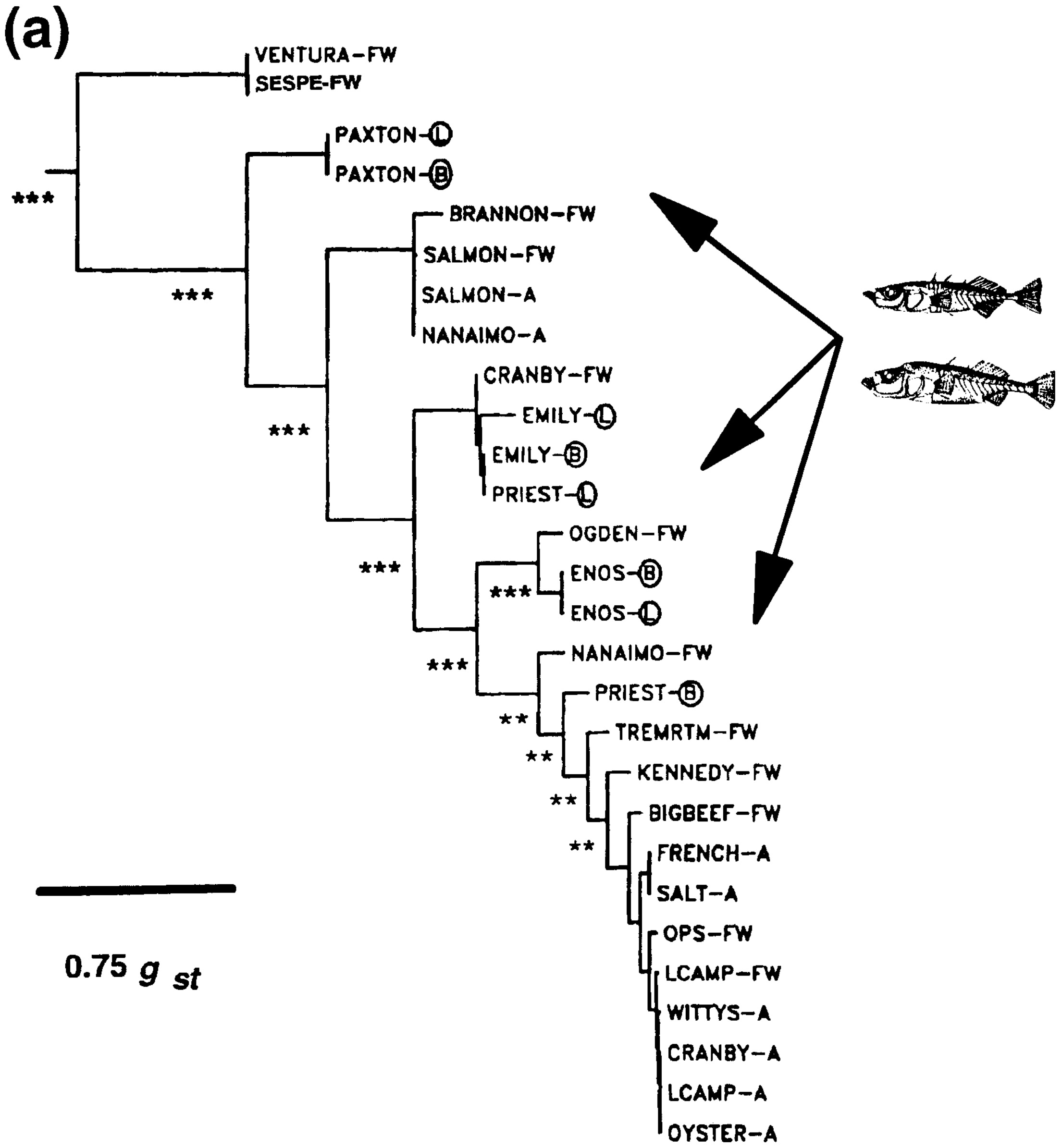

*Figure 2.* Parallel evolution of species pairs in sticklebacks and in sockeye salmon and kokanee. (a) Mitochondrial DNA phylogeny of benthic (B) and limnetic (L), solitary (FW) fresh water, and anadromous (A) sticklebacks from southwestern British Columbia. Tree represents a hierarchical clustering of net mtDNA sequence divergence among populations ($g_{st}$; Taylor and McPhail, 1999). Asterisks represent groups of populations to the right of bifurcations of the tree that are significantly divergent from one another. The divergences between benthic and limnetic sticklebacks within Paxton Lake, Emily Lake/Priest Lake, and Enos Lake are found in distinct portions of the tree. Drawings at right represent limnetic (upper) and benthic (lower) sticklebacks. (b) Consensus tree from bootstrapped maximum likelihood analyses of DNA and mtDNA restriction site variation among sockeye salmon (S) and kokanee (K) populations from the North Pacific. Numbers along branches represent the percentage of replicate trees containing the group of populations to the right of that branch and give qualitative levels of support for different groups of populations. Sockeye and kokanee have diverged at least twice in the North Pacific as both are found in distinct 'Northwestern Pacific' (NWP) and 'Fraser–Columbia' (FC) assemblages of *Oncorhynchus nerka*. Drawings at right represent sockeye salmon (upper) and kokanee (lower). See Taylor et al. (1996) for details.

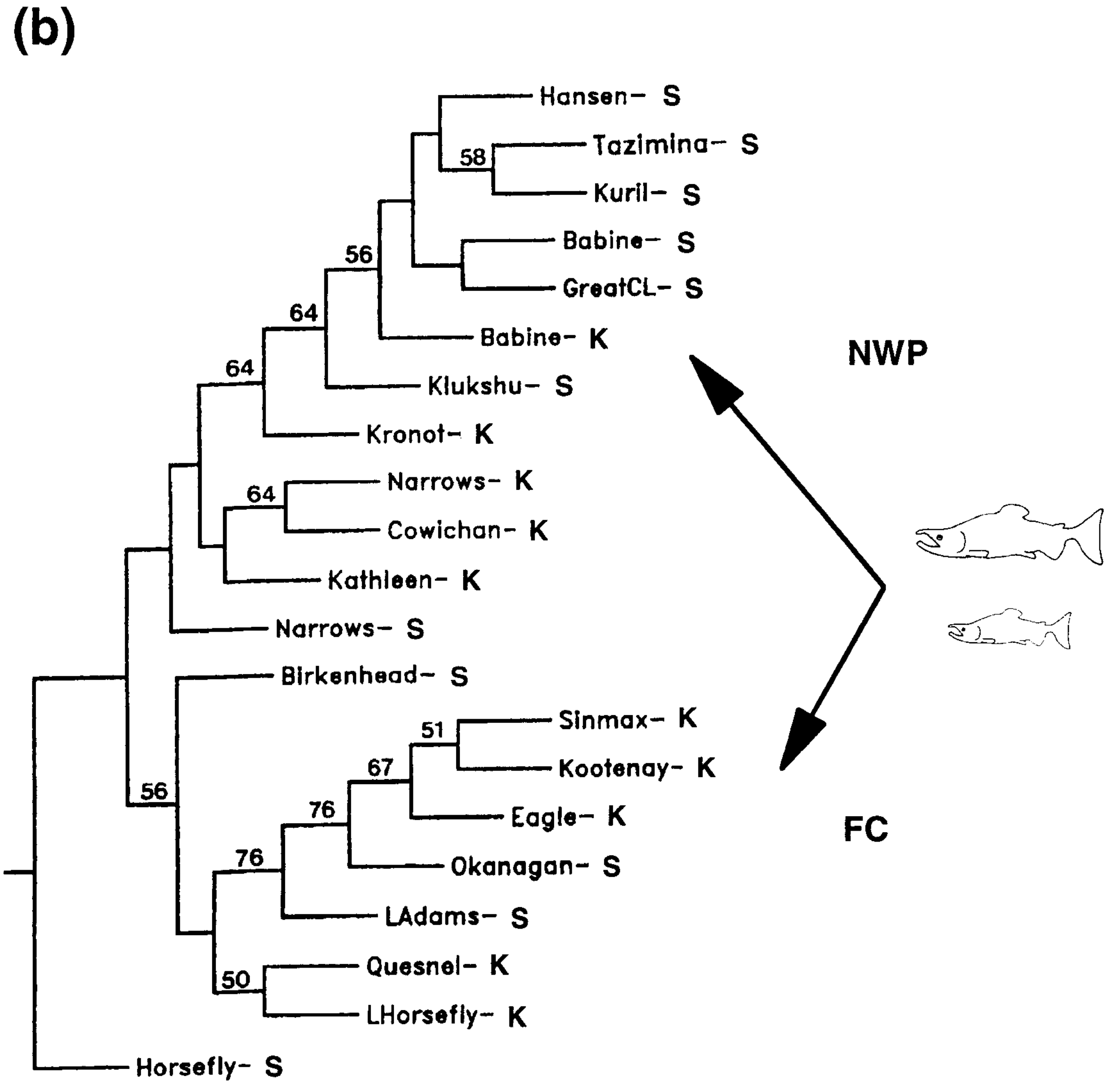

*Figure 2.* Continued.

pairs may have promoted microallopatric divergence within areas occupied by major phylogenetic lineages.

Despite continuing uncertainty about the geography of the initial stages of divergence in stickleback and salmon species pairs, what is clear is that the forms have diverged and remain genetically distinct despite some gene flow between them. If divergence was initially sympatric, then the gene flow must have been substantial. Alternatively, under an allopatric model of divergence between species pairs, both benthic and limnetic sticklebacks and sockeye salmon and kokanee maintain themselves as distinct gene pools in the face of gene flow which may have been substantial during initial secondary contact (as suggested by some mtDNA data in sticklebacks) and which persists at low levels (as suggested by behavioural and biochemical data for sockeye salmon and kokanee). These particular examples of species pairs in freshwater fishes, therefore, provide compelling evidence in favour of the idea that divergence to the level of biological species can proceed in the face of gene flow whether or not the initial divergence occurred in allopatry (Rice and Hostert, 1993).

### *Tempo of the divergences*

Species pairs in sticklebacks and salmon provide strong evidence that divergence to the level of biological species can occur rapidly. All the benthic–limnetic pairs are restricted to lakes that were covered by ice until the end of the Wisconsinan glaciation which ended about 10–15 000 years ago in southwestern British Columbia (Lindsey and McPhail, 1986; McPhail and Lindsey, 1986). Further, while some current sympatric sockeye and kokanee populations are found in areas that likely escaped Wisconsinan glaciation (Winans et al., 1996), the vast majority of sympatric pairs are restricted to habitats with a postglacial origin. A postglacial time frame is consistent with the very low levels of molecular divergence between these sympatric pairs. Nei's (1972) genetic distance based on allozymes is typically $<0.05$ for both benthic and limnetic stickleback species pairs (McPhail, 1994) and for sockeye salmon and kokanee from diverse areas (Foote et al., 1989; Wood and Foote, 1996; Winans, et al. 1996). As well, genetic distances between sympatric pairs are typically within the range of distances among random sets of allopatric populations (Figure 3). Not all sympatric pairs in sockeye salmon and kokanee, however, are necessarily so similar genetically. Winans et al. (1996) reported a genetic distance based on 22 loci of 0.1 between sockeye and kokanee from a lake in western Washington. There are no comprehensive data for mitochondrial DNA divergences between sockeye and kokanee, but net divergence between species pairs of sticklebacks ranges from 0.0001% to 0.06% (Taylor and McPhail, 1999). Estimating times-of-divergence based on these genetic distances is problematic, but comparison of genetic distances between closely related 'good' species within sticklebacks and salmon to those between members of sympatric pairs (Figure 4) suggests that the latter divergences have arisen relatively recently. Applying a molecular clock of 0.2–2.0% sequence divergence in mtDNA per million years (Avise, 1994, p. 103) suggests that stickleback species pairs originated within the mid-late Pleistocene and as recently as within the last 10 000 years. Even in more species-rich areas, divergence to the level of biological species can arise within such short time frames (e.g. species flocks of cichlids, Johnson et al., 1996). Finally, reproductive isolation between salmon and kokanee and between benthic and limnetic pairs of sticklebacks appears to be largely prezygotic (via mate or habitat preferences) or if postzygotic it is extrinsically based (i.e. ecological in nature). The general lack of intrinsic genetic incompatibilities that function in postzygotic reproductive isolation is consistent with a recent time frame for speciation (Coyne and Orr, 1989; Coyne, 1992; Hollocher et al., 1997).

## Comparisons with species pairs in other taxa

Although I have highlighted the ecological and genetic divergences in species pairs of threespine sticklebacks and sockeye salmon/kokanee, there are many other cases of species pairs in north temperate fishes. A brief examination of these other situations illustrate generalities of the nature and mechanisms of divergence in species pairs.

First, most other species pairs involve an ecotypic divergence along benthic/piscivorous and limnetic/planktivorous trophic axes. This differentiation is apparant in multiple cases of sympatric pairs of lake whitefish (Fenderson, 1964; Lindsey et al., 1970; Bodaly, 1979; Bernatchez et al., 1996), Arctic char (*Salvelinus alpinus*, Salmonidae) (Hindar et al., 1986; Skúlason et al., 1989), brown trout (*Salmo trutta*, Salmonidae) (Ferguson and Mason, 1981), and rainbow smelt (*Osmerus mordax*, Osmeridae) (Taylor and Bentzen, 1993) and in parapatric stream–lake pairs of threespine sticklebacks (Moodie, 1972; Reimchen et al., 1985; Thompson et al., 1997). In all these cases, differences in morphology and behaviour between sympatric species pairs likely serve as specializations to alternative trophic niches as illustrated by benthic and limnetic sticklebacks. Further, where trophic ecology does not appear to be the primary axis of divergence, there are many cases of sympatric and reproductively isolated migratory life history types (anadromous and nonanadromous) in Arctic charr (Hindar et al., 1986), Atlantic salmon (*Salmo salar*, Salmonidae) (Verspoor and Cole, 1989; Birt et al., 1991) and possibly in brown trout (Ferguson, 1989). Putative species pairs of lampreys consist of anadromous and nonanadromous populations as well as parasitic and nonparasitic feeding ecotypes (McPhail and Lindsey, 1970; Beamish and Withler, 1986). As in sockeye salmon and kokanee, the divergent populations of brown trout, Atlantic salmon, Arctic charr, and lampreys show body size differences with the resident form typically being smaller.

There are, however, at least some situations in other species pairs that do not mirror the typical

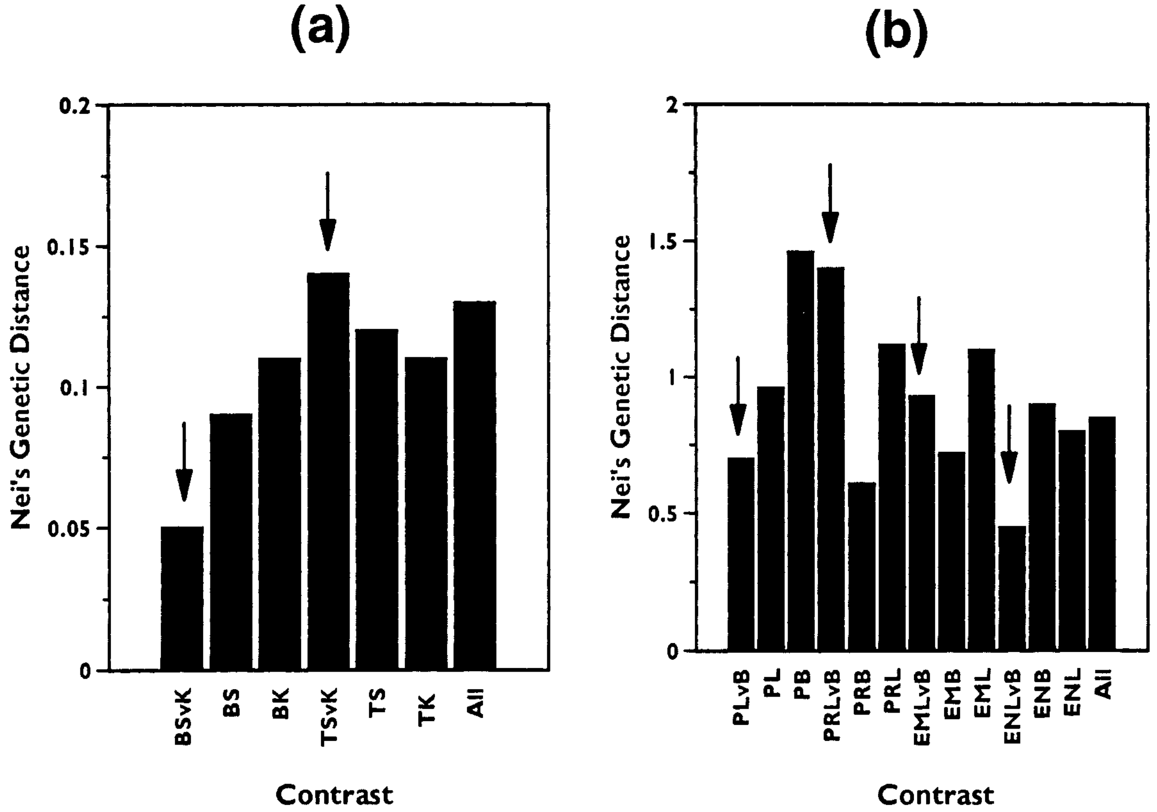

*Figure 3.* (a) Nei's (1972) standard genetic distance between sympatric sockeye salmon and kokanee in Babine Lake (BSvK) and Takla Lake (TSvK), British Columbia, relative to distances between each member of the species pairs and 10 allopatric populations of sockeye and kokanee. Allopatric comparisons are the means of 10 pairwise comparisons and also shown is the mean pairwise distance among all populations ("All"). Distances are based on two minisatellite and four allozyme loci (Foote et al. 1989; Taylor et al. 1996). (b) Nei's genetic distance between sympatric limnetic and benthic sticklebacks from Paxton (PLvB), Priest (PRLvB), Emily (EMLvB), and Enos (ENLvB) lakes and between the members of each pair and 17 allopatric freshwater and anadromous populations. Allopatric comparisons are the means of 17 comparisons across six microsatellite loci (E.B. Taylor, unpublished data). Also shown is the mean pairwise distance among all populations ("All"). Arrows indicate sympatric pair comparisons and note that there is an approximately tenfold difference in genetic distance scales between (a) and (b).

morphological or ecological differences as illustrated by sticklebacks and sockeye salmon/kokanee. For instance, although data for sympatric sockeye salmon and kokanee or between sympatric reproductive ecotypes of kokanee suggest little segregation in trophic ecology (Taylor et al., 1997b; Wood et al., 1999), there is at least one case of divergence of sympatric kokanee into benthic and limnetic trophic ecotypes (Kurkenov, 1977) in Kamchatka. Also, there are instances in lake whitefish (Chouinard et al., 1996) and rainbow smelt (Pigeon et al., 1998) where sympatric populations are recognized by molecular analyses yet demonstrate no detectable size-independent morphological, spatial, or trophic differentiation. In sum, although migratory and trophic ecology seem to be general factors that drive divergences between sympatric species pairs, other factors such as intrinsic genetic incompatabilites (Lu and Bernatchez, 1998) or reproductive ecology unrelated to body size differences (e.g. Taylor et al., 1997b) may be the objects of divergence.

The evidence for distinct gene pools in species pairs other than sticklebacks and sockeye salmon/kokanee is widespread enough to indicate that this is a general phenomenon in north temperate fishes. Allozymes, mtDNA, minisatellite and microsatellite DNA assays have produced compelling evidence for the existence of sympatric reproductively isolated populations of Arctic charr (Hindar et al., 1986; Hartley et al., 1992), Atlantic salmon (Verspoor and Cole, 1989; Birt et al., 1991), lake whitefish (Lindsey et al., 1970; Kirkpatrick and Selander, 1979;

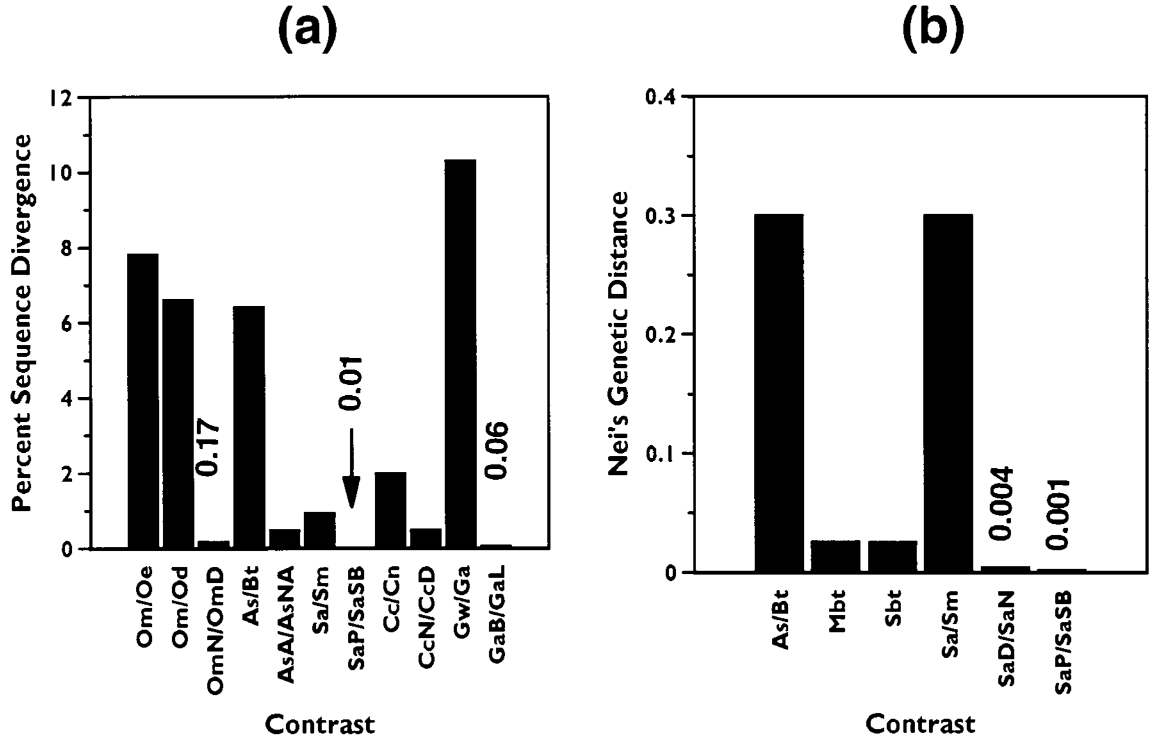

*Figure 4.* Comparative genetic distances between sympatric species pairs and sister species within the same genus based on (a) mtDNA sequence divergence and (b) Nei's (1972) genetic distance derived from allozyme surveys. Om, *Osmerus mordax* (Osmeridae); Oe, *O. eperlanus*; Od, *O. dentex*; OmN, normal *O. mordax*; OmD, dwarf *O. mordax* (Taylor and Bentzen, 1993; Taylor and Dodson, 1994); As, *Salmo salar*; Bt, *Salmo trutta*; Mbt, Loch Melvin *S. trutta*; Sbt, Swedish *S. trutta*; AsA, anadromous *S. salar*; AsNA, nonanadromous *S. salar* (Ryman et al., 1979; Gyllensten and Wilson, 1987; Birt et al., 1991); Sa, *Salvelinus alpinus*; Sm, *S. malma*; SaP, planktivorous *S. alpinus*; SaSB, small benthivorous *S. alpinus*; SaD, dwarf *S. alpinus*; SaN, normal *S. alpinus* (Hindar et al., 1986; Magnusson and Ferguson, 1987; Grewe et al., 1990; Danzmann et al., 1991); Cc, *Coregonus clupeaformis* (Salmonidae); Cn, *C. nasus*; CcN, normal *C. clupeaformis*; CcD, dwarf *C. clupeaformis* (Bernatchez et al., 1991; Bernatchez and Dodson, 1990); Gw, *Gasterosteus wheatlandi* (Gasterosteidae); Ga, *G. aculeatus*; GaB, benthic *G. aculeatus*; GaL, limnetic *G. aculeatus* (Ortí et al., 1994; Taylor and McPhail, 1999).

Bernatchez and Dodson, 1990; Bodaly et al., 1992), rainbow smelt (Taylor and Bentzen, 1993; Bernatchez, 1997), and brown trout (Ryman et al., 1979; Ferguson and Taggart, 1991). In lake whitefish species pairs, the genetic differences between sympatric species are apparent over at least a 20 year time span (Fenderson, 1964; Lindsey et al., 1970; Bernatchez and Dodson, 1990; Bernatchez et al., 1996). Quantitative genetic differences in morphology and behaviour provide strong evidence for separate gene pools in sympatric Arctic charr in Thingvallavatn, Iceland (Skúlason et al., 1989, 1993). As with benthic and limnetic sticklebacks and sockeye/kokanee, biochemical and molecular divergence between sympatric pairs is typically low (e.g. Nei's genetic distance <0.05, per cent sequence divergence <0.5%) and gene pool differentiation typically takes the form of distinctive frequencies of common alleles or closely related haplotypes. Consequently, genetic distances between sympatric pairs are similar to differences between random sets of allopatric populations (Kirkpatrick and Selander, 1979). Further, where species pairs are replicated within a particular taxon (e.g. lake whitefish, smelt), genetic differentiation between sympatric species can vary considerably among lakes (Bodaly et al., 1992; Taylor and Bentzen, 1993a; Bernatchez et al., 1996). Again, however, some exceptions to these general patterns are apparent. For instance, Lough Melvin in Ireland contains three coexisting ecotypes of brown trout: ferox (piscivore), gilaroo (benthivore) and sonaghen (plankitivore). Although gilaroo and sonaghen fit the pattern of low molecular differentiation, the ferox form is considerably more distinct (e.g. Nei's *D* of 0.08, 1.2% sequence divergence in mtDNA) and is characterized by nearly fixed allelic differences at some allozyme loci and mtDNA restriction fragment length polymorphisms (RFLPs; Ferguson and Taggart, 1991; McVeigh et al., 1995; Hynes et al., 1996). Finally, it is assays of biochemical and molecular loci that have provided the best evidence of sympatric species pairs of fishes in some marine environments where morphological or ecological differentiation is cryptic (Higuchi and Goto, 1996; Planes and Doherty, 1997).

The ecological and genetic factors contributing to reproductive isolation between most species pairs are not well understood. Spatial or temporal isolation during spawning may contribute to reproductive isolation (Frost, 1965; Behnke, 1972; Kirkpatrick and Selander, 1979; Smith and Todd, 1984; Ferguson and Taggart, 1991; Taylor and Bentzen, 1993b), but the extent to which mate choice promotes reproductive isolation between members of a species pair spawning sympatrically has not been well studied. Similarly, the role of intrinsic genetic factors in reproductive isolation has not been studied with the exception of research on dwarf and normal whitefish by Lu and Bernatchez (1998). These authors reported no differences in fertilization success between pure species or in reciprocal hybrid crosses of dwarf and normal lake whitefish. There was, however, a 2.4–4.7 times greater daily embryonic mortality rate in hybrid progeny which Lu and Bernatchez (1998) suggested may point to intrinsic genomic incompatibilities contributing to reproductive isolation in species pairs. The crosses between dwarf and normal whitefish, however, were not made between ecotypes from the same lake, but involved fish from different lakes. In addition, the different ecotypes belonged to different mtDNA clades (estimated to have diverged at least 150 000 years ago) and dwarf and normal ecotypes can arise *within* each of these clades (Bernatchez et al., 1996; Pigeon et al., 1997). In this experiment ecotypic differences were confounded both with environmental (i.e. source lake) and phylogenetic (i.e. mtDNA) differences. It is possible, therefore, that the increased hybrid mortality was due to either a lake or mtDNA clade effect and may not necessarily contribute to reproductive isolation between sympatric dwarf and normal whitefish. Consequently, as in sticklebacks and sockeye salmon/kokanee, there remains little evidence of strong intrinsic barriers to gene flow between sympatric species. In addition, more studies are needed to examine performance of advanced-generation hybrids between sympatric species and backcrosses to test for hybrid breakdown (Shaw et al., 1986; Hatfield and Schluter, 1999).

The maintenance of species pairs that may occasionally hybridize may also be facilitated by reduced fitness of hybrid genotypes driven by exogenous ecological interactions. As most species pairs differ in aspects of trophic or migratory ecology, it is possible that similar mechanisms as proposed for sticklebacks and sockeye salmon and kokanee may constrain gene flow in other species pairs in nature. Given, however, that hybrid genotypes are not necessarily less fit than parental genotypes under many situations (Arnold and Hodges, 1995; Arnold, 1997) and that experiments or surveys to test this idea have not been attempted in species pairs other than sticklebacks and sockeye salmon and kokanee, critical tests of the ecological nature of reproductive isolation are lacking.

Phylogeographic analyses of species pairs other than sticklebacks and sockeye salmon and kokanee have also addressed the geography of speciation. Svärdson (1961) was the first to posit multiple postglacial invasions of fresh waters by allopatrically derived forms to account for species pairs in Scadinavian fishes. Sympatric populations of brown trout (Ferguson and Mason, 1981; Hynes et al., 1996), Arctic charr (Hindar et al., 1986; Hartley et al., 1992) and rainbow smelt (Behnke, 1972; Bernatchez, 1997) have also been suggested to be the result of allopatric divergence followed by secondary contact from multiple invasions of postglacial environments. Perhaps the best examples of multiple invasions from distinct refugia involve the brown trout of Lough Melvin and the dwarf and normal whitefish of several lakes in northeastern North America and Yukon Territory (Bernatchez and Dodson, 1990; Bernatchez et al., 1996; Pigeon et al., 1997; but see Bodaly et al., 1992). In these cases the sympatric species within some lakes belonged to distinct phylogenetic lineages and these lineages had geographic distributions outside each lake that were strongly associated with distinct glacial refugia. The sympatric lineages presumably resulted from double invasions of the lakes in postglacial times by colonists from the different refugia. Interestingly, however, while these studies strongly suggest that the *phylogenetic* lineages were allopatrically derived, it is possible that these lineages were initially phenotypically similar and that the differences in ecology and morphology arose, or at least were magnified, after colonization of the lakes in question (Thompson et al., 1997).

As in sticklebacks and sockeye salmon and kokanee, somewhat more controversial has been the suggestion that coexisting species pairs have arisen sympatrically from a common ancestral population. Sympatric divergence has been suggested as a possible mechanism of divergence for some pairs of brown trout (Ferguson and Taggart, 1991; McVeigh et al., 1995), rainbow smelt (Taylor and Bentzen, 1993a), Arctic charr (Hindar et al., 1986) and lake whitefish (Lindsey et al., 1970; Behnke, 1972; Kirkpatrick and Selander, 1979; Bodaly et al., 1992; Pigeon et al., 1997). These cases for sympatric speciation all largely rest on the observation that distinct phenotypes within each lake are more closely related to each other, as inferred from genetic data, than is either phenotype to comparable forms outside each lake. Again, however, these data are open to an alternative interpretation of within-lake monophyly: the species diverged allopatrically, but appear descended from a recent ancestor within the lakes because of introgression following secondary contact (Taylor et al., 1997a; Taylor and McPhail, 1999). Analyses of patterns of phylogenetic relationships that can distinguish between sympatric divergence versus allopatric divergence/introgression (e.g. Wang et al., 1997) have yet to be attempted for these other northern species pair assemblages. Finally, it should be pointed out that neither allopatric nor sympatric origins should be expected to provide a ‘generic’ mechanism for the geography of species pair evolution. Rather, it is more likely that unique geological and ecological conditions in particular systems may promote one, either or both mechanisms (Ferguson and Taggart, 1991; Bodaly et al., 1992; Bernatchez et al., 1996; Pigeon et al., 1997).

## Prevalence of species pairs in temperate lakes

In all examples of species pairs discussed so far, there is general concordance in the directions and levels of ecological, morphological and genetic differentiation as well in as factors identified as contributing to reproductive isolation. Why have northern freshwater fish lineages repeatedly diversified along similar axes via similar mechanisms, particularly when contrasted with more southerly geographic areas where ‘older’ divergences tend to predominate? There are at least four features of northern aquatic environments and of their fish faunas that might promote species pair formation in recent times: (1) depauperate environments; (2) repeated vicariance and dispersal events; (3) environmental heterogenity in lakes; and (4) adaptive flexibility of morphological features and the occurrence of genome duplications.

First, species pairs tend to be found in ecosystems that are generally depauperate owing to the repeated disturbance and extinction events associated with the twenty or so Pleistocene glaciation events over the last two million years (Martinson et al., 1987). In general, temperate environments in the Holarctic regions that have been exposed to direct effects of glaciation have many fewer freshwater fish species than other temperate, subtropical or tropical areas (Helfman et al., 1997; Robinson and Schluter, 1999). As such, the prevalence of species pairs in these regions may represent the filling of ‘empty niches’ via character release facilitated by an absence of competitors that might prevent the occupation of such niches in more species-rich areas (Lindsey, 1981; Bell and Andrews, 1997; Robinson and Schluter, 1999). Perhaps even the presence of certain predators in more species-rich areas could constrain the occupation of niches characteristic of species pairs. Postglacial lake environments, therefore, may represent islands in the biogeographic sense; they are isolated, depauperate, represent novel ecological opportunities, and have been subject to sporadic colonization events. Such environments in terrestrial habitats are often associated with extensive radiations of closely related species (Carson et al., 1970; Jackman et al., 1994; Grant, 1998).

Second, watersheds with species pairs are those that have been exposed to multiple and shifting interconnectedness during glacial advances and retreats. Such geomorphological activity would have created repeated opportunities for isolation and divergence in contrasting environments followed by recontact between divergent populations through postglacial dispersal. Coupled with the characteristic spawning site fidelity of many taxa in newly colonized habitats, these factors likely promoted species pair formation via allopatric divergence and secondary contact (Svärdson, 1961; Smith and Todd, 1984; Bernatchez and Dodson, 1990).

Third, Smith and Todd (1984) summarized arguments that lake environments themselves represent a rich source of physical gradients (e.g. depth, shoreline development, substrate) with associated variation in prey species and reproductive habitat characteristics that have promoted ecological segregation.

Fourth, two features of fish themselves may promote rapid diversification. For instance, morphological features of the head, jaws, and visual system are all involved in prey detection, manipulation, and ingestion, and 'key innovations' in these systems (e.g. jaw protrusion) are thought to be major driving factors in fish evolution (Alexander, 1967; Liem, 1973). This inherent feature of fishes to exhibit feeding specializations (see also Skúlason and Smith, 1995), coupled with alternative trophic niches in depauperate northern freshwater environments, would tend to promote diversification. In addition, the indeterminate nature of fish growth results in inherent phenotypic plasticity (e.g. in body size owing to habitat productivity differences). Such variation in body size may promote speciation through allometrically based feeding specializations (Strauss, 1984). Further, because body size appears to be important in mate selection, such variation may predispose fishes to assortative mating by form via size differences between them (e.g. sockeye and kokanee) or size-related differences in reproductive habitat choice (e.g. dwarf and normal smelt populations, Taylor and Bentzen, 1993a, b). Finally, species pair formation may be promoted in salmonid fishes by the ancestral tetraploidy of Salmonidae. Gene duplication events may have resulted in adaptive divergence in gene function that could have contributed to the development of morphology and life history variation that is so characteristic of species pairs (Allendorf and Thorgaard, 1984).

## Species status of sympatric pairs

The material reviewed above provides compelling evidence that there are many cases of reproductively isolated, sympatric populations of fishes that occupy distinct ecological niches in (mostly) freshwater environments. Most studies of sympatric species pairs lack a strong temporal component to examine the stability of reproductive isolation, but where this has been examined, there is no evidence that divergent pairs are collapsing into a single gene pool and sympatric pairs appear stable for decades (Lindsey et al., 1970; Behnke, 1972; Bodaly et al., 1992; McPhail, 1994). A time frame spanning a few decades or less is small on a evolutionary scale, but has been sufficient to homogenize gene pools between even more divergent lineages that have come into contact (Busack and Gall, 1981). Sympatric pairs in sticklebacks, sockeye salmon and kokanee, lake whitefish and certain brown trout populations (e.g. Lough Melvin), therefore, fulfil the criteria for recognition as biological species, i.e. genetically distinct populations in sympatry, each fulfilling distinct ecological roles (Mayr, 1963). Such populations also fulfil the criteria of some other recent alternative species concepts such as the 'genotypic cluster' concept of Mallet (1995) and the 'cohesion species' concept of Templeton (1989). Species pairs, as decribed above, however clearly would not be considered as valid phylogenetic species (*sensu* Cracraft 1983). This is because members of most species pairs are not *diagnosable* by the possession of unique characteristics, but rather are distinguished from members of other species by different *frequencies* of shared character states (e.g. allele frequencies, gill raker counts).

Even in the rare cases where sympatric pairs are diagnosable (e.g. dwarf and normal lake whitefish in Cliff Lake, Maine, are fixed for differences in mtDNA lineages), one or both members of species pairs are usually not diagnosable *outside* the area of sympatry. For instance, dwarf and normal lake whitefish that are diagnosable using mtDNA within Cliff Lake are, by the same criterion, indistinguishable from many comparable as well as distinct phenotypes outside the lake (Bernatchez and Dodson, 1990). In addition, because species pairs within a particular taxon are thought to have arisen independently, phylogenies of species pairs clearly show that phenotypes are poly- or paraphyletic (Foote et al., 1989; Taylor and Bentzen, 1993a; Bernatchez et al., 1996; Taylor et al., 1996) and such taxa are anathema to the phylogenetic species concept (Schluter and Nagel, 1995). There are at least three reasons, however, why a 'final decision' on the taxonomic status of sympatric species pairs may be an overly simplistic and unrealistic goal: (1) the problem of taxonomy; (2) the mutifaceted nature of species and speciation; and (3) a misguided emphasis on diversity of names relative to ecological and genetic diversity.

First, assuming a preference for the biological species concept, a solid case can be made for distinct species status for members of pairs in particular areas (e.g. Enos Lake benthic and limnetic sticklebacks, Babine Lake sockeye salmon and kokanee, Cliff Lake dwarf and normal whitefish, Lough Melvin brown trout), but this is not the real problem. The real problem associated with sympatric pairs involves their nomenclature, i.e. the issue is not a conceptual one, but largely an operational one. For instance, under our current system of binomial classification, sympatric species could be given distinct names. Behnke (1972) addressed the problem of species pair taxonomy and suggested that giving members of sympatric species pairs distinct and new names as a matter of course could “get out of hand” and would reduce the meaning and “evolutionary significance of the species category”. It doesn’t seem intuitive, however, to set an ‘upper limit’ on the number of biological species within a taxon (e.g. within the genus *Gasterosteus*), given that many other taxa consist of highly speciose groups such as the 800 or more species of Hawaiian *Drosophila* (Kambysellis and Craddock, 1997). Rather, the problem with species pair taxonomy appears to be the issue of taxonomic categorization of members of species pairs when their phylogenetic relationships to closely related forms outside the zone of sympatry (e.g. a particular lake) are polyphyletic, ambiguous or unknown. Because such uncertainties are observed in allopatric comparisons and cannot be assessed by sympatry against the ‘acid test’ of the BSC (Mayr, 1963; Avise, 1994) assigning a distinct specific name to each member of a sympatric species pair is naive and cannot be done without a thorough examination of multiple traits, including reproductive isolation (Rundle and Schluter, 1998), within the ‘species complex’ as a whole.

Second, Grant and Grant (1997) discussed reproductively isolated sympatric populations of finches and argued that their designation as distinct species would be difficult given the variety of species definitions that *could* be employed (see also Endler, 1989). Grant and Grant (1997) also summarized comments by Huxley (1942) who argued that it is naive to expect a ‘generic’ species definition because species may arise in so many different ways. Therefore, while many who adopt the BSC or its derivatives would recognize many sympatric pairs as distinct species, the taxonomy of such species is not trivial, and valid arguments for alternative species concepts (which species pairs may not fit) can be made. Perhaps it is inevitable that different species concepts must be applied to different biological situations (e.g. sexual versus nonsexual organisms, allopatric versus sympatric populations, see papers in Claridge et al., 1997). With such a pluralistic approach to species identification, it then becomes difficult to justify conventional taxonomic designation as the common currency of biodiversity enumeration and conservation.

Third, many previous workers (Behnke, 1972; Ferguson and Mason, 1981; Carson, 1987; McPhail, 1989) have argued that the crucial issue is to document and to recognize the ecological and genetic diversity represented by species pairs whether they are recognized taxonomically or not.

## Taxonomy and the conservation of sympatric pairs

What might be the implications for conservation of species pairs if members of such pairs cannot be taxonomically resolved? For instance, the designation of species pairs within a particular taxon as a ‘species complex’ (Hagen and McPhail, 1970) may be unsatisfactory to many taxonomists and conservation bureaucrats, but that term does indeed reflect the *reality* that evolutionary and ecological complexity exists within a particular Latin binomial that cannot operationally be accommodated by our current system of nomenclature. We require, therefore, a change of thinking to recognize that Latin binomials can obscure evolutionary diversity where it is greatest. We must, therefore, recognize that such ‘hidden’ diversity should be incorporated into management and conservation programmes and legislation even in the absence of formal taxonomic recognition (Behnke, 1972).

Toward these ends several non-Linnaean categorization systems for diversity as exemplified by species pairs have been proposed (Ryder, 1986; Lindsey, 1988; Waples, 1995), but the challenge that remains is to establish universal criteria for diversity units within a single ‘named’ species. In fact, some jurisdictions do not require official taxonomic status for legal protection, although it may still help (Avise, 1989, 1994). For instance, the ‘distinct population segment’ and ‘Evolutionary Significant Unit’ provisions of the US Endangered Species Act (Utter, 1981; Waples, 1995) can afford legal protection for differentiated populations designated under the same Latin binomial. Because the definition of distinct populations typically integrates aspects of phenotype and genotype (Utter et al., 1993; Bernatchez, 1995) the evolutionary distinctiveness of members of particular species pairs should easily be recognized and warrant protection if necessary under such a system.

A potential limitation of explicit categorization of species pairs as ‘species complexes’ or ‘superspecies’ within a taxon is that individual populations within such complexes may be considered ‘less important’ than ‘good’ (i.e. named) species. For instance, named species are typically interpreted as deeper evolutionary divisions that may be considered as ‘less replaceable’ than members of more recently derived species complexes (O’Brien, 1994; Smith et al., 1995). As currently practised, however, formal taxonomic classification is often an imperfect indicator of the depth of evolutionary divergence (Behnke, 1972; O’Brien and Mayr, 1991) and even members of species pairs are probably irreplaceable over a human lifespan. In addition, if speciation is recognized as a *process* (Avise and Walker, 1998), then it is logical to expect to find some groups at intermediate stages of this process (Utter, 1981) and it is not obvious why one should prioritize existing named species over lineages in the process of speciation. In fact, it could be argued that in order to help maintain biodiversity, we need information on how biodiversity arises. The best chance to obtain such knowledge is by conserving and studying groups that are still in the process of speciation such as most species pairs where reproductive isolation is incomplete.

In conclusion, formal taxonomic categorization is an important and useful endeavour in evolutionary and conservation biology, but it should not necessarily be the minimal requirement for legal protection. Rather, and as others have emphasized (Behnke, 1972; Ferguson and Mason, 1981; Carson, 1987; McPhail, 1989; Bernatchez and Wilson, 1998), the identification of populations and population groups with independent evolutionary histories (and likely different future tendencies), and the hierarchical relationships among such groups, should be the focus of conservation efforts regardless of taxonomic identity. Such a philosophy recognizes that independent lineages represent the maximum genetic potential for future evolutionary change, a key aspect of long-term persistence of a taxon. This approach is especially important for north temperate species pairs, most of which inhabit ephemeral habitats where extinctions result from cyclic glaciation events and associated climatological changes (McPhail, 1994; Bell and Andrews, 1997). Recognition of the evolutionary significance of divergent sympatric populations, therefore, represents an important step towards the conservation of a significant component of biodiversity in temperate aquatic ecosystems.

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