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Review: The geography of speciation and adaptive radiation in coregonines

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with 1 figure and 4 tables

Abstract: Coregonines are becoming a model system for studying rapid speciation and adaptive radiation. Radiations have occurred in large lakes throughout the Northern Hemisphere following deglaciation. Some radiations are characterized by limited genetic diversity and display either poorly and/or well differentiated ecotypes. Other radiations contain high levels of total genetic diversity, but little genetic differentiation between ecotypes. This variation in the relationship between total genetic diversity, the distribution of genetic variance and the degree of morphological divergence provides an interesting model for studying the origins of sympatric species diversity. We review the evidence for three alternative speciation scenarios within all three coregonine genera: *Prosopium*, *Stenodus* and *Coregonus*. Reviewing genetic, morphological and biogeographical data we estimate the relative importance of (i) geographic speciation where in situ diversity builds up by multiple invasions, (ii) speciation by divergent selection without geographical isolation from a single founder population, and (iii) speciation involving divergent selection during secondary contact with hybridization. In the context of this third scenario we discuss three alternative mechanisms: the maintenance and strengthening of allopatrically arisen reproductive isolation through classical reinforcement; the persistence of allopatrically arisen phenotypic differentiation in the absence of reproductive isolation; complete collapse of genetic and phenotypic structure into a hybrid swarm from which new incipient species arise in sympatry. Using the speciation mode predictions developed in this review, hybrid swarm and genomically-driven reinforcement appeared the most prevalent in the Coregoninae. Putative cases of sympatric speciation were also identified.

Introduction

Adaptive radiation, the evolution of phenotypic and ecological diversity in a rapidly multiplying lineage (SCHLUTER 2000), has recently received much attention by ecological and evolutionary biologists as a possible major source of functional biological and species diversity (e.g. BERNATCHEZ 2004). North temperate fish occupying young, postglacial environments are one of the best emerging model systems for adaptive radiation research, because several taxa have rapidly generated species and ecological diversity on multiple occasions, providing

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the kind of variation required to test quantitative predictions of speciation and adaptive radiation theory (SCHLUTER 1996).

The subfamily Coregoninae is one of the most phenotypically and ecologically diverse freshwater fish groups in the Northern Hemisphere. It is currently split into three genera, the monotypic, piscivorous genus *Stenodus*, the predominantly benthic-feeding *Prosopium* and the ecologically variable genus *Coregonus*. However genetic evidence places *Stenodus leucichthys* within the genus *Coregonus* (BERNATCHEZ et al. 1991, BODALY et al. 1991, REIST et al. 1998, POLITOV et al. 2004). This subfamily has a largely north temperate distribution. Over the past 700,000 years this region has been severely affected by multiple episodes of glaciation, large areas being repeatedly covered by ice. Coregonine species would have survived in distinct lake and river refugia around the edge of the ice, expanding outwards during the relatively brief interglacials, allowing secondary contact and introgression between the different glacial isolates. The differences in pattern and extent of the advance/retreat cycles of the glacial ice in different geographical areas would create refugial populations of different ages and different histories of isolation and admixture (HEWITT 1996).

Following the latest retreat of the ice around 15,000 years ago, vast areas of unoccupied habitat became available, notably in postglacial lakes and other water bodies left behind. The temporal instability of freshwater interconnections, the cold climate and/or the need for anadromy to colonise, meant that only a limited subset of the preglacial fish fauna could invade these new habitats from their refugia. The resulting lack of competition would have created ecological opportunity for the successful colonists, which has been hypothesised to have led to the formation and/or persistence of genetically weakly-differentiated sympatric taxa in many north temperate fish species, especially within the Salmonidae (TAYLOR 1999). These sympatric forms mainly differ along four axes: (i) diet ranging from zoobenthos to limnetic zooplankton (e.g. BERNATCHEZ et al. 1999), (ii) water depth of feeding niche (e.g. TURGEON et al. 1999), (iii) degree of anadromy (e.g. SHUBIN et al. 1997) and (iv) temporal and spatial location of spawning (e.g. SCHULZ & FREYHOF 2003). The number of morphotypes or incipient species co-existing, varies in number between water systems, within and between evolutionary lineages. Thus coregonine species such as *P. cylindraceum*, *S. leucichthys* and *C. autumnalis* remain largely undifferentiated across their respective ranges, where as other "species" such as *C. artedi*, *C. lavaretus* and *C. albula* have produced diverse sympatric forms and species flocks in many water bodies (NIKOLSKY & RESHETNIKOV 1970, TURGEON & BERNATCHEZ 2003), and should be referred to as species complexes. The ecological and morphological differentiation patterns between sympatric forms are repeated in parallel in multiple water bodies, suggesting the action of natural selection in the generation or maintenance of these taxa. This variety in the number of sibling species, incipient species and intraspecific forms, within the genera of one subfamily, make the Coregoninae a very interesting model system for the study of adaptive radiation and speciation.

In coregonine incipient species groupings, most of the four criteria of adaptive radiation (proposed by SCHLUTER 2000): common ancestry, phenotype-environment correlation, trait utility and rapid speciation; have been inferred to occur, however not all have been strictly tested (BERNATCHEZ 2004). Implicit in this view of adaptive radiation is speciation; the evolution of reproductive isolation between taxa (SCHLUTER 1996), allowing their coexistence in sympatry. In coregonines artificial and natural hybrids are possible between many of the species, at least within the genus *Coregonus*. Natural hybrids have even been reported between *C. clupeaformis* and *S. leucichthys*, and *C. autumnalis* and *S. leucichthys* (ALT 1971).

Temporal persistence of many taxa in sympatry despite the potential for introgression, implies the existence of some type of extrinsic barrier to gene flow between incipient species. However there is evidence that these barriers can break down (TODD & STEDMAN 1989). This dynamic potential for introgression and differentiation makes it difficult to infer mode of speciation and evolutionary process from purely molecular phylogenetic patterns.

The aims of this paper are to review the coregonine literature, to describe the diversity of divergent sympatric incipient species radiations within the subfamily and to ascertain what is known about the primary modes of, and processes involved in species formation in each case.

Methods

Literature search methods

The data for this review was gathered in four different ways. The primary method was to use Web of Science and Google Scholar to find relevant literature, with the following specific search terms: Coregon*, whitefish AND speciation, *Stenodus* OR inconnu, *Prosopium*, cisco*, vendace and lake herring. Following this, the reference sections of papers found, were cherry-picked for relevant material, especially older references. Finally researchers were contacted personally for information or elusive references and, ichthyological journals not covered by the search engines were searched exhaustively by hand. From these references, water bodies, for which multiple sympatric coregonine taxa were described, were recorded with the relevant speciation information. This information is the raw data for the review (supplementary Table A, available on request from the corresponding author).

Genetic tests of alternative speciation scenarios

Genetic tests to discern between speciation in isolation (allopatry) and speciation with gene flow have been developed and include the Wang, Wakeley and Hey (WWH) Test (WANG et al. 1997) and the Linkage Disequilibrium (LD) Test (MACHADO et al. 2002). Available methods to discern between sympatric speciation from a single population and introgression scenarios include phylogenetic tree-based methods such as the Homoplasy Excess Test (SCHLIEWEN & KLEE 2004, SEEHAUSEN 2004, KIDD et al. 2006) and the comparing of divergence times between neutral loci (WU 2001).

At the time of writing, none of these tests had yet to be applied to coregonine population genetic data. In the absence of such tests and yet the existence of a large body of literature documenting coregonine speciation, we here develop a set of predictions using both biogeography and genetics to distinguish different speciation scenarios. For instance genomic and ecological reinforcement scenarios, make explicit biogeographical assumptions about the origins of the sympatric species. If there is no evidence for multiple refugia, equaling or exceeding the number of sympatric species in a system, this would be evidence to refute reinforcement scenarios. Unlike genomic reinforcement, the ecological reinforcement hypothesis predicts that the same phenotype occurring in several lakes should often have the same biogeographic origin, e.g. being of the same glacial refugial lineage. The hybrid swarm hypothesis requires that more than one refugial lineage, or more than one significantly differentiated lineage within a refugial clade be present in a water system, but these can be fewer than the number of species now co-existing in any one system. The single lineage, multiple invasions scenario requires proof that the water system was connected at multiple times to the source population, with intermittent isolation periods having lasted sufficiently long to allow for genetic differentiation.

Speciation models and prediction tests

In this section six different scenarios for the emergence of sympatric coregonine diversity are described and predictions are generated that we hope are testable (summarized in Table 1.).

Table 1. Sets of criteria for distinguishing speciation modes (A–F).

	Phylogenetic (Ph)	**Population Genetics (PG)**	**Biogeography (BG)**	**Morphological/Ecological Differentiation (Mo)**
A. Allopatric Speciation	(1) Sister taxon of each species found outside system. (2) No phylogenetic discordance beyond levels of lineage sorting	(1) Higher genetic differentiation between sympatric taxa, than between sympatric and some allopatric taxa	(1) Distinct multiple refugia equal to or larger than the number of taxa; sympatric taxa found in areas of overlap. (2) Every sympatric species also occurs allopatrically	(1) Similar ecological diversity among allopatric and among sympatric populations unless character displacement occurs in sympatry. (2) Genetic differentiation not necessarily associated with morphological/ ecological differentiation
B. Genomically Driven Reinforcement: An allopatric phase is followed by reinforcement of RI with maintenance of pre-existing genomic differentiation, and possible evolution of ecological character displacement	(1) Sympatric or allopatric forms may be sister taxa, depending on amount of introgression prior to completion of reinforcement. (2) Yet each taxon should be genomically closer to a different allopatric progenitor. (3) Cytogenomic discordance possible, nuclear-nuclear discordance expected.	(1) May have higher genetic differentiation between sympatric taxa, than between sympatric and allopatric taxa.	(1) Distinct multiple refugia for allopatric progenitors, equal/more than the number of sympatric taxa (2) Every sympatric species also occurs allopatrically. (3) sympatric taxa found in areas of overlap	(1) Ecological diversity larger among sympatric than among allopatric populations. (2) Genetic differentiation not necessarily associated with morphological/ecological differentiation. (3) Hybrids have lower intrinsic fitness than individuals of parent taxa.

Table 1. cont.

C. Ecologically Driven Reinforcement: An allopatric phase is followed by reinforcement of RI with maintenance of pre-existing ecological differentiation	(1) Sympatric or allopatric forms may be sister taxa, depending on amount of introgression prior to completion of reinforcement. (2) Cytogenomic discordance possible, nuclear-nuclear discordance expected.	(1) Unlikely to have higher genetic differentiation between sympatric taxa, than between sympatric and allopatric taxa.	(1) Distinct multiple refugia for allopatric progenitors, equal/more than the number of sympatric taxa (2) Every sympatric species also occurs allopatrically. (3) Similar phenotypes in different water bodies belong to the same colonizing lineage. (4) Sympatric taxa found in areas of overlap	(1) Ecological diversity among allopatric populations is larger than or equal to that among sympatric populations. (2) Genetic differentiation not necessarily associated with morphological/ecological differentiation. (3) Hybrids have lower extrinsic fitness than parent taxa. (4) Phenotypic differentiation preceded secondary contact, and thus each sympatric taxon is morphologically closest to an allopatric taxon.
D. Hybrid Swarm Radiation: An allopatric phase is followed by fusion of gene pools, followed by the evolution of new ecological and genomic diversity	(1) Sympatric forms are sister taxa. (2) Cytogenomic discordance possible, nuclear-nuclear discordance expected. (3) Sympatric forms unlikely to be fixed for alternative mtDNA haplotype lineages	(1) Higher genetic differentiation between allopatric taxa, than between sympatric taxa	(1) Sympatric taxa found in areas of overlap between two or more refugia.	(1) Ecological diversity is larger among sympatric than among allopatric populations. (2) Genetic differentiation correlates with morphological/ecological differentiation. (3) Natural selection generated de novo differentiation at non-neutral loci. (4) Parallel divergence in different lakes may be achieved through identical genetic pathways by selection on the same genetic polymorphisms that resulted from admixture

Table 1. cont.

E. Sympatric Speciation from a Single Founder Lineage	(1) Sympatric forms are sister taxa. (2) No cytogenomic discordance. (3) Levels of nuclear-nuclear discordance between neutral and divergently selected sequences exceed those expected by lineage sorting	(1) Higher genetic differentiation between allopatric taxa, than between sympatric taxa	(1) Lack of evidence of more than one refugium in area and/or historic fragmentation of the water system	(1) Genetic differentiation correlates with morphological/ecological differentiation. (2) Natural selection generated de novo differentiation at non-neutral loci. (3) Parallel patterns of divergence expected in different water systems. (4) Parallel divergence may be achieved through different genetic pathways
F. Single Lineage, Multiple Invasion (with or without hybridization)	(1) Sympatric or allopatric forms may be sister taxa, depending on level of RI between sympatric forms. (2) May show cytogenomic and nuclear-nuclear discordance	(1) The final invader should be genomically more similar to the common progenitor	(1) Geological/hydrological evidence that water system has had multiple connections to source, with long isolation between connections. (2) Lack of evidence of more than one refugium	(1) The final invader should be more similar phenotypically to the common progenitor

Modes of speciation have traditionally been arranged hierarchically; with the primary split being between the build up of reproductive isolation in geographic isolation (allopatric speciation) and its development in situ within a single population, with gene flow, under divergent selection (sympatric speciation). Allopatry and sympatry represent the two extremes of geographic isolation in the process of speciation (MAYR 1963, BUSH 1975, GAVRILETS 2004). Intermediate scenarios involve an initial period of genetic divergence in allopatry, which is followed by secondary contact with incomplete reproductive isolation and varying levels of introgression. The level of gene flow and allopatric isolation is represented in the order in which we present the alternative speciation modes.

Allopatric speciation

A purely allopatric speciation scenario requires divergence of ancestral populations in geographical isolation, followed by independent invasions of the descendent forms into a lake (or a river system). Preexisting reproductive isolation prevents admixture upon secondary contact. As the newly sympatric species have diverged elsewhere, each will have left its closest relatives outside the zone of secondary contact.

Genomically driven reinforcement

Classical reinforcement, as a concept first developed by DOBZHANSKY (1940), can occur if sets of genes from different parents, that come together in the hybrid offspring, reduce the intrinsic viability or fertility of hybrids through epistasis. Hybridization would then be selected against due to intrinsic factors (SERVEDIO & NOOR 2003). This process presupposes some level of post-zygotic reproductive isolation has built up in allopatry, before secondary contact. The process is most likely to operate at moderate levels of hybridization, so that the strength of selection against the production of hybrids can counteract gene flow breaking up co-adapted differences in mate choice between the populations (NOSIL et al. 2003). Depending on the speed of reinforcement and concomitantly the amount of introgression, sympatric populations may or may not appear as sister taxa on phylogenetic trees and there may be phylogenetic discordance between different nuclear genes and/or between nuclear and cytoplasmic factors (cytonuclear discordance). Fixation of alternative haplotypes, despite nuclear evidence for introgression, may be taken as an indication of reinforcement, because the fixation of different mitochondrial haplotypes in different sympatric taxa is unlikely in scenarios with large amounts of gene flow at neutral loci.

Ecologically driven reinforcement

The second introgression scenario is similar to a scenario postulated by SVÄRDSON (1957, 1998), specifically to explain sympatric coregonine diversity. During a past period of isolation, now-sympatric populations have differentiated in phenotype and ecological niche, which generates some level of extrinsic (ecology-based) post-zygotic and possibly pre-zygotic isolation. Introgression and ecological selection against hybrids, which fall between the parental niches, might reinforce the development of pre-zygotic isolation. Like in genomic reinforcement the rate at which pre-mating isolation is reinforced will determine the patterns of relatedness seen in phylogenetic and population genetic tests.

Hybrid swarm radiation

Hybridization can be a source of heritable variation and novel phenotypes, which may be selected for in new environments (LEWONTIN & BIRCH 1966). Building on this, a hybrid swarm adaptive radiation model was developed, in the context of the ecological theory of adaptive radiation (SEEHAUSEN 2004). Here, genetic differentiation, which had built up in geographic isolation is lost upon secondary contact, generating a fused population with large genetic variance; a hybrid swarm. Release from selection due to the under-utilized habitats and lack of competitors in the postglacial aquatic environments may promote such hybridization on colonization, as hybrids would not initially experience any ecological fitness reduction compared to the parental types. The elevated genetic variation in the resulting population and the new adaptive trait combinations in some hybrid genotypes, may facilitate the exploitation of different under-utilized ecological niches by different genotypes and provide material for directional selection to work on. Transgressive segregation, whereby phenotypic traits are generated that exceed the range in parental values, has been shown to occur at a relatively high frequency (35% of traits studied) in animal quantitative-genetics hybridization studies (RIESEBERG et al. 1999), adding support to the idea of hybridization as a source of novel variation. At an early stage of the radiation, the hybrid swarm may form a syngameon, with incipient species maintained by ecological selection despite considerable gene flow. Gene flow would become less over time as niches are filled, pre-mating isolation being ecologically reinforced as hybrids more often fall between peaks in the adaptive landscape and are selected against. The hybrid swarm therefore gives rise to an adaptive radiation in sympatry through sympatric ecological speciation, but starting from a genetically enriched population. Taxa resulting from hybrid swarm speciation within a water body, will be each other's sister species. The hybrid origin of the taxa and the fact that only a few loci under divergent selection during ecological speciation will experience reduced gene flow, mean that nuclear-nuclear discordance is expected. Additionally there may be cytonuclear discordance.

Sympatric speciation from a single founder lineage

In sympatric speciation, divergent natural or sexual selection causes the split of a single founder population into sympatric differentiated forms, reproductive isolation among which builds up gradually in situ. Incipient species that have resulted from sympatric speciation from a single population will tend to cluster on phylogenetic trees as each other's closest relatives. Like in allopatric speciation there will be little cytogenomic and nuclear-nuclear discordance among neutral loci. However unlike among allopatrically evolved forms, divergence with gene flow in sympatry, predicts discordance between neutral and divergently selected loci in the distribution of alleles between species. Alleles that are under positive selection in one incipient species may be selected against in the niche of another incipient species, and such a locus will therefore experience reduced gene flow between incipient species compared to neutral loci (MACHADO et al. 2002). This leads to discordance at different nuclear loci, with neutral loci giving more recent divergence times (if any) than those loci under divergent selection between the nascent populations.

Single lineage, multiple invasions scenario

Perhaps the most difficult speciation scenario to prove is single lineage, multiple invasions, which can be seen as a special case of the scenarios detailed above. Here the colonisation of a lake or river system by one ancestral lineage is followed by a period of geographic isolation from the source populations, before another invasion from the same source population into the same water body takes place. The now sympatric populations may remain reproductively isolated (allopatric speciation) or follow any of the introgression scenarios. The most well known putative examples of multiple invasions from the same lineage, are the lacustrine sympatric stickleback species pairs on islands in the Strait of Georgia, British Columbia (TAYLOR & MCPHAIL 2000). In this scenario phylogenetic trees could show sympatric taxa either as sister species or the second invader as sister group to the source population of both, depending on the level of introgression and time spent in isolation. Whether there is any nuclear-nuclear or cytonuclear discordance will depend on the length of time between invasions and the amount of gene flow between the sympatric taxa. In allopatric speciation and both reinforcement scenarios, but not in the hybrid swarm scenario, the taxon resulting from the last invasion will be genetically and possibly phenotypically closer to the common progenitor stock, than the taxon resulting from the first invasion.

Table 2. Speciation criteria evidence for individual radiations (important negative evidence is shown in italics).

Species Complex	Available Evidence[1]	Water System	No. of Sympatric taxa in system	A. Complete Speciation in Allopatry	B. Genomically Driven Reinforcement	C. Ecologically Driven Reinforcement	D. Hybrid Swarm Radiation	E. (One founder lineage) Sympatric	F. Single Lineage, Multiple Invasions	Most Likely Speciation Scenario	References
***Prosopium coulteri* complex**	Mo	Lakes Aleknagik, Naknek & Chignik, Alaska	2–3	Forms similar in meristic counts to taxa found in allopatry	Two or three forms similar in meristic counts to different taxa found in allopatry. Greater range in meristic counts in sympatry, may show an increase in ecological diversity. Biogeographic evidence for more refugia than sympatric taxa	Biogeographic evidence for more refugia than sympatric taxa	Two forms similar in meristic counts to populations found in allopatry, third form may have arisen through hybridization. Greater range in meristic counts in sympatry may show an increase in ecological diversity	No evidence	No evidence	Any	McCart (1970), Lindsey & Franzin (1972), Bird & Roberson (1979)
***Prosopium* sp.**	Ph Mt, Ph Nuc, PG, Mo	Bear Lake, Utah	3	Surrounding hydrology suggests repeated fragmentation of lake systems into refugia. No cytogenomic discordance. Morphologically similar fossils found in allopatry	Some of the sympatric taxa resemble fossils found in allopatry	Some of the sympatric taxa resemble fossils found in allopatry	Sympatric taxa are sister species on nuclear population tree. Genetic differentiation low. Parallel divergence in fossil allopatric taxa?	Sympatric taxa are sister species on nuclear population tree. No cytogenomic discordance. Genetic differentiation low. Parallel divergence in fossil allopatric taxa?	Morphologically similar fossils found in allopatry	Sympatric or Introgression Scenario	Smith & Todd (1984), Bernatchez et al. (1991), Vuorinen et al. (1998)
Coregonus	Ph Mt, Ph	Lake Superior,	4	No evidence	Sympatric taxa group closely on nuclear tree. Two glacial mtDNA lineages in system. Possibly some hybrid inviability	Sympatric taxa form monophyletic	Sympatric taxa group closely, but two refugial lineages present with high levels of admixture. Evidence of no more	No evidence	No evidence	Hybrid swarm spe-	Brown JR (1970), Turgeon et al. (1999),Turgeon & Bernatchez

Table 2. cont.

***artedi* complex**	Nuc, PG, BG, Mo	Laurentian Great lakes			as highly skewed sex ratios in favour of homogametic sex have been observed.	clade, low genetic differentiation.	than two refugial races in lake systems, yet four taxa described in lake system.			ciation most likely	(2001a, b), Turgeon & Bernatchez (2003)
	Ph Mt, Ph Nuc, PG, BG, Mo	Lake Nipigon, Laurentian Great Lakes	4	No evidence	Sympatric taxa are sister species on nuclear tree. Two glacial mtDNA lineages in system. Possibly some hybrid inviability as highly skewed sex ratios in favour of homogametic sex have been observed.	Sympatric taxa form monophyletic clade. Non-significant genetic differentiation between some described taxa.	Sympatric taxa form monophyletic clade, but two refugial lineages present with high levels of admixture. Evidence of no more than two refugial races in lake systems, yet four taxa described in lake system.	No evidence	No evidence	Hybrid swarm speciation most likely	Brown Jr (1970), Turgeon et al. (1999), Turgeon & Bernatchez (2001a, b), Turgeon & Bernatchez (2003)
	Ph Mt, Ph Nuc, PG, BG, Mo	La Grande Reservoir, Quebec	2	No evidence	Sympatric taxa are sister species on nuclear tree. Two glacial mtDNA lineages in system. Possibly some hybrid inviability as highly skewed sex ratios in favour of homogametic sex have been observed with the same introgressing lineages in other lakes. Large form also found in allopatry	Sympatric taxa form nuclear monophyletic clade. Two refugial haplotype races present, equal to the number of sympatric taxa. Low genetic differentiation between forms. Large form also found in allopatry	Sympatric taxa form nuclear monophyletic clade but two refugial mtDNA lineages present with high levels of admixture.	No evidence	No evidence	Reinforcement after massive introgression or hybrid swarm radiation	Brown Jr (1970), Turgeon et al. (1999), Turgeon & Bernatchez (2001a, b), Turgeon & Bernatchez (2003)
					Sympatric taxa are sister species on nuclear tree. Two glacial mtDNA lineages in system. Possibly some hybrid inviability	Sympatric taxa form nuclear monophyletic clade. Two refugial haplotype races present,	Sympatric taxa form nuclear monophyletic clade but two refugial mtDNA lineages			Reinforcement after massive	Brown JR (1970), Turgeon et al. (1999), Turgeon &

Table 2. cont.

	Ph Mt, Ph Nuc, PG, BG, Mo	Lake Cormorant, Manitoba	2?	No evidence	as highly skewed sex ratios in favour of homogametic sex have been observed with the same introgressing lineages in other lakes. Dwarf form also found in allopatry	equal to the number of sympatric taxa. Non-significant genetic differentiation between forms. Dwarf form found also in allopatry	present with high levels of admixture. Heterozygotic deficiency in both morphotypes suggests possible existence of more sympatric taxa	No evidence	No evidence	introgression or hybrid swarm radiation	Bernatchez (2001a, b), Turgeon & Bernatchez (2003)
	Ph Mt, Ph Nuc, PG, BG, Mo	Barrow Lake, Alberta	2	No evidence	Sympatric taxa are sister species on nuclear tree. Two glacial mtDNA lineages in system with possibly some hybrid inviability as highly skewed sex ratios in favour of homogametic sex have been observed with the same introgressing lineages in other lakes.	Sympatric taxa form nuclear monophyletic clade. Two refugial haplotype races present, equal to the number of sympatric taxa. Low genetic differentiation between forms.	Sympatric taxa form nuclear monophyletic clade but two refugial mtDNA lineages present with high levels of admixture. Low genetic differentiation between forms.	No evidence	No evidence	Reinforcement after massive introgression or hybrid swarm radiation	Brown Jr (1970), Turgeon et al. (1999), Turgeon & Bernatchez (2001a, b), Turgeon & Bernatchez (2003)
***Coregonus clupeaformis* complex**	Ph Mt, Ph Nuc, PG, BG, Mo	Cliff Lake, St John River Drainage, Maine	2	No evidence	Sympatric forms fixed for different refugial mt haplotypes. Embryonic mortality rates in *C. clupeaformis* refugial crosses (atlantic versus arcadian) found to give a selection coefficient of 0.24–0.47.	Sympatric forms fixed for different refugial mt haplotypes. *Same phenotypes in different lakes are fixed for different refugial mt haplotypes. No morphological traits consistently differentiate allopatric populations from different ecological races.* Yet at putative loci under ecological selec-	Two glacial refugial lineages present. At putative loci under selection, morphs are sister taxa to same phenotypes from other lakes	No evidence	No evidence	Genomic reinforcement most likely	Bernatchez & Dodson (1990), Chouinard et al. (1996), Pigeon et al. (1997), Lu & Bernatchez (1998), Bernatchez et al. (1999), Campell And Bernatchez (2004)

Table 2. cont.

					tion, morphs are sister taxa to same phenotypes from other lakes.					
Ph Mt, Ph Nuc, PG, BG, Mo	East Lake, St John River Drainage, Quebec	2	No evidence	No evidence	At putative loci under ecological selection, morphs are sister taxa to same phenotypes from other lakes.	At putative loci under selection, morphs are sister taxa to same phenotypes from other lakes	Only one refugial mt haplotype group found. Little evidence of admixture at neutral nuclear markers. Sympatric forms are monophyletic in mt and neutral nuclear genes	Only one refugial lineage present	Sympatric speciation from single lineage most likely	Bernatchez & Dodson (1990), Pigeon et al. (1997), Lu & Bernatchez (1999), Bernatchez et al. (1999), Lu et al. (2001), Campbell and Bernatchez (2004)
Ph Mt, Ph Nuc, PG, BG, Mo	Indian Pond, St John River Drainage, Maine	2	No evidence	Nuclear DNA shows admixture of two refugial lineages in both forms. Embryonic mortality rates in *C. clupeaformis* refugial (atlantic versus arcadian) crosses found to give a selection co-efficient of 0.24–0.47.	*The same phenotypes in different lakes are fixed for different refugial mt haplotypes. No morphological traits consistently differentiate allopatric populations from different ecological races.* Yet at putative loci under ecological selection, morphs are sister taxa to same phenotypes from other lakes.	Nuclear DNA shows admixture of another refugial lineage in both forms. At putative loci under selection, morphs are sister taxa to same phenotypes from other lakes	No evidence	No evidence	Genomically driven reinforcement or speciation from hybrid swarm	Bernatchez & Dodson (1990), Pigeon et al. (1997), Lu & Bernatchez (1998), Lu & Bernatchez (1999), Lu et al. (2001), Cambell and Bernatchez (2004)

Table 2. cont.

Ph Mt, Ph Nuc, BG	Spider Lake, St John River Drainage, Maine	3	No evidence	Nuclear DNA shows admixture of two refugial lineages in both extant forms. Embryonic mortality rates in *C. clupeaformis* refugial (atlantic versus arcadian) crosses found to give a selection coefficient of 0.24–0.47.	*The same phenotypes in different lakes are fixed for different refugial mt haplotypes. No morphological traits consistently differentiate allopatric populations from different ecological races.*	Two glacial refugial lineages present, evidence of introgression in mt DNA. Number of forms described higher than the number of refugial lineages present	No evidence	No evidence	Genomically driven reinforcement or speciation from hybrid swarm	Fenderson (1964), Bernatchez & Dodson (1990), Lu & Bernatchez (1998), Lu et al. (2001)
Ph Mt, Ph Nuc, PG, BG, Mo	Témiscouata Lake, St John River Drainage, Quebec	2	No evidence	Nuclear DNA shows admixture of two refugial lineages in both forms. Embryonic mortality rates in *C. clupeaformis* refugial (atlantic versus arcadian) crosses found to give a selection co-efficient of 0.24–0.47.	*The same phenotypes in different lakes are fixed for different refugial mt haplotypes. No morphological traits consistently differentiate allopatric populations from different ecological races.*	Nuclear DNA shows high admixture of two refugial lineages in both forms	No evidence	No evidence	Genomically driven reinforcement or speciation from hybrid swarm	Bernatchez & Dodson (1990), Pigeon et al. (1997), Lu & Bernatchez (1998), Lu & Bernatchez (1999), Bernatchez et al. (1999), Lu et al. (2001)
Ph Mt, Ph Nuc, PG, BG, Mo	Webster Lake, St John River Drainage, Maine	2	No evidence	Nuclear DNA shows admixture of two refugial lineages in both forms, though sympatric forms nearly fixed for different refugial mt haplotypes and F_{st} is high. Embryonic mortality rates in *C. clupeaformis* refugial (atlantic versus arcadian) crosses found to give a	*The same phenotypes in different lakes are fixed for different refugial mt haplotypes. No morphological traits consistently differentiate allopatric populations from different ecological races.* Yet at putative loci under ecological selection, morphs are sister taxa to same	Nuclear DNA shows admixture of two refugial lineages in both forms. At putative loci under selection, morphs are sister taxa to same phenotypes from other lakes	No evidence	No evidence	Genomic reinforcement most likely	Bernatchez & Dodson (1990), Pigeon et al. (1997), Lu & Bernatchez (1998), Lu & Bernatchez (1999), Bernatchez et al. (1999), Lu et al. (2001), Cam-bell and

Table 2. cont.

				selection co-efficient of 0.24–0.47.	phenotypes from other lakes.					Bernatchez (2004)
Mt & Nuc	Lake Musquacook II, Allegash Basin, Maine	2	No evidence	Mt DNA shows admixture of two refugial lineages in dwarf form. Embryonic mortality rates in *C. clupeaformis* refugial (atlantic versus arcadian) crosses found to give a selection co-efficient of 0.24–0.47.	*The same phenotypes in different lakes are fixed for different refugial mt haplotypes. No morphological traits consistently differentiate allopatric populations from different refugial races.*	Mt DNA shows admixture of two refugial lineages in dwarf form	No evidence	No evidence	Genomically driven reinforcement or speciation from hybrid swarm	Kirkpatrick & Selander (1979), Bernatchez & Dodson (1990), Lu & Bernatchez (1998)
Ph Mt & Mo	Lake Caniapiscau, Quebec	2	No evidence	No evidence	No Evidence	No evidence	Only one refugial lineage in system. Dwarf and normal forms fixed for the same mitochondrial haplotype group	No evidence	Sympatric speciation from single lineage or hybrid swarm	Bernatchez & Dodson (1990), Pigeon et al. (1997), Bernatchez et al. (1999), Lu et al. (2001)
Ph Mt, PG & Mo	Lake Como, Ontario	2	No evidence	Nuclear DNA shows admixture of two refugial lineages in both forms. Embryonic mortality rates in *C. clupeaformis* refugial (atlantic versus arcadian) crosses found to give a selection co-efficient of 0.24–0.47.	*The same phenotypes in different lakes are fixed for different refugial mt haplotypes. No morphological traits consistently differentiate allopatric populations from different refugial races.*	Nuclear DNA shows admixture of two refugial lineages in both forms.	No evidence	No evidence	Genomically driven reinforcement or speciation from hybrid swarm	Bernatchez & Dodson (1990), Vuorinen et al. (1993), Lu & Bernatchez (1998), Bernatchez et al. (1999), Lu et al. (2001)
				Sympatric forms fixed for different mitochondrial						

Table 2. cont.

Ph Mt, Ph Nuc Mo	Dezadeash Lake, Yukon	2	Sympatric forms not monophyletic in mt DNA	haplotype groups within the same postglacial lineage. High F_{st} values for mt DNA between morphs suggest low gene flow. Cytogenomic discordance: nuclear genes suggest sympatric taxa are sister taxa, however mt data places allopatric populations within the same refugial lineage closer to the different sympatric taxa.	*The same phenotypes in different lakes are fixed for different refugial mt haplotypes. No morphological traits consistently differentiate allopatric normal morphs from different refugial races.*	No evidence	No evidence	Cytogenomic discordance: nuclear DNA suggest sympatric taxa sister taxa, however mt data places allopatric populations within the same refugial lineage closer	Genomically driven reinforcement or speciation from hybrid swarm (Probably single lineage multiple invasions)	Bernatchez & Dodson (1990), Bernatchez et al. (1996), Bernatchez et al. (1999), Lu et al. (2001)
Ph Mt & Mo	Little Teslin Lake, Yukon	2	No evidence	Nuclear DNA shows admixture of two refugial lineages in both forms, though sympatric forms nearly fixed for different refugial mt haplotypes and F_{st} is high. Embryonic mortality rates in *C. clupeaformis* refugial (atlantic versus arcadian) crosses found to give a selection co-efficient of 0.24–0.47	*The same phenotypes in different lakes are fixed for different refugial mt haplotypes. No morphological traits consistently differentiate allopatric normal morphs from different refugial races.*	Cytogenomic discordance: nuclear genes suggest sympatric taxa are sister taxa, however mt data places allopatric populations closer to the different sympatric taxa.	No evidence	No evidence	Genomically driven reinforcement or speciation from hybrid swarm	Bernatchez & Dodson (1990), Bernatchez et al. (1996), Bernatchez et al. (1999), Lu et al. (2001)
Ph Mt & Mo	Squanga Lake,	2	No evidence	Two glacial refugial lineages present. Embryonic mortality rates in *C. clupeaformis*	*The same phenotypes in different lakes are fixed for different refugial mt haplotypes. No morphological*	Two glacial refugial lineages present. Low F_{st} values	No evidence	No evidence	Genomically driven reinforcement or	Bernatchez & Dodson (1990), Bernatchez et al. (1996), Lu

Table 2. cont.

		Yukon			refugial (atlantic versus arcadian) crosses found to give a selection coefficient of 0.24–0.47.	*traits consistently differentiate allopatric normal morphs from different refugial races.*	and presence of hybrid individuals.			speciation from hybrid swarm	& Bernatchez (1998), Bernatchez et al. (1999), Lu et al. (2001)
***Coregonus lavaretus* complex**	Ph Mt, Ph Nuc, PG, Mo	Lake Brienz – Lake Thun, Switzerland	3/5–6	Two different nuclear phylogenetic lineages in system, even though only one refugial mt haplotype fixed in taxa studied. *Non-monophyletic lineage may be due to stocking*	Two different nuclear phylogenetic lineages in system, even though only one refugial mt haplotype fixed in taxa studied.	Lake flock diphyletic at neutral nuclear markers. Several taxa resemble morphologically similar eco-morphs in other lake systems.	Four of five sympatric taxa within lake system form a monophyletic clade at neutral nuclear markers. There are more species in this lake system than in all others nearby.	Four of five sympatric taxa within lake system form a monophyletic clade at neutral nuclear markers. Only one mt refugial lineage found in taxa studied. Non-monophyletic lineage may be due to stocking	Lake flock diphyletic at neutral nuclear markers within same refugial mt haplotype group. Non-monophyletic lineage may be due to stocking	Dual speciation scenario. Sympatric or hybrid swarm speciation in one of the two nuclear phylogenetic lineages. Allopatric speciation with or without introgression in the other. Unless divergent lineage is due to stocking.	Bernatchez & Dodson (1994), Douglas et al. (1999), Douglas & Brunner (2002), Douglas et al. (2005)
	Ph Mt, Ph Nuc, PG, Mo	Lake Konstanz, Austria / Switzerland / Germany	6?	No evidence	Two refugial mt haplotype groups present.	Low genetic divergence and admixture between two refugial mt lineages in three forms. Several taxa resemble eco-morphs in other lake systems.	Cytogenomic discordance: Two refugial mt haplotype groups present but studied parts of lake flock monophyletic at neutral nuclear markers. Low genetic divergence and admixture between mt lineages in three forms. There are more species in this lake system than in any other nearby.	No evidence, unless stocking and secondary hybridization is the cause of two mt lineages being present in several species	No evidence	Hybrid swarm speciation most likely	Bernatchez & Dodson (1994), Douglas et al. (1999), Douglas & Brunner (2002), Douglas et al. (2005), Østbye et al. (2005b)

Table 2. cont.

Ph Nuc, Ph Mt, PG, Mo	Lake Neuchâtel – Biel, Switzerland	2/2	No evidence	Two refugial mt haplotype groups present	Low genetic divergence and admixture between two refugial mt lineages in system. Taxa resemble ecomorphs from other lake systems	Cytogenomic discordance: Two refugial mt haplotype groups present but studied parts of lake flock monophyletic at neutral nuclear markers. Low genetic divergence and admixture between mt lineages in two forms.	No evidence, unless stocking and secondary hybridization is the cause of two mt lineages being present in several species.	No evidence	Speciation from reinforcement with high introgession or hybrid swarm. Sympatric speciation if stocking and secondary hybridization is the cause of two mt lineages being present in two species	Douglas et al. (1999), Douglas et al. (2005), Østbye et al. (2005b)
Ph Nuc, Ph Mt, PG, Mo	Lake Lucerne (Urn), Switzerland	3–4	Two different nuclear phylogenetic lineages in system. Two refugial mt lineages in system. *Non-monophyletic lineage may be due to stocking*	Two different nuclear phylogenetic lineages in system. Two refugial mt lineages in system.	Lake flock diphyletic at neutral nuclear markers. Low genetic divergence and admixture between two refugial mt lineages in system. Taxa resemble ecomorphs from other lake systems.	Cytogenomic discordance: Two refugial mt haplotype groups present, but studied parts of lake flock monophyletic at neutral nuclear markers in one of the colonizing nuclear phylogenetic lineages. Low genetic divergence and presence of rarer lineage in only one form at a low frequency, suggest high levels of admixture. There are more species in this lake system than in any other in geographic proximity.	No evidence, unless stocking and secondary hybridization is the cause of two refugial mt and two phlyogenetic nuclear lineages being present in the system.	Lake flock diphyletic at neutral nuclear markers. Non-monophyletic lineage may be due to stocking	Dual speciation scenario. Speciation from hybrid swarm in one of the nuclear phylogenetic lineages. Allopatric speciation with or without introgression in the other. Unless second mt and nuclear lineages present due to post-divergence stocking.	Douglas et al. (1999), Douglas & Brunner (2002), Douglas et al. (2005), Østbye et al. (2005b)

Table 2. cont.

Ph Nuc, Ph Mt, PG, Mo	Lake Zurich-Walen, Switzerland	3–4?/3–4?	No evidence	Two refugial mt haplotype groups present	Studied sympatric species monophyletic at neutral nuclear markers. Low genetic divergence and admixture between two refugial mt lineages in system. Taxa resemble ecomorphs from other lake systems.	Cytogenomic discordance: Two refugial mt haplotype groups present but studied parts of lake flock monophyletic at neutral nuclear markers. Low genetic divergence and presence of rarer lineage in only one form, at a low frequency, in one of the lakes (Walen). There also may be more taxa in this system (four) than refugial mt lineages (two)	Only one mt lineage found in Lake Zürich. Stocking and secondary hybridization may be the cause of two mt lineages being present at low frequencies in Lake Walen	No evidence	Speciation from hybrid swarm or sympatric speciation if stocking and secondary hybridization is the cause of two mt lineages being present in one of the lakes	Douglas et al. (1999), Douglas et al. (2005), Østbye et al. (2005b)
Ph Nuc	Lake Saimaa, Finland	4?	No evidence	No evidence	Low genetic differentiation between forms. Similar phenotypes found in other water systems.	Low genetic differentiation between forms. Similar phenotypes found in other water systems.	Low genetic differentiation between forms. Similar phenotypes found in other water systems.	No evidence	Sympatric speciation from single lineage or from hybrid swarm	Heinonen (1988)
Ph Nuc,					Q_{st}-F_{st} suggest traits related to trophic niche under selection. Most morphs have relatively low genetic differentiation and cluster together. No report of	No cytogenomic discordance. Q_{st}-F_{st} suggest traits related to trophic niche under selection. Most morphs have relatively low	Only one mt lineage found, most morphs have relatively low genetic differentiation and cluster together on nuclear data. Q_{st}-F_{st}	Assignment of one sympatric taxon closer to different allopatric source populations within the	Possibly one case of multiple invasion from the same mt clonal group with possi-	Naesje et al. (2004),

Table 2. cont.

Ph Mt, PG, Mo	Lake Femund, Norway	4	No evidence	No evidence	hybridization. Sympatric taxa generally morphologically resembling same ecotypes in other lake systems.	genetic differentiation and cluster together. Sympatric taxa generally morphologically resembling same ecotypes in other lake systems.	suggest traits related to trophic niche under selection. Sympatric taxa generally morphologically resembling same ecotypes in other lake systems.	same mt lineage. Relatively high genetic differentiation between "bay" morph and other sympatric taxa	ble introgression for one of the four morphs, plus sympatric radiation within the other lineage	Østbye et al. (2005a, b)
Ph Nuc, Ph Mt	Lake Isteren, Norway	2	No evidence	Two morphs cluster closer to nearby allopatric populations, than each other.	Two morphs cluster closer to nearby allopatric populations, than each other. Low genetic differentiation between two morphs	Low genetic differentiation between two morphs	Only one mt lineage present	Low genetic differentiation between two morphs, but cluster closer to nearby allopatric populations in microsat PCA plots, than to each other.	Sympatric speciation or multiple invasion within the same mt clonal group	Østbye et al. (2005a, b)
Ph Mt	Lake Mjøsa, Norway	2	No evidence	Two refugial mt haplotype groups present	Two refugial mt haplotype groups present	Two refugial mt haplotype groups present.	No evidence	No evidence	Introgression Scenario	Østbye et al. (2005b)
Ph Mt	Lake Sperillen, Norway	3	No evidence	Two refugial mt haplotype groups present in two of the forms	Two refugial mt haplotype groups present in two of the forms. Sympatric taxa generally morphologically resembling same ecotypes in other lake systems	Two refugial mt haplotype groups present in two of the forms. More sympatric taxa than the number of refugial groupings present in the system.	No evidence	No evidence	Introgression Scenario	Østbye et al. (2005b)

Table 2. cont.

	Ph Nuc, Ph Mt	Lake Ladoga, Russia	7?	No evidence	Two refugial mt haplotype groups present	Two refugial mt haplotype groups present. *Many sympatric taxa are morphologically similar.*	Sympatric taxa within a lake system are sister taxa at allozyme loci. Two refugial mt haplotype groups are present. There are more species in this lake system than in all others nearby	No evidence	No evidence	Hybrid swarm speciation most likely	Sendek (2004), Østbye et al. (2005b)
	Ph Mt, Ph Nuc	Lake Baikal, Russia	3	No evidence	No evidence	No evidence	Sister taxa are sympatric. Concordance between mitochondria and most nuclear markers. Low genetic differentiation. Evidence of hybridization between taxa.	Sister taxa are sympatric. Concordance between mitochondria and most nuclear markers. Low genetic differentiation.	No evidence	Sympatric speciation from single lineage or from hybrid swarm	Politov et al. (2000), Sukhanova et al. (2002, 2004)
Coregonus *migratorius* sp.	Ph Mt, Mo	Lake Baikal, Russia	3?	No evidence	Nuclear-nuclear discordance, with some allozyme loci grouping the omul with *C. autumnalis*. Evidence of hybridization with sympatric *C. lavaretus pidschian*	Nuclear-nuclear discordance, with some allozyme loci grouping the omul with *C. autumnalis*. Evidence of hybridization with sympatric *C. lavaretus pidschian*	Nuclear-nuclear discordance, with some allozyme loci grouping the omul with *C. autumnalis*. Evidence of hybridization with sympatric *C. lavaretus pidschian*. Sympatric taxa group together, low genetic divergence	Sympatric taxa group together, low genetic divergence	No evidence	Sympatric speciation from single lineage or from hybrid swarm	Smirnov (1969), Sukhanova et al. (1996), Brontet al. (1999), Politov et al. (2000), Burnham-Curtis et al. (2002), Politov et al. (2002), Sukhanova et al. (2004)

Table 2. cont.

Coregonus *albula* complex	PG, Ph Mt, Mo	Lake Breiter Luzin, Germany	2	No evidence	No evidence	Sympatric taxa generally morphologically resembling same ecotypes in other lake systems	Lower genetic distance between sympatric taxa than taxa in allopatry. Parallel occurrence of forms in other water systems	Lower genetic distance between sympatric taxa than taxa in allopatry. Parallel occurrence of forms in other water systems	No evidence	Sympatric or Introgression Scenario	Schultz et al. (2006)
	PG, Ph Mt, Mo	Lake Stechlin, Germany	2	No evidence	No evidence	Sympatric taxa generally morphologically resembling same ecotypes in other lake systems	Lower genetic distance between sympatric taxa than taxa in allopatry. Parallel occurrence of forms in other water systems	Lower genetic distance between sympatric taxa than taxa in allopatry. Parallel occurrence of forms in other water systems	No evidence	Sympatric or Introgression Scenario	Schultz & Freyhof (2003), Schultz et al. (2006)
	Ph Nuc	Lake Kajoonjärvi, Finland	2	No evidence	No evidence	Sympatric taxa generally morphologically resembling same ecotypes in other lake systems	Sympatric taxa within a lake system are sister taxa at allozyme loci, low genetic differentiation. Sympatric taxa generally morphologically resembling same ecotypes in other lake systems	Sympatric taxa within a lake system are sister taxa at allozyme loci, low genetic differentiation. Parallel occurrence of forms in other water systems	No evidence	Sympatric or Introgression Scenario	Vuorinen et al. (1981)

Table 2. cont.

Ph Nuc, Mo	Lake Sokojärvi, Finland	2	No evidence	No evidence	Sympatric taxa generally morphologically resembling same ecotypes in other lake systems	Sympatric taxa within a lake system are sister taxa at allozyme loci, low genetic differentiation. Sympatric taxa generally morphologically resembling same ecotypes in other lake systems	Sympatric taxa within a lake system are sister taxa at allozyme loci, low genetic differentiation. Parallel occurrence of forms in other water systems	No evidence	Sympatric or Introgression Scenario	Svärdson (1988)
Ph Nuc	Lake Ladoga, Russia	2?	No evidence	No evidence	Sympatric taxa generally morphologically resembling same ecotypes in other lake systems	Sympatric taxa within a lake system are sister taxa at allozyme loci, low genetic differentiation. Sympatric taxa generally morphologically resembling same ecotypes in other lake systems	Sympatric taxa within a lake system are sister taxa at allozyme loci, low genetic differentiation. Parallel occurrence of forms in other water systems	No evidence	Sympatric or Introgression Scenario	Sendek (2002)

[1] Refers to the types of speciation evidence criteria (described in Table 1.) known for that specific water system. Ph Nuc = Phylogenetic nuclear, Ph Mt = Phylogenetic mitochondrial, PG = Population genetics, BG = Biogeography, Mo = Morphological/Ecological differentiation.

Table 3. Summary of radiations where one mode of speciation could be singled out as most likely (A–F).

Speciation Scenario	Instances where Specific Scenario Implicated	Taxon	Lake System (number of incipient species)	References
A. Allopatric	0			
B. Genomic Reinforcement	2	*C. clupeaformis*	Cliff Lake (2) Webster Lake (2)	Lu et al. (2001) Pigeon et al. (1997)
C. Ecological Reinforcement	0	*C. artedi*	Lake Superior (4) Lake Nipigon (4)	Turgeon & Bernatchez (2003)
D. Hybrid Swarm Radiation	4	*C. lavaretus*	Lake Ladoga (7?)	Sendek (2004), Østbye et al. (2005b)
			Lake Konstanz (6)	Douglas & Brunner (2002), Østbye et al. (2005b)
E. Sympatric	1	*C. clupeaformis*	East Lake (2)	Lu et al. (2001)
F. Single Lineage, Multiple Invasions	0			

Results

In this study the available evidence extracted from the reviewed literature was used to test predictions of alternative speciation modes in individual coregonine radiations in specific water systems; this evidence is summarized in Table 2. The prevalence of each of these six specific modes (A–F) across the Coregoninae, implicated by the predictions in Table 1, is represented in Table 3. Where the mode of divergence cannot be narrowed down to one of the six speciation scenarios, the smallest possible composite of likely modes for each radiation are presented in Table 4. Fig. 1 shows the overall prevalence of each speciation scenario in the reviewed coregonine literature.

Out of over 200 individual sympatric coregonine radiations mined from the literature, 41 had the required evidence to test the speciation mode predictions developed. In seven of these 41 radiations, the most likely speciation scenario could be singled out. *Coregonus clupeaformis* species pairs in Cliff and Webster lakes are fixed or almost fixed for alternative mitochondrial haplotype lineages and display relatively large genetic differentiation between forms making genomically driven reinforcement the most likely scenario. Ecologically driven reinforcement can be ruled out by the fact that eco-morphological forms in *C. clupeaformis* are not specific to refugial lineages (Lu et al. 2001). The East Lake species pair of *C. clupeaformis* forms a monophyletic clade in both mitochondrial and nuclear phylogenies and shows no sign of genetic admixture from other glacial lineages, largely ruling out all modes of speciation, other than sympatric speciation from a single lineage (Lu et al. 2001). The number of described sympatric forms (four) in the Lakes Superior and Nipigon *C. artedi* flocks (Todd & Smith 1992, Turgeon et al. 1999), is higher than the known number of glacial lineages (two) that have extensively admixed in these lakes, ruling out reinforcement and making the

Table 4. Summary of radiations for which more than one mode of speciation appears equally likely.

Speciation Scenario Subsets	Instances where Specific Subsets of Specific Scenario Implicated	Taxon	Lake System (number of incipient species)	References
B/C/D/E/F	7	*Prosopium* sp.	Bear Lake (3)	Vuorinen et al. (1998)
		C. lavaretus	Lake Neuchâtel/Biel (2/2)	Douglas et al. (1999), Østbye et al. (2005b)
		C. albula	Lake Kajoonjärvi (2)	Vuorinen et al. (1981)
			Lake Sokojärvi (2)	Svärdson (1988)
			Lake Ladoga (2?)	Sendek (2002)
			Lake Breiter Luzin (2)	Schulz et al. (2006)
			Lake Stechlin (2)	
D/E/F	7	*C. clupeaformis*	Lake Caniapiscau (2)	Lu et al. (2001)
		C. lavaretus	Lake Thun/Brienz (3/5–6)	Douglas et al. (1999), Østbye et al. (2005b)
			Lake Urn (3–4)	
			Lake Zürich/Walen (3–4/3–4)	
			Lake Baikal (3?)	Sukhanova et al. (2002)
			Lake Saimaa (4?)	Heinonen (1988)
		C. migratorius	Lake Baikal (3?)	Sukhanova et al. (2004)
B/D	7	*C. clupeaformis*	Indian Pond (2)	Bernatchez & Dodson (1990), Lu et al. (2001)
			Spider Lake (3)	
			Témiscouata Lake (2)	
			Lake Musquacook II (2)	Kirkpatrick & Selander (1979), Lu et al. (2001)
			Lake Como (2)	Vuorinen et al. (1993)
			Little Teslin Lake (2)	Bernatchez et al. (1996)
			Squanga Lake (2)	
B/C/D	5	*C. artedi*	La Grande Reservoir (2)	Turgeon & Bernatchez (2003)
			Lake Cormorant (2)	
			Barrow Lake (2)	
		C. lavaretus	Lake Sperillen (3)	Østbye et al. (2005b)
			Lake Mjøsa (2)	
E/F	2	*C. lavaretus*	Lake Isteren (2)	Østbye et al. (2005a, b)
			Lake Femund (4)	
B/D/F	1	*C. clupeaformis*	Lake Dezadeash (2)	Bernatchez et al. (1996)
A/B/C/F	2	*C. lavaretus*	Lake Thun/Brienz (3/5–6)	Bernatchez & Dodson (1994), Douglas & Brunner (2002)
			Lake Urn (3–4)	Douglas & Brunner (2002), Østbye et al. (2005b)
A/B/C/D/E/F	3	*P. coulteri*	Alaskan Lakes (2–3)	McCart (1970)

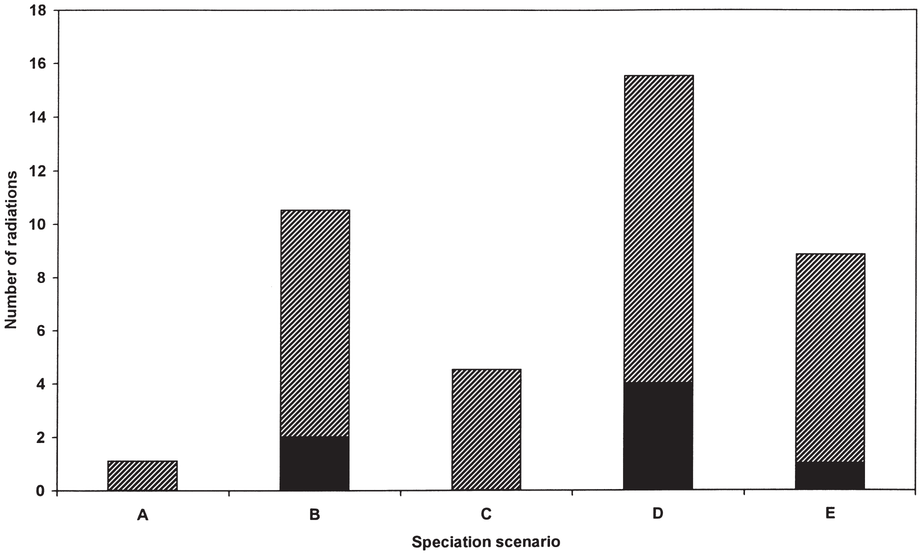

Fig. 1. The prevalence of each speciation mode across coregonine radiations included in this study. Black series equals the number of cases where a one mode of speciation was found to be the most likely (taken from Table 3). The hatched series equals the number of instances in which a number of speciation scenarios appear equally likely. The number of instances where the mode of radiation has been narrowed down to a composite of equally likely speciation scenarios (detailed in Table 4), was divided by the number of equally likely speciation modes, to keep the data points in Fig. 1 independent. A = allopatric speciation, B = genomically driven reinforcement, C = ecologically driven reinforcement, D = hybrid swarm radiation, E = sympatric speciation from a single founder lineage.

hybrid swarm scenario the most likely (TURGEON & BERNATCHEZ 2003). In Lake Ladoga, there are around seven described forms, with only two refugial lineages being found admixed in the two forms analyzed. The difference between the number of invading lineages and the minimum number of forms present, make hybrid swarm radiation again seem the most likely scenario (SENDEK 2004, ØSTBYE et al. 2005b). Similarly for Lake Konstanz, five to six species have been recorded, yet only two glacial refugial lineages are known from this region. The five taxa investigated form a monophyletic clade in microsatellite markers (DOUGLAS & BRUNNER 2002). Three of these taxa, included in a large mitochondrial phylogeography, show admixture between the same two distinct refugial haplotype lineages (ØSTBYE et al. 2005b).

For the 34 remaining radiations, at least some conclusions can be drawn and the range of possible modes of speciation can mostly be narrowed down.

Speciation mode subsets B/C/D/E/F

This subset is comprised of individual coregonine radiations in which the available evidence cannot distinguish between sympatric speciation and introgression scenarios in the formation of the endemic taxa. This subset includes cases in which the sympatric taxa cluster together on phylogenetic trees, but only one genetic marker has been used and/or phylogeographic data is limited preventing the discrimination of sympatric speciation from a single lineage, from multiple invasions and high gene flow introgression scenarios, only allopatric speciation being ruled out. A special case in this subset are the connected lakes Neuchâtel/ Biel, in which sympatric forms in each water system form a monophyletic clade on a micro-satellite phylogeny (DOUGLAS et al. 1999). The presence of two refugial mitochondrial haplotype lineages, plus the fact that the number of taxa within the lake system is equal to the number of refugial mitochondrial lineages present, means that the different introgression scenarios cannot be distinguished from sympatric speciation with anthropogenic stocking (DOUGLAS et al. 1999, ØSTBYE et al. 2005b).

Speciation mode subsets D/E/F

This subset of possible modes of speciation, includes lakes for which the traces of hybrid swarm and sympatric speciation cannot be teased apart. For all the examples in this subset, sympatric taxa cluster together on phylogenies, ruling out allopatric speciation with complete isolation upon secondary contact. Allopatric divergence followed by reinforcement can also be ruled out, because of the large number of sympatric taxa and lack of evidence for a correspondingly large number of possible refugia (Swiss *C. lavaretus* lakes) and/or the absence of multiple haplotype lineages within the water body (*C. clupeaformis*, lake Caniapiscau)(LU et al. 2001, ØSTBYE et al. 2005b). In some of these examples hybrid swarm speciation cannot be ruled out because mitochondrial phylogeographic data is lacking, so the input of genetic material from multiple refugia cannot be ruled out (Lake Saimaa) or its presence cannot be distinguished with the available data from the effects of stocking (most Swiss *C. lavaretus* lakes)(HEINONEN 1988, ØSTBYE et al. 2005b). For Lake Caniapiscau, hybrid swarm speciation cannot be ruled out because little investigation of the nuclear genome has been carried out, so the presence of multiple haplotype lineages, with the fixation of one in the sympatric taxa in the time since colonisation cannot be ruled out (LU et al. 2001). In a special case of this speciation subset, the Baikal whitefish (*C. lavaretus*) and omul (*C. migratorius*), mitochondrial and nuclear markers both suggest monophyly of the sympatric taxa and low genetic divergence. The presence of allozyme alleles of the allopatric *C. autumnalis* in the omul suggests high introgression. However, there is, as yet, no way to tell when this happened, whether before of after speciation. Hence hybrid swarm, sympatric speciation or single lineage, multiple invasion scenarios all remain valid (POLITOV et al. 2000, SUKHANOVA et al. 2004).

Speciation mode subsets B/D & B/C/D

The next groupings of putative speciation scenarios shown in Table 4, are found in those water bodies where phylogeographic studies have shown (a) evidence of multiple refugial lineages entering the water body, ruling out sympatric speciation from a single founder lineage, and (b) low genetic differentiation and cytonuclear discordance as evidence of hybridization between the lineages, ruling out purely allopatric speciation. The first of these groupings (B/D) is made up *C. clupeaformis* species pairs in water bodies such as Indian Pond, Spider and Témiscouata Lakes, where ecologically driven reinforcement can be ruled out due to the fact that incipient species ecomorphological phenotypes are not specific to genetic refugial lineages (Bernatchez & Dodson 1990, Bernatchez et al. 1996, Lu et al. 2001). The latter grouping (B/C/D) contains radiations in three lakes (Barrow, Cormorant and La Grande Reservoir) made up of *C. artedi* species pairs, where although there is data from both mitochondrial and nuclear markers, any of the introgression scenarios remain possible (Turgeon & Bernatchez 2003). This subset also contains two Norwegian *C. lavaretus* lakes (Sperillen and Mjøsa) where mitochondrial data shows two invading lineages and hybridization, but no published research on the nuclear genome has been carried out to help distinguish the different speciation scenarios (Østbye et al. 2005b).

Speciation mode subsets E/F & B/D/F

In Lake Femund in Norway, nuclear markers show one of the sympatric forms is genetically closer to forms in allopatry, within the same mitchondrial refugial lineage, with relatively high genetic differentiation between it and other sympatric taxa. This suggests a single sympatric origin of the Femund taxa or two (or more) invasions from taxa within the same mitochondrial lineage, with radiation in sympatry of one of the lineages (E/F). The sympatric taxa in Lake Isteren, similarly, group closer to individual Lake Femund taxa, also within the same refugial lineage, suggesting the same possible scenarios (Østbye et al. 2005a, b). The Lake Dezadeash *C. clupeaformis* species pair form a sister group relationship on a nuclear phylogenetic tree, however although belonging to the same mitochondrial lineage, the taxa are placed closer to different forms in allopatry, again within the same mitochondrial lineage, on a mitochondrial phylogeny. This suggests multiple invasions of the same lineage with gene flow at nuclear but not mitochondrial loci (B/D/F) (Bernatchez et al. 1996).

Speciation mode subsets (A/B/C/F)

In certain Swiss *C. lavaretus* lakes the sympatric taxa form diphyletic clades. In Lakes Thun/Brienz and Lucerne the sympatric taxa form monophyletic clades on nuclear phylogenies, apart from one divergent form. These divergent forms could be the result of two independent lineages colonizing the lake system, with allopatric speciation with or without low level introgression in the divergent lineage, the remainder of the sympatric taxa radiating from the other phylogenetic lineage through sympatric or hybrid swarm speciation (see above). However this pattern could also result from stocking of the allopatric populations into these lakes (Douglas & Brunner 2002).

Speciation mode subsets (A/B/C/D/E/F)

The Alaskan lake *P. coulteri* sympatric forms, although having data on possible multiple refugia and clines in morphology over the range of *P. coulteri*, has no genetic work to date and therefore none of the speciation scenarios could be ruled out (McCart 1970).

In summary, radiation from hybrid swarms, followed by genomically driven reinforcement, out of all the speciation scenarios detailed**,** have been found to be the most likely or possible modes of speciation across the Coregoninae, being implicated in 34.38% and 25.43% respectively of the taxon radiations (Fig. 1). Sympatric speciation from a single lineage was the third most often invoked mode (23.43%), followed by ecologically driven reinforcement (13.48%). Allopatric speciation with complete reproductive isolation on secondary contact, was the least likely mode of speciation in coregonine taxa (3.28%).

Discussion

Prevalence of speciation modes in adaptive radiations of the Coregoninae

It may be startling that in all the incidences of sympatric coregonine incipient species radiations that have been studied, there is no case in which the mode of speciation is known with certainty. Using the predictions outlined in Table 1, hybrid swarm radiation and genomically driven reinforcement are the most commonly implicated speciation scenarios in the origin of sympatric species diversity with in coregonine fish. This suggests that a period of allopatry may be important, followed by secondary contact and introgression. However our results also highlight the difficulty to distinguish between different introgression scenarios and speciation from a single lineage in sympatry. Possible cases of sympatric speciation from a single founder lineage are the third most frequent, suggesting this mode of speciation may not be uncommon in Coregoninaes.

The near-absence of evidence supporting allopatric speciation without hybridization maybe surprising considering its assumed prevalence as a mechanism of speciation, especially given the island-like characteristics of postglacial lakes. However hybridization is known to be common between closely-related fish taxa (Scribner et al. 2001). The different coregonine colonising lineages have probably only been isolated for the duration of the last ice-age (<150,000 years (Lu & Bernatchez 1998)), which may be too short for sufficient genetic divergence to cause complete reproductive isolation upon secondary contact. More interesting perhaps is the level of genetic differentiation built up in allopatry and its influence on what happens in secondary sympatry. Reinforcement requires some level of post-mating isolation, either intrinsic or extrinsic, acting against hybrids for increased pre-mating isolation to be selected for. The mean range of Nei's genetic distance (D), between three *C. clupeaformis* glacial lineages, of 0.05–0.17 (Bodaly et al. 1992) would predict the potential occurrence of some hybrid disadvantage, when compared to the range of possible values seen in post-zygotic isolation in *Drosophila* (>0.071)(Coyne & Orr 1989, 1997). Indeed there is some evidence for post-zygotic isolation, in the increased hybrid embryo mortality in crosses of two *C. clupeaformis* refugial lineages (Lu & Bernatchez 1998) and perhaps the skewed sex ratios in introgressing populations of Laurentian Great Lake ciscoes (Brown jr. 1970, Turgeon et al. 1999). More research certainly needs to be carried out across coregonine species complexes to test for evidence of intrinsic/extrinsic selection against hybrids of sympatric taxa. The lack of obvious prevalence of reinforcement as a speciation mechanism in coregonine, other than in two lakes containing species pairs in the *C. clupeaformis* complex, might be explained by the relatively short time of isolation between glacial refugial lineages. Alternatively this could be explained by the difficulty of distinguishing reinforcement from other speciation modes, both using the predictions developed in this review and during specific investigations of reinforcement as an evolutionary mechanism (Jiggins 2006).

The hybrid swarm radiation hypothesis, states that genetically divergent lineages hybridize forming a hybrid swarm, providing the enrichment with functional genetic variation that fuels rapid adaptive radiation in sympatry (Seehausen 2004). In theory, the potential for this enrichment is positively correlated with the level of genomic divergence between the hybridizing lineages, just as the potential for genomic reinforcement is. However the latter almost certainly requires more strongly divergent genomes than the former. Hence the probability of genomic reinforcement should increase with increasing genetic differentiation, relative to the probability of hybrid swarm radiation. It is important to point out that there are even lakes (Aylmer, Allagash, Haymock and Carr Pond in Maine) which contain only one species, however more than one refugial haplotype is admixed in these populations, showing that genetic differentiation in allopatry alone does not always lead to further differentiation in sympatry (Lu et al. 2001). However, these are generally small lakes that may not offer the ecological opportunity for more than one species. The collapse of refugial lineages into a single panmictic population in such cases is additional evidence against the strength of intrinsic reproductive isolation mechanisms and for the importance of ecology in coregonine speciation.

In this review, the single lineage, multiple invasions scenario has only been ruled out in radiations where more than one postglacial lineage has been admixed. In all other water systems the specific biogeography has yet to be investigated. Multiple invasions from the same lineage may in many cases be impossible to rule out. However it seems a plausible mode of speciation in Lakes Dezadeash, Isteren and Femund, given the available evidence (see Results section). Multiple invasions from the same lineage is the most likely mode of speciation in British Columbian threespine sticklebacks (*Gasterosteus aculeatus*) benthic/limnetic species pairs. Although intra-lacustrine stickleback species pairs are generally sister taxa at mitochondrial markers, the limnetic morphs tend to show a more recent nuclear ancestry with, and are closer morphologically and in salinity tolerance to marine populations (Taylor & McPhail 2000). Geological evidence supports this secenario; there were two marine transgressions submerging this area with 1,500 to 2,000 years between them (Taylor & McPhail 2000).

Within the *C. lavaretus* complex there are two water systems where more than one taxon radiation can be postulated. In both lakes Thun and Lucerne, Switzerland, one of the sympatric taxa groups with allopatric Lake Konstanz taxa on a microsatellite-based phylogenetic tree. All the other sympatric taxa form monophyletic clades within each lake system. It cannot be ruled out that recent stocking is involved, though this could be the case for any of the commercially-important coregonine taxa (Douglas et al. 1999, Douglas & Brunner 2002).

Biogeographic and taxonomic prevalence of speciation scenarios

Explanations of the most likely origin of sympatric coregonine diversity vary between evolutionary lineages and between biogeographic areas.

In the *Coregonus lavaretus* complex the presence in Europe of three distinct *C. lavaretus* mitochondrial refugial lineages has been shown. Of the two most studied lineages, one has a more southerly distribution in the Central Alpine area of Switzerland, along the Rhine through to Danish populations. The other lineage is more broadly distributed across Scandinavia and into Siberia. There is admixture of these lineages across a broad geographic area in *C. lavaretus* populations. In these secondary contact zones, the high numbers of sympatric taxa in most lakes suggest hybrid swarm radiation is usually the most likely mode of speciation. The third European refugial lineage is found mostly in Russian *C. lavaretus* taxa, however sampling is so far limited (Østbye et al. 2005b). In general, relatively few large scale phylogeographic or phylogenetic studies involving Russian coregonine taxa have been published. Therefore, although Russia has a high diversity of endemic coregonine and a large proportion of the *C. lavaretus* and *C. albula* species complex diversity (NIKOLSKY & RESHETNIKOV 1970), there is little information to test different speciation scenarios in this area. In Lake Ladoga, with seven sympatric *C. lavaretus* taxa recorded and with only two mitochondrial lineages present, hybrid swarm speciation seems likely. However as only two Ladogan taxa have been included in mitochondrial phylogeographic analysis and that the area surrounding the lake (especially to the east) was not extensively sampled, this does not preclude that other mitochondrial refugial lineages are or were present in the lake or surrounding water systems (ØSTBYE et al. 2005b). This coupled with the facts that allozymes and morphology show little differentiation between some of the sympatric taxa (SENDEK 2004), mean this conclusion should be treated with caution until further research rules out other introgression scenarios. In Lake Baikal the sympatric taxa form a monophyletic clade in both nuclear and mitochondrial phylogenetic trees suggesting sympatric speciation from a single lineage. The lack of a broader phylogeographic context, however, means hybrid swarm speciation cannot be ruled out (SUKHANOVA et al. 2002, 2004). Indeed there is still confusion over the taxonomic position of one of the constituent sympatric taxa, the Baikal omul (*C. migratorius*). Different allozyme loci suggest either a hybrid origin of this taxon from *C. lavaretus/C. autumnalis* (BODALY et al. 1994, SUKHANOVA et al. 2004), or an ancestral position to these species, with more recent hybridization with *C. lavaretus* (POLITOV et al. 2004). The lack of a thoroughly sampled phylogeographic context mean the Baikal omul and its three eco-morphological forms could have arisen from single lineage sympatric speciation or high gene flow introgression scenarios (SUKHANOVA et al. 1996).

Genetically the best studied of the coregonine species complexes, the North American *C. clupeaformis* radiations largely consist of dwarf/normal species pairs. The geographically disjunct occurrence of these species pairs (Southern Yukon, Ontario, Maine and Quebec) is hypothesised to be due to competitive exclusion of the zooplanktivorous dwarf form, by *C. artedi* in Central Canada (FENDERSON 1964). Five phylogenetic lineages (BODALY et al. 1992, LU et al. 2001) have introgressed across a wide region, the only introgression scenario ruled out in most cases being ecologically driven reinforcement, as morphological phenotypes can be fixed for mitochondrial haplotypes of different refugial lineages (BERNATCHEZ & DODSON 1990). The strongest case for sympatric speciation from a single lineage comes from the species pair of East Lake in the St. John River Basin, however the proximity of allopatric populations containing mitochondrial haplotypes from other refugial lineages and the fact that sympatric taxa group with other allopatric populations of the same morphotype on trees derived from putative loci under selection (CAMPBELL & BERNATCHEZ 2004), means that hybrid swarm speciation with a disproportionately higher genetic input from one lineage, cannot be completely ruled out. Potentially one of the most interesting *C. clupeaformis* lakes, is Spider lake, where unlike other water bodies in this species complex, three forms have been reported; mature dwarf forms with a similar gill raker number range to the sympatric normal form have been found alongside the standard, high gill raker dwarf form (FENDERSON 1964). Sadly this third form now appears to be extinct following smelt introduction.

Although less work has been done on the ecology of speciation in *C. artedi*, the phylogeography and phylogenetics of the complex are relatively well known. This system is more complex than the *C. clupeaformis* system and is more reminiscent of the European *C. lavaretus* complex, with around seven recognized sympatric forms in the Laurentian Great lakes

(Todd et al. 1981). Phylogeographic results show that fish from two distinct refugia have mixed across a large proportion of the range of *C. artedi*, supporting a radiation hypothesis that involves multiple invasions into a lake, with large scale introgression following (Turgeon et al. 1999, Turgeon & Bernatchez 2003). However unlike the *C. lavaretus* and *C. clupeaformis* species complexes, there is as yet no evidence for sympatric speciation from a single colonising lineage in this group. One of the most interesting lakes in this complex is Lake Cormorant, Manitoba, where the two morphotypes are not significantly differentiated genetically, but both morphs display heterozygote deficiencies, perhaps suggesting the presence of other sympatric populations. If the existence of these extra taxa is confirmed, this would be good evidence for hybrid swarm speciation having taken place in this lake (Turgeon & Bernatchez 2003).

The radiations in the *C. albula* complex largely consist of species pairs containing a morphologically typical form, with either a large piscivorous form or a deeper-dwelling, spring-spawning form. Relatively little work has been done on the phylogenetics and phylogeography of sympatric *C. albula* species, with genetic studies generally showing low differentiation within lakes and that the sympatric taxa group together (Vuorinen et al. 1981, Sendek 2002, Schulz et al. 2006). In Lake Breiter Luzin, Schulz et al. (2006) suggest hybridization of *C. sardinella* mitochondrial haplotypes into both coregonine taxa in this lake. The genetic evidence presented is inconclusive and larger phylogeographies of both the closely related *C. sardinella* and *C. albula* complexes need to be undertaken to resolve this. Mostly however, the signatures of sympatric speciation and allopatric diversification, with introgression on secondary contact, cannot be teased apart in the *C. albula* complex.

Of the *Prosopium* species complexes, only the phylogenetic relationships of the Bear Lake species have received some attention. Genetic markers indicate a sister species relationship and low genetic divergence, with no cytonuclear discordance between the three sympatric lacustrine species (Vuorinen et al. 1998). Incipient species in the *P. coulteri* complex occur as two to three sympatric taxa, in only three lakes in close proximity in the Bristol Bay area of Alaska (McCart 1970). This curious distribution (possibly an artefact of sampling and *P. coulteri*'s generally secretive nature) warrants further investigation. Morphological evidence of single forms in allopatry with meristic character counts similar to sympatric forms, suggest multiple invasions of distinct lineages is possible, however genetic studies are needed to corroborate this (McCart 1970, Lindsey & Franzin 1972, Bird & Roberson 1979).

None of the cases of anadromous/resident or riverine sympatric taxa, found in the reviewed literature, have been studied enough to draw any conclusions regarding the mode of speciation. Also no conclusions can be drawn about modes of speciation in many of the sympatric taxa in, for example: *Prosopium williamsoni*, *Coregonus sardinella*, *C. muksun*, and *C. nasus*, which remain understudied.

Conclusions

Despite the great number of coregonine sympatric incipient speciation cases described, relatively little is known about the geographic modes of speciation in this group. Reviewing a large body of literature, we found no evidence for purely allopatric speciation without introgression on secondary contact. We did find evidence for three different speciation modes: 1.

allopatric divergence followed by reinforcement on secondary contact, 2. sympatric speciation from a hybrid swarm into which several divergent lineages had collapsed, 3. sympatric speciation from a single founder lineage. Explicit tests for distinguishing between these modes need to be developed and more research needs be undertaken to resolve the principle causes and modes of rapid speciation. In general more research is needed to explain the unusual propensity to rapid speciation and adaptive radiation in coregonine.

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