Advancing mate choice studies in salmonids

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Abstract Mate choice in most organisms is not random, but determined by a suite of interacting traits and environmental factors. While the selective pressures underlying differences in mate choice between species, populations, individuals and even within individuals has been gaining interest, there still remains unexplained variation in mate preferences especially in non-model systems. Despite being of social, environmental and economic importance there is comparatively little known about how salmonids and other tetraploids make mate choice decisions in the wild and the resultant reproductive success (i.e. the number of offspring which survive to sexual maturity). Resolving questions related to salmonid mate choice is of particular importance given that humans have been supplementing salmon populations through aquaculture for decades. Despite these efforts, hatchery produced fish have lower reproductive success relative to their wild counterparts and salmon populations are declining. Most studies on mate choice and

reproductive success in salmonids focus on body size and major histocompatibility complex based choice. However, mate choice can also be affected by other factors including other genetic factors, predation risk and social environment. Here, we (a) synthesize what is presently known about mate choice and reproductive success in salmonids, (b) identify gaps in knowledge and areas where there is a lack of consensus in results, and (c) suggest interdisciplinary ways of advancing our understanding of mate choice in salmonids and other polyploids.

Keywords Captive breeding · Mate choice · Polyploidy · Salmonids · Sexual selection

Introduction

Resolving selection pressures and mechanisms behind the skew in reproductive success (i.e. the number of offspring which survive to sexual maturity) in animal populations has long intrigued biologists. Mate choice studies have revealed a diversity of mating systems and mating preferences that are individual (e.g. Godin and Auld 2013; Edward and Chapman 2013), species and/or population dependent (Endler and Houde 1995) and affirmed that both males and females use multiple cues to assess a number of interacting factors, including chemical, morphological, and behavioural

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traits for choosing among potential mates (see Candolin 2003 for a review). Factors that affect mate choice include physical, behavioural and genetic traits, as well as environmental conditions. Examples of traits that affect mate preferences and reproductive success include body size, ornamentation, courtship displays, personality, immune system compatibility, age, condition, social environment, and sperm competition.

Despite these advancements, there is a relatively less work geared towards understanding mate choice in non-model species (e.g. animals other than *Drosophila*, zebra finches (*Taeniopygia guttata*), Trinidadian guppies, (*Poecilia reticulata*), zebrafish (*Danio rerio*)) and it is unclear how what is known about mate choice and reproductive success in model species may extend to other species, including species of social and economic importance. Current management strategies for such species often involves artificial breeding programs where humans select and breed individual mate pairs either randomly (to avoid bias), or based on morphological characteristics of choice such as increased body size (e.g. Hanson and Smith 1967; Fleming and Gross 1994) or growth rates. However, in nature mate choice is not random and the observed higher reproductive success of wild over captive origin parents in a natural context [e.g. in coho, *Oncorhynchus kisutch* (Whitcomb et al. 2014)] indicates that fitness (i.e. reproductive success) advantages may result from the complex natural phenomenon of mate choice among individuals themselves (Andersson and Simmons 2006).

Salmonids comprise an important group of animals that are frequently artificially bred in captivity. In many hatcheries, fish are mated and offspring released into the wild to supplement depleted wild populations or to support commercial, tribal or recreational harvest (Fleming and Petersson 2001; Katz et al. 2013) often resulting from human activities such as over-harvesting and/or habitat destruction. However, there is relatively little known about how salmonids choose mates in the wild and insufficient experimental evidence on how to maintain genetic diversity in these populations (Fraser 2008). Maintenance of genetic diversity may help populations adapt to changing environments (e.g. Reusch et al. 2005). Mismatch among human selected mating partners in fish could account for some of the observed reduced reproductive success of hatchery fish relative to wild

fish (e.g. Nordeide 2006; Araki et al. 2008; Reed et al. 2015; Falica et al. 2017).

It is likely that salmonids, like other animals, use multiple behavioural and morphological cues to evaluate potential mates. However, most research on mate choice in salmonids has focused on preference for increased body size (e.g. Hanson and Smith 1967; Fleming and Gross 1994), arrival time at spawning grounds (e.g. Fleming 1996; Bentzen et al. 2001), and immune system compatibility among mates (e.g. Landry et al. 2001; Consuegra and de Leaniz 2008; Garner et al. 2010; Whitcomb et al. 2014). While research on other aspects of salmonid mate choice is increasing, there remain large gaps in our knowledge of how salmonids make mate choice decisions and how choice varies both within and between populations. Factors evident from work in other species include: courtship displays (e.g. Zuk et al. 1995), colour patterns (Hughes et al. 2013), relatedness (Pusey and Wolf 1996), and social aspects of both individual's rearing (e.g. Adkins-Regan and Krakauer 2000) and current environments, including in the context of sex ratio (e.g. Jirotkul 1999) and presence of sexual competitors (e.g. Auld and Godin 2015). A lack of focus on these important factors in salmonid mate choice and reproductive success studies could account for our limited understanding about fitness differences between wild and hatchery fish populations (e.g. Fleming and Gross 1992; Fleming et al. 1997). Moreover, because salmonids, like other important groups of fishes, are of polyploid origin (Le Comber and Smith 2004) and are still undergoing rediploidization, they have genetic inheritance patterns that differ from those of commonly studied diploids (e.g. Liu et al. 2016).

In this review, we synthesize what is known about mate choice and reproductive success in salmonids and highlight unanswered questions that can generate testable predictions to resolve uncertainties for both fisheries managers and theoretical biologists. We highlight what is already known about inter and intrasexual competition for both males and females including pre- and post-spawning processes, from both a behavioural and genetic standpoint. We also identify cross-disciplinary methodologies that could provide further insight into these processes, and propose possible avenues of research to help fill gaps in our understanding of mate choice and reproductive success in this ecologically, culturally, and economically

important group of fish. Ultimately, we hope that this synthesis will help salmonid and other captive-context mate-choice research move forward and overall lead to improved hatchery practices.

Salmonid mating system

Salmonids are bony fish of polyploid origin that include taimen (*Hucho*, *Parahucho*), Pacific salmon and trout (*Oncorhynchus*), Atlantic salmon (*Salmo salar*) and trout (*Salmo*), charr (*Salvelinus*), long-finned charr (*Salvelinus*), whitefish (*Coregonus* and *Stenodus*), round whitefish (*Prosopium*), lenoks (*Brachymystax*) and graylings (*Thymallus*) and the extinct *Eusalmo*. They are native to high latitudes of the northern hemisphere, but have been introduced around the world for commercial aquaculture or fisheries (e.g. Chile, New Zealand).

All salmonids spawn in freshwater, but breeding patterns vary across species and populations (De Gaudemar 1998). For example, some salmonids are iteroparous (reproduce multiple times) and others semelparous (breed only once). Similarly, some salmonids spend their adult life in marine environments returning to freshwater only to spawn and others spend their entire lives in freshwater. Those trout and salmon that spend their adult lives in the ocean return to their natal stream reaches to spawn (Quinn et al. 1999, 2006) (Fig. 1a). The spawn timing for salmonids is largely genetically determined and varies

between species and populations within species (Bentzen et al. 2001). In most species of salmon, males arrive at the spawning grounds earlier than females (Morbey 2000), and once paired with a female, will attempt to exclude other males (Morbey 2002). Once females arrive at spawning grounds they compete with other females for access to preferred spawning habitat (Tentelier et al. 2016) and are territorial with and without the presence of males (e.g. Foote 1990).

Within large populations of salmonids inhabiting a single river system there is evidence of subpopulations inhabiting different tributaries (e.g. Verspoor 1997). For example, Ryman (1981) demonstrated population differentiation in brown trout (*Salmo trutta*) that were separated by less than 10 km. Brown trout have also been found to form subpopulations within a less than a 5 km stretch of stream (Kazyak et al. 2016). Another study by Skaala and Nævdal (1989) found genetic differentiation among trout in different streams whose spawning areas were less than 2 km apart. Even low genetic differentiation can lead to differences, such as growth rate, in Atlantic Salmon (Aykanat et al. 2015). Given discrete genetic differences between populations despite spawning in relatively close proximity it is likely that individuals are reproducing with genetically similar mates.

Alternative reproductive tactics are present in salmonid mating systems with precocious males (jacks) maturing a year or more earlier than sexually

Fig. 1 **a** Chinook salmon (*Oncorhynchus tshawytscha*) on spawning grounds of Fall Creek in Oregon, **b** adult male Chinook salmon with developed kype and teeth

mature adults (Gross 1984). Instead of competing with larger adult males for access to females, jacks more often assume a subordinate position in the mating hierarchy and perform sneak mating whereby they monitor the interactions between females and adult males and attempt to synchronize their sperm release with the dominant male; however, sneaking can be performed by both adults and jacks. Jacks are important in mating systems since the precocious males are unlikely to mate with their sisters who remain at sea and thus decrease the overall incidence of inbreeding (Perrier et al. 2014). Males in some species also form leks in which less attractive males (e.g. subdominant) gather around more attractive males (e.g. dominant) who are likely to attract females (Figenschou et al. 2004).

As adult males prepare to spawn and return to their natal streams they undergo development of numerous secondary sexual characteristics that can include the appearance of red coloration, thickening of skin, and enlargement of snout and teeth (Johnson et al. 2006) (Fig. 1b), which can be used to compete with rivals (Keenleyside and Dupuis 1988), and changes to fins (Thorn and Morbey 2016). Protein and stored fat are used for the development of secondary sexual characteristics, upriver migration, and egg production (Hendry and Berg 1999). Underdeveloped secondary sexual characteristics may be indicators of overall poor nutrition and foraging ability during the ocean phase of life. The development of these secondary sexual characteristics increases an individual's chance of reproductive success via intrasexual competition for access to spawning sites or mates and/or intersexual competition through attraction of potential mates (Fleming and Gross 1994). In salmonids, the effective population size is usually male biased resulting in exaggerated secondary sexual characteristics in males, competition for fertilization opportunities and differences in reproductive success between males than females (Quinn and Foote 1994).

Males and females are promiscuous (e.g. Bentzen et al. 2001) with evidence of mutual mate choice. Males can demonstrate a choice for a female by competing with other males for access to her during spawning and releasing sperm as she releases eggs for fertilization. Males also control the amount of sperm they release (Makiguchi et al. 2016a), with males releasing more sperm when spawning with larger and presumably more fecund females. When multiple

females of varying quality (e.g. fecundity) are spawning, males should exhibit mate choice (Edward and Chapman 2011) as they are likely to face sperm depletion after several matings or mating attempts (Mjølnerød et al. 1998). Females can exhibit mate choice by delaying egg release until a preferred male is in position to fertilize her eggs (e.g. Berejikian et al. 2000). Males and females are likely able to synchronize gamete release using a combination of vibration and visual communication systems (e.g. Tautz and Groot 1975; Satou et al. 1994; De Gaudemar and Beall 1999).

To protect fertilized eggs from potential predators and/or from being swept downstream in a current, females will cover their eggs with gravel. Embryos develop within the gravel substrate before emerging as alevins and developing into juveniles (Groot and Margolis 1991). After hatching, there is no parental care from either parent even in iteroparous species. Hence, mate choice is likely to be strongly based on good or compatible genes that can be transmitted to offspring, rendering factors such as access to food and/or parental care that may be important to other mating systems of no consequence to salmonids.

Post-spawning sexual selection

Even if a male is able to spawn with a female, he is not guaranteed egg fertilization or reproductive success. Two post-spawning processes affecting fertilization success are sperm competition (see Birkhead and Møller 1998) from other males and cryptic female choice (see Eberhard 1996), which will be discussed below. After ejaculation, sperm must compete with sperm from other males for fertilizations and may have differential success based on sperm characteristics, such as velocity (Gage et al. 2004; Liljedal et al. 2008; Egeland et al. 2015) (Table 1). Recent studies have also demonstrated a role of seminal fluid in the activation (Rudolfson et al. 2015) and competitive ability of sperm (e.g. Rosengrave et al. 2009; Lewis and Pitcher 2017). For example, in the grass goby (*Zosterisessor ophiocephalus*) sneaker male sperm increased velocity when in contact with the seminal fluid of a territorial male (Locatello et al. 2013). Conversely, the sperm velocity of territorial males decreased in the presence of sneaker male seminal fluid (Locatello et al. 2013). The ability of males to respond to apparent risk and/or intensity of sperm

Table 1 Traits linked to mate choice and/or offspring production in salmonids

Trait	Sex	Preference or trait	Species	References
Body size	♀	Larger males	Chinook (<i>Oncorhynchus tshawytscha</i>)	Berejikian et al. (2000), Neff et al. (2008)
	♂	Larger females	Coho (<i>O. kisutch</i>)	Sargent et al. (1986)
	♀♂	Assortative mating	Japanese Charr (<i>Salvelinus leucomaenis</i>)	Maekawa et al. (1994)
	♀♂	Assortative mating	Brown trout <i>Salmo trutta</i> L.	Serbezov et al. (2010)
	♂	Preference for males larger than themselves		Labonne et al. (2009)
	♂	Assortative mating	Sockeye and kokanee (<i>O. nerka</i>)	Hanson and Smith (1967), Foote (1988)
Colour	♂	Red coloration	Sockeye	Craig and Foote (2001), Foote et al. (2004)
	♀	Brighter, blue green males	Chinook	Neff et al. (2008)
	♀♂	Assortative		Lehnert et al. (2016a, b)
	♂	Darker sired more viable offspring	Brown trout	Wedekind et al. (2008)
	♂	Fertilization potential inversely related to coloration	Arctic charr (<i>S. alpinus</i>)	Liljedal et al. (1999)
	♀	More brightly coloured females had less reproductive potential	Arctic charr	Janhunen et al. (2011)
Ornamentation	♂	More ornamented males sired higher quality offspring	Alpine whitefish <i>Coregonus</i> sp.	Wedekind et al. (2001)
	♀	More ornamented females had larger offspring		Kekäläinen et al. (2010)
Adipose fin	♀	Larger	Brown trout	Petersson et al. (1999)
	♀	Larger	Atlantic salmon	Järvi (1990)
MHC	♀♂	Dissimilar	Atlantic salmon <i>Salmo salar</i>	Evans et al. (2012), Landry et al. (2001), Consuegra and de Leaniz (2008)
	♀	Similar		Yeates et al. (2009)
	♀♂	Random		Promerová et al. (2017)
	♀	Intermediate	Brown trout	Forsberg et al. (2007)
	♀	Dissimilar	Chinook	Neff et al. (2008), Garner et al. (2010)
	♂	Random		Neff et al. (2008)
	♂	♀ with whom they would produce offspring with intermediate diversity at MHC II		Evans et al. (2013)
	♀♂	More similar at MHC I-A1 and random at MHC II-B1		Lehnert et al. (2017)
	♂	Great fertilization success if heterozygous	Arctic charr	Skarstein et al. (2005)
	♀	Greater fertilization for similar sneaker males	Atlantic salmon	Weir et al. (2012)
	♀♂	Variable across years	Coho	Whitcomb et al. (2014)
Density	OSR	No evidence	Chinook	Neff et al. (2008)
		Density of males affected offspring production	Atlantic salmon	Weir et al. (2012)

Table 1 continued

Trait	Sex	Preference or trait	Species	References
Dominance	♀	Preference for dominant mate	Arctic charr	Sørum et al. (2011)
		Increased fertilization success	Coho salmon	Berejikian et al. (2001)
Kinship	♀	Dissimilar	Atlantic salmon	Garant et al. (2005)
	♀♂	Random		Landry et al. (2001)
	♀♂	Variable		Houde et al. (2011)
Life History	♀♂	Assortative mating	Sockeye and kokanee	Footo and Larkin (1988), Thériault et al. (2007)
		No assortative mating	Brook charr (<i>S. fontinalis</i>)	
Origin	♀	Context-dependent preference for males from the same population	Brown trout	Bolgan et al. (2017)
Ovulation	♂	Courtship towards ♀ who had ovulated	Masu salmon <i>O. masu</i> and Biwa trout (<i>O. rhodurus</i>)	Honda (1982)
Courtship	♀	More intense ♂ courtship	Atlantic salmon	De Gaudemar et al. (2000)
Immediate social environment		No known studies		
Parasite load		No known studies		
Predation risk		No known studies		
Cognition		No known studies		
Familiarity		No known studies		
Gene Drive		No known studies		
Personality		No known studies		
Ploidy		No known studies		

competition (e.g. through release of more sperm) should increase their reproductive success (Bretman et al. 2009).

Sperm competition can play a role in the reproductive success of salmonids. Salmon sperm (milt), which is immobile until it is activated by water, is viable for approximately 30 s and female eggs can be fertilized for approximately 40 s after which the micropyle closes and no sperm are able to enter (Hoysak and Liley 2001); however, in sockeye salmon (*Onchorhynchus nerka*) a contact time of 5–10 s for egg and sperm is sufficient to ensure high levels of fertilization (Hoysak and Liley 2001). For a given male to be able to successfully fertilize eggs he needs to appropriately time sperm release and would benefit from having fast sperm that can reach eggs before other sperm fertilize the eggs. Pitcher et al. (2009) found adult male coho salmon with less red reflectance

and high UV reflection in their body coloration had higher sperm velocity compared to males with more red coloration suggesting a tradeoff between attractive coloration leading to a better position in the dominance hierarchy and sperm quality. They found no relationship between body size and sperm velocity, longevity, or any morphological sperm trait. Similarly, in Alpine whitefish (*Coregonus zugensis*), older males on average maintain a higher position in the dominance hierarchy, but also had slower sperm relative to younger males (Rudolfson et al. 2008). Moreover, males with less ornamentation had higher sperm motility and greater fertilization success, but produced less viable embryos (Kekäläinen et al. 2015). Differences in competitive ability of sperm may in part explain differences in reproductive success between hatchery and wild males; however, Camarillo-Sepulveda et al. (2015) found most sperm characteristics of

wild and farmed Atlantic salmon similar with the exception of wild salmon sperm having a longer flagellum, but this did not translate into increased fertilization rates. Their study had a relatively low sample size of 10 wild males, 21 farmed males, and 8 females each of wild and farmed origin. Lumley et al. (2016) also showed no benefit to Atlantic salmon offspring when there was opportunity for sperm competition and cryptic female choice; however, they only looked at offspring growth and survival for 140 days and so there is no measure of lifetime reproductive success. Any increase in offspring growth and survival may be apparent later in life. There are apparently no studies that compare fertilization rates between wild and hatchery males in other salmonids.

Males who are able to circumvent premating female choice and/or males who produce sperm that reach eggs before rival sperm may still be excluded from fertilizations by cryptic female choice (e.g. Rosengrave et al. 2008, 2016; Lehnert et al. 2016a, 2017). Cryptic female choice occurs when a female or an extension of the female (i.e. eggs or ovarian fluid) favors certain sperm over others. For internal fertilizers, this occurs within the reproductive tract of the female. It was initially thought that cryptic female choice was limited to internal fertilizers, but recent studies demonstrate the ability of cryptic female choice, mediated by ovarian fluid, to occur in external fertilizers such as Chinook salmon (*Oncorhynchus tshawytscha*) (Rosengrave et al. 2008, 2016; Lehnert et al. 2016a, 2017; but see Wedekind et al. 2004; Lumley et al. 2016), and trout (e.g. Galvano et al. 2013; Yeates et al. 2013). Also, Arctic charr (*Salvelinus alpinus*) sperm from dominant males had greater motility in ovarian fluid (Egeland et al. 2016). This increased mobility could be cryptic female choice, via ovarian fluid, for dominant male sperm or dominant male sperm could simply be better at moving through ovarian fluid (Egeland et al. 2016); however, the experiment could not disentangle the two competing hypotheses. Makiguchi et al. (2016b) found that ovarian fluid differentially affects the sperm of precocious parr and anadromous masu salmon (*Oncorhynchus masu*). Based on their results, they encourage further study on seminal protein in salmonids including genetic effects, biochemical mechanisms of reproductive success and the use of proteomics to identify relevant proteins. They also

note the importance of including ovarian fluid in studies of fertilization dynamics.

Mate choice and reproductive success in salmonids: what is known?

(a) *Body size*

Throughout the animal kingdom, body size is known to affect mate choice and sexual competition with both males and females generally demonstrating a preference for larger bodied mates (e.g. Ryan 1980; Côte and Hunte 1989; Howard et al. 1998; Aquiloni and Gherardi 2008). Male preference for female body size is thought to be driven, at least in part, by the ability of larger females to produce more eggs compared to smaller females. Moreover, larger females may out-compete smaller females for access to resources including nesting habitat (Fleming and Gross 1994). Furthermore, larger females can also better defend their nests, compared to smaller females (Van den Berghe and Gross 1984). Females demonstrate preferences for larger males even in instances when males provide no direct resources such as food, shelter or parental care (e.g. Auld et al. 2016). In non-resource based mating systems larger males may provide an indirect benefit of advantageous genes for offspring (e.g. Calsbeek and Sinervo 2002). While individuals in a wide array of taxa often prefer relatively large mates, there may be disadvantages to this preference including increased competition for the most desirable mates. For example, because large females are preferred by many males, there is a greater risk of males incurring both pre-mating competition for access to large females and post-mating sperm competition. As a result, males do not always exhibit a preference for larger females over smaller ones. In many populations, there remains variation in both male (e.g. Godin and Auld 2013) and female (e.g. Endler and Houde 1995) preference for body size.

Body size is one of the best-studied mate choice preferences in salmonids. There are multiple studies wherein male salmonids demonstrate a preference for large females as mates (e.g. Hanson and Smith 1967; Sargent et al. 1986; Foote 1988; Maekawa et al. 1994; Serbezov et al. 2010) (Table 1) as they are presumably more fecund and will therefore have increased

reproductive output (e.g. Van den Berghe and Gross 1989); however, this is not always the case (Garant et al. 2001; Dickerson et al. 2005). Larger females are also capable of digging deeper redds (e.g. Quinn and Foote 1994; Steen and Quinn 1999) which has the advantage of decreasing the likelihood of gravel damage to eggs during heavy runoff (Van den Berghe and Gross 1984) or another female excavating the redd (Hanson and Smith 1967), improving chances of juvenile survival. Similarly, female salmonids generally prefer to mate with larger males (e.g. Foote 1989; Maekawa et al. 1994; Berejikian et al. 2000; Neff et al. 2008; Serbezov et al. 2010) (Table 1). In general, larger males produce more sperm (e.g. Watanabe et al. 2008) and are therefore able to fertilize a larger proportion of eggs (see Dickerson et al. 2005 for an exception), can outcompete smaller males for access to spawning females (e.g. Thomaz et al. 1997), and they may also have increased energy reserves to perform courtship displays, which can be attractive to females. For example, larger Arctic charr males invest more in courtship behaviours towards females compared to smaller males (Bolgan et al. 2017). Furthermore, larger males may have ‘good’ genes they will pass on to their offspring giving them a competitive advantage in growth and reproduction with larger females producing more eggs and larger males being more competitive for access to females. Despite these general trends, variation in mate choice among salmonids remains. For example, large brown trout females prefer to spawn with males larger than themselves while smaller females prefer mates of similar size (Labonne et al. 2009) and the effect of adult body size on the production of offspring in steelhead (*Oncorhynchus mykiss*) trout varies from year to year (Seamons et al. 2004). Observed variation in mate choice for body size may result in part from prevailing environmental factors. For example, in coho salmon the benefit of larger body size in competing for access to spawning females can be context-dependent with the benefit decreasing as density increases (Fleming and Gross 1994). Mutual mate preference for large body size often leads to size-assortative mating, which appears to be common in salmonids (Table 1). Despite some variation in preference for larger body (e.g. Fleming and Gross 1994), it is one of the most consistent preferences observed in salmonid mate choice.

(b) Dominance

Males often engage in contests, battles or displays to establish dominance that grants access to sexually receptive females. Other than in primates, there is consistent evidence that dominant or higher-ranking males achieve greater offspring production than do subordinate males (Ellis 1995). Increased juvenile offspring production for dominant males is observed in salmonid mating systems, wherein males often compete for a top place in the dominance hierarchy (Berejikian et al. 2001) (Table 1). In a controlled experimental study, wild coho males exhibited dominance over captive reared males in approximately 80% of trials (Berejikian et al. 1997). This behavioural difference would account for some of the differential reproductive success between adult wild and hatchery males in coho. In coho or other species, age may also affect dominance hierarchies, such as older male Alpine Whitefish on average holding higher dominance positions compared to younger males (Rudolfson et al. 2008).

Despite the apparent advantage of dominant males in some salmonids with regard to egg fertilization, female brown trout do not always experience benefits via offspring quality from mating with larger and more dominant males (Jacob et al. 2007). Similarly, Figen-schou et al. (2007) found no difference in larval length, yolk area or red yolk pigment between dominant and subordinate offspring of Arctic charr. Moreover, they found subordinate males sired more offspring than dominant males. A study on Chinook salmon demonstrated frequency dependent selection for success of adults, which more often occupy dominant positions in a hierarchy, than jacks (Berejikian et al. 2010). Together, these results suggest that the advantage of being a dominant male is not ubiquitous and raise questions regarding which conditions incur dominance benefits. Further investigation into factors influencing this variation is needed.

(c) Density

Density of potential mates and competitors can affect individual mate choice decisions and offspring production (e.g. Fleming and Gross 1994; Atwell and Wagner 2014). With access to multiple prospective mating partners, individuals can increase choosiness because they are more likely to encounter high quality

and/or compatible mates compared to when there are relatively few potential mates (e.g. Dawkins 1969). Conversely, the presence of competing rivals can decrease an individual's ability to mate with preferred partners, with a disproportionate effect on less competitive individuals (Wong and Candolin 2005). The effect of density on mating behaviour (e.g. Mathisen 1962) and success has been documented in salmonids. For example, sneaker males mating at low densities or in the absence of dominant males can monopolize fertilization of a female's eggs, whereas at high densities or when dominant males are present, multiple sneaker males will fertilize some smaller proportion of eggs (Berejikian et al. 2010; Weir et al. 2012) (Table 1). Moreover, the operational sex ratio (OSR), which is the ratio of sexually mature males to sexually mature females, differs between spawning grounds and affects male reproductive behaviour (Quinn et al. 1996). Fleming and Gross (1994) also observed a negative correlation between density and the advantage of large body size for access to females. It is therefore important to incorporate measures of density and alternative mating tactics when assessing mate choice and reproductive success for a population at any given time. However, to our knowledge it is currently unknown if similar patterns occur in salmonids other than coho and Atlantic salmon. Experimental manipulation of density and OSR during spawning could provide further insight into the effects of density and sex ratio during spawning on reproductive success in salmonids.

(d) *Return time*

In birds and salmon that migrate to breeding habitat, the time of arrival on mating grounds can affect their likelihood of successfully reproducing (e.g. Tryjanowski et al. 2010). Female sockeye salmon who return to the spawning grounds earlier typically have the opportunity to gain access to better spawning habitat, and irrespective of size, both males and females who arrived on the spawning grounds early had longer opportunities for reproduction (Hendry et al. 2001) (Table 1). Similarly, pink salmon (*Oncorhynchus gorbuscha*) males that arrived earlier often held more dominant social positions and sired more offspring, but female reproductive success was not linked to return time (Dickerson et al. 2005). Another benefit of arriving early is avoidance of over ripening of eggs because this can reduce egg viability (De

Gaudemar and Beall 1998). However, in steelhead trout the effect of arrival time on offspring production varies from year to year although differences in sample size between years could have contributed to observed inter-annual variation between years (Seamons et al. 2004). Similar to other factors affecting mate choice and reproductive success, the influence of return time on the number of healthy offspring produced differs among species, contexts and over time.

(e) *Ornamentation*

Since Darwin, elaborate traits and conspicuous ornamentation have been a central focus in mate choice and sexual selection (Zahavi 1975). Bright colours and other costly traits are thought to signal 'good genes' in potential mates but (Pitcher and Neff 2007) found no relationship between sexually selected traits of a sire and the survival or growth of his offspring in Chinook salmon. While mate choice studies involving ornamental traits have traditionally focused on female preference for male ornaments, there is increasing evidence that males also use female ornamentation (e.g. colour) as a mate choice cue (Amundsen and Forsgren 2001). This evidence exists for salmonids as several studies have shown male and/or female mate choice and/or offspring production linked to coloration (Table 1). For example, male sockeye salmon have demonstrated a mating preference for models of red females over green morphs (Foote et al. 2004). The use of female models in this experiment controls for other differences that may exist between natural females. The ability of red morphs to better sequester carotenoids from the environment via diet may be indicative of 'good genes' and drive this preference (Craig and Foote 2001). In Chinook salmon (*O. tshawytscha*), which has red and white morphs, (Lehnert et al. 2016b) found some assortative mating based on colour morph. In another study, male Chinook with brighter lateral blue/green hues sired more offspring compared to less bright males, when spawning in experimental channels (Neff et al. 2008); however, in other salmonids red coloration in males, contrary to expectation, was not associated with increased offspring production or higher quality offspring. Brown trout males with greater amounts of dark pigmentation sire more viable offspring compared to males with greater levels of carotenoid pigmentation (Wedekind et al. 2008) and

their offspring were more resistant to parasitic infection (Jacob et al. 2010), suggesting that levels of dark, but not red, pigmentation may be valid signals of good genes. Similarly, male fertilization potential of Arctic charr was negatively correlated with red spawning coloration (Liljedal et al. 1999) and offspring of brightly coloured males showed no advantage in embryo survival or growth (Janhunen et al. 2011). Red coloration is positively correlated with offspring length, but only in smaller males (Eilertsen et al. 2009) suggesting an interaction between length and coloration. Increased red coloration in females was negatively correlated with their reproductive potential. Moreover, the offspring they produced were less viable compared to paler counterparts (Janhunen et al. 2011). It is unclear what is driving the differences in preference/offspring production related to colour in different species/populations or whether the observed variation is the result of different methodologies. In salmonids, an improved understanding of factors contributing to these differences will allow researchers and hatchery managers to better understand mate choice and incorporate these findings into breeding decisions and strategies.

Ornamental traits other than colour can signal good genes or otherwise be attractive to the opposite sex. Evidence of this in salmonids exists from studies of whitefish, where increasing size of breeding tubercles positively correlates with survival of eggs between 30 days post gamete release and time of hatching (Wedekind et al. 2001). In their study, there was also a significant interaction of maternal and paternal effects suggesting genetic incompatibility unrelated to tubercle length (Wedekind et al. 2001). Incorporation of genetics in whitefish mate choice studies would improve our understanding of the importance of these genetic compatibilities and allow researchers to design experiments that tease apart the effects of ornamentation on mate choice in these species. Additionally, offspring of highly ornamented males and females have higher swimming speeds, better predator avoidance, while offspring of highly ornamented females, but not males, were larger than the offspring of less ornamented females (Kekäläinen et al. 2010). Huuskonen et al. (2009) found a paternal effect only of first feeding in larval offspring, but found a maternal effect in swimming ability, contrary to Kekäläinen et al. (2010). Differences in study results may be attributed to evolutionary history of fish used in each study.

Huuskonen et al. (2009) used fish from Koitajoki River in eastern Finland while Kekäläinen et al. (2010) used fish from Oulujoki in western Finland. Small sample size may also have affected the observed outcome with eggs from only two females used in one experiment (Huuskonen et al. 2009). Investigation of biotic or abiotic factors contributing to observed differences and higher sample sizes would allow for more accurate recognition of patterns that shape mate choice in salmonid fishes.

(f) *Major histocompatibility complex*

Over the past decades there has been a lot of interest in the effect of immune system compatibility on mate choice in a wide array of vertebrates. The immune system is instrumental to survival and protection from infectious bacteria, viruses, and parasites that an individual will be exposed to throughout life. The role of major histocompatibility complex (MHC) in mate choice has been examined in various groups of salmonids with much variation among findings (Table 1). Several studies have concluded that Atlantic salmon choose mates dissimilar to themselves at MHC loci (Landry et al. 2001; Consuegra and de Leaniz 2008; Evans et al. 2012), but Yeates et al. (2009) found preferential selection for sperm with similar MHC alleles. Promerová et al. (2017) found no evidence for non-random fusion of gametes at MHC II. Weir et al. (2012) found sneaker males had greater fertilization success with eggs of MHC similar females. Few studies directly explore underlying mechanisms that explain these differences. A study on brown trout concluded females preferentially selected mates with intermediate differences in MHC (Forsberg et al. 2007) while another study found brown trout MHC dissimilar offspring were more parasite resistant (Jacob et al. 2010). A study of Arctic charr showed greater male fertilization success when heterozygous at MHC alleles (Skarstein et al. 2005). In Chinook, there is evidence that resistance to pathogens was increased for captive bred MHC heterozygotes and individuals who were outbred (Arkush et al. 2002), but tests of mate choice in the wild show conflicting results. Neff et al. (2008) found female Chinook preferentially mating with males dissimilar to themselves at MHC loci, but males in their study mated randomly at MHC loci. Conversely, Lehnert et al. (2016b) found assortative mating at

MHC I-A1 and random mating at MHC II-B1. Evans et al. (2013) found male Chinook more aggressive towards females with whom they would produce offspring with high or low diversity at MHC class II and their offspring showed greater diversity at MHC class I. In coho salmon, mating preferences at MHC loci differed between fish of wild and hatchery origin and between years (Whitcomb et al. 2014).

While some observed differences in MHC based mate choice may be attributable to differences in methodology or sample size (Hoover and Nevitt 2016), collectively the findings of these studies suggest that mate preferences based on MHC compatibility may differ among populations (see contrasting findings from Landry et al. 2001; Consuegra and de Leaniz 2008; Evans et al. 2012 compared to Yeates et al. 2009), environmental conditions (Larson et al. 2016), and/or temporally (Evans et al. 2012). To better understand mate choice based on immune system compatibility and use this information to effectively manage breeding in hatcheries, we need improved understanding of the importance of observed variation and to develop testable hypotheses that verify MHC is indeed relevant to how individuals of different species and populations choose mates under different circumstances. A comprehensive meta-analysis and comparison of species, populations and environmental conditions at time of study may help explain the observed differences in MHC based mate choice in salmonids and other species.

(g) *Relatedness*

Many studies have addressed whether or not degree of relatedness to potential sexual partners affects mate choice in a variety of species. In many populations, individuals preferentially mate with non-kin presumably to avoid negative effects associated with inbreeding depression (see Pusey and Wolf 1996); however, this trend is not ubiquitous and individuals from some populations preferentially mate with kin (e.g. Bateson 1982).

Juvenile Atlantic (Brown and Brown 1992, Rajakaruna et al. 2006) and coho salmon (Quinn and Busack 1985), rainbow trout (*Oncorhynchus mykiss*) (Brown and Brown 1992) and brook charr (*Salvelinus fontinalis*) (Rajakaruna et al. 2006), and Arctic charr (Olsén et al. 1998) are able to distinguish kin versus non-kin, but there are only a few studies that test

whether adults discriminate against or favor kin as mating partners in the wild (e.g. Landry et al. 2001; Garant et al. 2005) (Table 1) and those studies yielded inconsistent results. Garant et al. (2005) found genetic diversity amongst offspring and an increased number of mates led to higher offspring production in female Atlantic salmon, but only an increased number of mates led to higher offspring production in males of the same species. They concluded that females mated with more outbred males, but it is unclear whether the finding increased matings for outbred males was the result of intrasexual or intersexual competition or whether it was the result of pre-spawning selection (mate choice) or post-spawning selection (cryptic female choice or sperm competition). Further, it cannot be ruled out that other mate pairings were made and the offspring not viable. Landry et al. (2001) concluded that Atlantic salmon chose mates that were MHC dissimilar, but found no genome wide evidence that mate choice was a mechanism to avoid inbreeding. As above, the experimental design did not enable the authors to tease apart the mechanism of competition. Furthermore, results from studies on the effects of inbreeding on salmonid offspring also differ. Kincaid (1976) found that inbreeding (mating full-sibs) in rainbow trout resulted in crippled young and decreased survival compared to mating of outbred half-sibs. Alternatively, Turner et al. (2009) found no relationship with genome wide relatedness and survivability in Atlantic salmon. In this study, fish were mated randomly and survival was compared to parental relatedness, rather than categorically comparing survival of offspring between pairs of mates that were related and those that were unrelated.

Outbreeding can also be disadvantageous, especially for populations adapted to specific environments, but in some circumstances salmonids will mate with individuals from a different species. For example, female Atlantic salmon will mate with male brown trout (Castillo et al. 2010). Similar to inbreeding, effects of outbreeding in salmonids are variable. In masu salmon offspring production of dispersers was lower compared to individuals returning to their natal stream (Kitanishi and Yamamoto 2015) suggesting disadvantages may result from at least a certain level of outbreeding. A study on Chinook salmon found no evidence of outbreeding depression nor evidence of beneficial heterosis in examined traits (Lehnert et al. 2014). Similarly, Houde et al. (2010) found no effect

of inbreeding or outbreeding in their study population of Atlantic salmon. Houde et al. (2011) evaluated the potential effects of inbreeding and outbreeding depression on three populations of Atlantic salmon and concluded the effects were population dependent (Table 1). They recommend that potential effects of inbreeding and outbreeding depression should be evaluated on a population-level basis. Although some inbreeding occurs naturally as a result of strong homing and return timing of spawning individuals (Wang et al. 2002), there are apparently no studies that test whether males and females preferentially choose to mate with more or less related individuals in Pacific salmon.

Together, these results suggest that the effects of inbreeding and/or outbreeding differ among species and/or populations. However, differences in results may also be due to differences in methodology (e.g. natural spawning versus artificial crosses). To tease apart which factors are contributing to the observed findings (e.g. differences between species, populations or methodology) there needs to be standardized testing of inbreeding either across species or testing of different methodologies within a single species or population. While these studies provide interesting results as to whether mating events produced offspring, they are unable to tease apart the mechanism that led to the production of offspring (e.g. pre or post-spawning mechanisms). These questions could be explored by the incorporation of complementary behavioral tests of mate choice based on inbreeding. Further, it would be useful/interesting to test whether inbreeding affects not only survival of young, but ultimately whether they reach sexual maturity (Lehnert et al. 2014) and produce offspring.

(h) Fins

Recent work has demonstrated preference for fin size in some fishes. In medaka (*Oryzias latipes*) females prefer males with relatively longer anal and dorsal fins (Fujimoto et al. 2014) and in a cichlid (*Pelvicachromis taeniatus*) males prefer females with larger pelvic fins (Baldauf et al. 2010). In some species of salmonid there is evidence that the adipose fin is a sexually selected characteristic (e.g. Westley et al. 2008) and that females demonstrate a preference for males with larger adipose fins relative to body size (e.g. Järvi 1990; Petersson et al. 1999) (Table 1). The size of the

adipose fins of Atlantic salmon males who occupy a subordinate place in the hierarchy shrink after several days of interactions with dominant males (Haugland et al. 2011) and so larger adipose fins may be indicative of a socially dominant male, which are generally better competitors for access to females and may also be preferred by females. It is still unknown whether this apparent preference for relatively larger adipose fins persists in other salmonids including Pacific salmon. Typically, Pacific salmon produced in hatcheries have their adipose fins clipped for identification (Van der Haegen et al. 2005). It is an important question as to whether a preference for larger adipose size, including competition with males completely lacking adipose fins, leads to greater offspring production/reproductive success for males with relatively larger adipose fins.

Recent evidence also shows a mechanosensory role for adipose fins in the catfish (*Corydoras aeneus*). The adipose fin of this catfish is highly sensitive and able to detect small changes in lateral fin deflection (Aiello et al. 2016). This line of evidence has led to the hypothesis that the adipose fin is able to detect changes in water flow or turbulence. In a study of caudal fin kinematics in steelhead trout, Reimchen and Temple (2004) found that amputation of the adipose fin showed the greatest effect on caudal fin kinematics in turbulent conditions. If the adipose is able to detect and provide information regarding water flow, its absence could affect a male's ability to properly position himself and time the release of gametes in a mating situation in a flowing stream.

Similarly, there is evidence that the female anal fin is a secondary sexual characteristic in kokanee salmon (*Oncorhynchus nerka*) as it grows larger when females become sexually mature; however, because the female anal fin is often in the gravel during nest digging, it is unlikely to influence male preference, but may assist in egg deposition (Thorn and Morbey 2016). This fin enlargement did not occur with pectoral or pelvic fins at maturity. It is unknown whether this enlargement of the anal fin is consistent across salmonid species and populations or whether it is dependent on other external factors.

Incorporation of genetic analyses could provide further insight into whether the absence and/or size of an adipose fin affects male and female reproductive success and whether males incur a reproductive

benefit of mating with females with larger anal fins in the wild.

(i) *Life history*

Assortative mating can occur based on behaviours and life history strategies. For example, melon flies (*Bactrocera cucurbitae*) mate assortatively based on development duration (Miyatake and Shimizu 1999). Assortative mating with respect to life history strategies also occurs within at least some (e.g. Foote and Larkin 1988), but not all (see Thériault et al. 2007), salmonid mating systems. Some species of salmonid exhibit distinct morphs (e.g. Hendry and Quinn 1997; Moreira and Taylor 2015) and life history strategies (e.g. sockeye and kokanee), including different spawning morphotypes (e.g. beach, stream, or glacial (Ramstad et al. 2010)), which can lead to reproductive isolation (Hendry et al. 2000). For example, individuals that spawned in streams instead of lakes had half the offspring production as natal stream spawners. There was no difference in offspring production of stream spawners who did not spawn in their natal stream compared to those spawning in their natal stream suggesting the reduced lifetime offspring production of lake spawners may be attributable to differences in morphotypes between lake and stream spawners (Peterson et al. 2014) (Table 1). This suggests the possibility of genetic or behavioural differences that result in lowered egg survival of lake spawners in faster flowing streams. For example, in fast flowing stream environments there may be increased payoff for females to increase the depth of their redds to prevent eggs from being swept away in the current. Due to differences in stream flow there may also be different selective pressures of sperm characteristics such as velocity and longevity. It is unknown whether finer scale differences in stream characteristics, such as velocity and depth, lead to assortative mating within habitats as well as between habitats. Fine-scale differences in optimal spawning habitat could be important in maintaining genetic diversity within populations.

Future directions and priorities

There are multiple factors known to influence mate choice in other species that have not yet been tested as

a mechanism of mate choice in salmonids, including personality, cognition, predation, and gene drive. As such, there remain many unresolved questions involving mate choice in salmonids that could be important not only for our general understanding of mate choice in salmonids and potentially other polyploid species, but that could also contribute to improved conservation and hatchery practices. For the remainder of this review we will discuss (i) topics relevant to mate choice studies that have not been well studied in salmonids, but could potentially affect sexual competition in salmon (ii) the need for integration of different methodologies to enable a broader understanding of the factors that affect mate choice in salmonids and the underlying mechanisms, including what is driving observed differences in sexual competition between individuals, populations and species, and (iii) testable theory related to if and how mate choice patterns are impacted by increased ploidy.

Relatively unexplored topics in salmonid mate choice

(a) *Condition*

The state or condition of individuals can affect mating effort, mating preferences, attractiveness to others, gamete quality, and ultimately reproductive success (Bakker et al. 1999; Hebets et al. 2008; Schultzhaus et al. 2017; Evans et al. 2017). An individual's overall condition is influenced by factors including, but not limited to, diet (e.g. Schultzhaus et al. 2017), and parasite load (Hamilton and Zuk 1982). The effect of parasites on fish behaviour has been relatively well studied. Studies have shown that parasite infection can affect fish behaviour in multiple ways including altering their mate choice (Lopez 1999; Mazzi 2004) and an individual's likelihood of being selected as a mate (Milinski and Bakker 1990; Barber et al. 2000). Parasitic infection can diminish an individual's nutrition and energy reserves causing a decrease in attractive signals such as colour (Hamilton and Zuk 1982) and/or in reproductive effort including performing fewer courtship displays (e.g. Kennedy et al. 1987; Pélabon et al. 2005). Infection of visible parasites or changes in behaviour also signal the health of an individual's immune system to prospective mates who may choose to reject mates based on

infection (Zahavi 1975). Furthermore, parasitic infection can impact male reproductive success by negatively affecting ejaculate quality (e.g. Liljedal et al. 1999; Kekäläinen et al. 2014). Because sperm is genetically different to one's self, the body will initiate an immune response towards it. Therefore, males may benefit from immune system suppression to protect their sperm prior to ejaculation (Liljedal et al. 1999; Skau and Folstad 2005); however, immune system suppression in males with infection may not be beneficial for their own survival. In salmonids, male Arctic charr with high levels of infection produced lower quality ejaculates compared to uninfected individuals. Males who resist parasite infection may therefore be able to produce higher quality ejaculates (Liljedal et al. 1999). We are unaware of any other studies that explicitly test how parasite infection affects mate choice in salmonids.

(b) Predation

Change in predation pressure can affect mate choice, mating behaviour, and sexual selection (Andersson 1994). This effect has been documented in insects (e.g. Hedrick and Dill 1993), amphibians (e.g. Tuttle et al. 1982), and fish (e.g. Endler 1987; Johnson and Basolo 2003). Because showy ornaments and displays are conspicuous and attract the attention of potential predators, in high predation environments selection should favor males who are less conspicuous and/or strategically adjust courtship displays in the presence of predators. For example, in the presence of a predator, male guppies from a high predation environment altered their conspicuous courtship displays whereas those from a low predation population did not adjust their courtship displays according to predation risk (Magurran and Seghers 1990). Changes in ambient predation pressure can affect mate choice and reproductive success by increasing predation on certain phenotypes over others, such as more conspicuous males.

Salmonids play an important role in ocean, freshwater and terrestrial ecosystems as an important food source for other species including bears (*Ursus* species) (e.g. Hilderbrand et al. 1999), marine mammals (e.g. Keefer et al. 2012; Wasser et al. 2017), birds (e.g. Quinn and Buck 2001), and humans. These predation pressures can cause selection on morphological and behavioural characteristics related to mating and reproductive success. This effect is

documented in sockeye salmon (Quinn and Kinnison 1999; Quinn et al. 2001). Several studies reported that variation in predation pressure led to size selective mortality within and between populations (Quinn and Kinnison 1999; Quinn et al. 2001; Quinn and Buck 2001) with avian predators mainly targeting females and smaller fish and bears targeting males and larger fish. Predation from brown bears (*Ursus arctos*) was typically higher in smaller, shallow streams. With greater predation pressure from brown bears in these streams typical dominance of larger males for access to females was not observed (Quinn et al. 2003). Size selective fishing by humans can also affect OSR and opportunity for sexual selection (Kendall and Quinn 2013). Because populations are subject to different predators spatially and temporally (Keefer et al. 2012) effects of predation on sexual competition and reproductive success likely differ according to location, composition of predator populations, and timing; however, we do not know of any studies that directly compare salmonid mate choice in the presence or absence of predators or examine the effect of predator composition or density on mate choice. Understanding how predation shapes mate choice in salmonids will provide a better overall understanding of the factors affecting individual reproductive success in different environments.

(c) Gene drive

Selfish genetic elements (SGEs) (e.g. transposable elements, meiotic drivers, post segregation killers) (Werren 2011), ubiquitous in eukaryotes, frequently result in reproductive incompatibility that can lead to reduced reproductive success in males (Price and Wedell 2008; Lindholm et al. 2016). SGEs occur more than would be expected by chance in gametes and/or offspring and are associated with costs such as reduced fertility and sex bias in offspring (Wedell 2013). There is some evidence that individuals can avoid potential mates that may transmit SGEs by using morphological characteristics (Wilkinson et al. 1998) or odor cues (Lenington 1991). One example of a morphological trait associated with gene drive (the system that enables the increased transmission of SGEs) is the length of eyestalks in stalk-eyed flies (*Diopsidae*) (Wilkinson et al. 1998). There is also evidence from mice (*Mus musculus*) that sperm competition can suppress gene drive; however, it is not known whether

this type of selection against gene drive happens at the gamete level in polyploids, which have different inheritance patterns than diploid individuals. If gene drive is occurring in salmonids, lack of sperm competition in some artificial breeding designs could be producing hatchery males with SGEs that are later avoided by females (Manser et al. 2017). While identification of SGEs is difficult, new technologies are helping move the field forward and new insights are being made. An improved understanding of SGEs and how they impact mate choice decisions and genetic inheritance in salmonids will help resolve theoretical questions surrounding SGEs in polyploids in general and provide insight into improved breeding practices for commercially important polyploid species, including salmonids.

(d) Epigenetics

Over the last two decades, there has been an increased interest in epigenetic effects on animal behaviour (e.g. Weaver et al. 2004; Curley et al. 2011), including reproductive behaviours (Crews et al. 2007), and offspring performance (e.g. Ducatez et al. 2012; Mashoodh et al. 2012; Valtonen et al. 2012). These epigenetically mediated changes are frequently the result of genome methylation and have been documented in insects (e.g. Crean et al. 2014), fish (e.g. Taborsky et al. 2013), and mammals (e.g. Crews et al. 2007; Jašarević et al. 2011; Skinner et al. 2014). They can influence the development of sexually selected characteristics (e.g. Jašarević et al. 2011, 2012) including behaviours such as courtship (Jašarević et al. 2012). Importantly, these epigenetic changes are heritable. For example, exposure to an endocrine-disrupting chemical can alter mate preferences in mice for three generations (Crews et al. 2007).

For external fertilizers, such as salmonids, and possibly some internal fertilizers, the recent pre- and post-release environments of sperm can affect its phenotype and the phenotype of any resultant offspring (see Marshall 2015 for a review). For example, the marine invertebrate broadcast spawner, *Galeolaria gemineoa*, produce offspring that are more resistant to hyposalinity when the sperm that sired them were also exposed to a similar hyposalinity (Ritchie and Marshall 2013). These epigenetic changes could have important implications for salmonids bred and/or reared in artificial environments during captivity, their gametes and/or offspring are likely exposed to

different compounds and/or different concentrations of compounds than they would in a completely wild experience. A recent study by Le Luyer et al. (2017) demonstrated differences in genome methylation between hatchery and wild coho. Areas of the genome showing differences in methylation include genes related to salinity tolerance and behaviour, amongst others. Hatchery induced epigenetic changes such as those identified by Le Luyer et al. (2017) could affect mate choice decisions over subsequent generations in salmonids. For a comprehensive understanding of the factors affecting mate choice in salmonids, including differences between wild and captive bred individuals, we need to better understand how epigenetic changes affect their mating behaviour, mate choice and reproductive success.

(e) Cognition

Teleost fish display individual variation in cognitive abilities with sources of variation including sex differences, personality and degree of brain lateralization, which are heritable (Lucon-Xiccato and Bisazza 2017). Cognitive differences could contribute to individual differences in the ability to achieve fertilizations that produce offspring which survive to maturity. In vertebrates, including fishes (Shohet and Watt 2009), females often prefer to mate with males with good cognitive abilities (Boogert et al. 2011). In addition to being preferred by females, improved cognitive abilities could help individuals make good mate choice decisions and/or enhance their ability to compete intrasexually.

Recently, the effects of social competence and plastic behaviour on fitness have been gaining attention (Taborsky and Oliveira 2012). With respect to mate choice, socially competent individuals would be able to accurately assess their own ability to compete for females and direct efforts strategically. Because environmental change has been linked to enhanced cognitive abilities (e.g. Kotrschal and Taborsky 2010) and many salmonid habitats are currently undergoing rapid human induced environmental change (Gross 1991; Sih et al. 2011), it is important to understand if/how environmental change can alter mate choice and reproductive success of salmonids.

Most fish reared in a hatchery experience a less stimulating and more crowded environment than is typical for wild fish during early life. There is evidence

that cognitive, swimming (e.g. (Ahlbeck Bergendahl et al. 2017), foraging (Brown et al. 2003; Rodewald et al. 2011)), and other abilities are decreased when reared in less complex (e.g. Brown et al. 2003; Salvanes et al. 2013; DePasquale et al. 2016) and more crowded environments (Brockmark et al. 2010, but see Näslund et al. 2017). Research on other species has further suggested that the method of sensory (i.e. visual, chemical, or auditory) enrichment may have long-lasting effects on the ability of individuals to learn using specific sensory systems (Dolivo and Taborsky 2017). These hypotheses should be tested in salmonids to explore whether rearing in more complex environments also improves the reproductive success of hatchery fish. Because there is evidence that differences in personality and cerebral lateralization are at least in part heritable, a greater understanding of their genetic basis in salmonids will give us a better understanding not only of salmonid relative reproductive success, but also of the evolution of cognition in polyploids.

(f) *Personality*

Individuals often prefer certain behavioural characteristics in mates including elaborate courtship displays and innate personality traits, which are consistent across contexts and repeatable over time, such as boldness; however, preference for boldness is not consistent through the animal kingdom. For example, female guppies prefer to mate with bolder males (e.g. Godin and Dugatkin 1996), but female rainbow kribis (*Pelvicachromis pulcher*) preferentially mate with males who display a dissimilar level of boldness to themselves (Scherer et al. 2017), and pairs of great tits (*Parus major*) that mated assortatively at either extreme of the boldness spectrum had the greatest reproductive success (Both et al. 2005). A meta-analysis by Smith and Blumstein (2008) on multiple taxa, including fishes, found a significant positive correlation between boldness and reproductive success in captive animals. This relationship was significant for both males and females in captivity, but was found to be strongest for captive males. Fleming et al. (1996, 1997) found first-generation hatchery bred Atlantic salmon were bolder compared to wild counterparts. Further research is needed to understand the variation in preference for personality and whether

differences in personality play a role in salmonid mate choice and reproductive success.

Personality traits such as boldness are also correlated with an individual's likelihood of using social information during decision-making such as strategically adjusting their mate choice in the presence of an audience of sexual competitors (Bierbach et al. 2015). Since social information can provide important and energetically inexpensive information regarding the quality of potential mates, differences in personality could further affect an individual's ability to make good mate choice decisions that lead to increased reproductive success; however there have been few studies on the effect of behavioural traits and individual personality on reproductive success in salmonids despite observations that this taxon displays repeatable personality characteristics (e.g. Sneddon 2003; Wilson and Stevens 2005; Adriaenssens and Johnsson 2010) that are heritable (Vilhunen et al. 2008; Kortet et al. 2014) and evidence that personality can affect mate choice (e.g. Godin and Dugatkin 1996; Both et al. 2005; David and Cézilly 2011; Scherer et al. 2017).

(g) *Courtship*

Males who perform acts of courtship such as presentation of nuptial gift, performance of song or elaborate displays are often preferred by females in polygamous mating systems wherein males compete for access to sexually receptive females (Andersson 1994); however, courtship is energetically costly and often highly conspicuous to nearby predators. An alternative tactic to achieve fertilizations is sneak mating attempts. In general, sneak mating secures a lesser proportion of fertilizations compared to males who perform courtship acts (e.g. Berejikian et al. 2010). Differential fertilization success may be a function of female preference since sneaker males have greater gonad investment (e.g. Vladić et al. 2010), and more competitive sperm (e.g. greater velocity) (Rudolfson et al. 2006; Young et al. 2013), although it is often released after that of courting males (e.g. Sørum et al. 2011).

Upon arrival at spawning grounds, both male and female salmonids engage in distinct pre-mating behaviours including female redd digging and male courtship. Exhibition of these behaviours can signal to potential mating partners and other conspecifics about

an individual's quality (e.g. fecundity) and readiness to spawn. Pre-mating behaviours include males approaching females, darting towards nest-digging females, hovering nearby, quivering and crossing over (reviewed in Esteve 2005) (Fig. 1a). Female status and behaviour affect male courtship displays. For example, male Atlantic salmon perform more courtship displays towards females digging redds (De Gaudemar et al. 2000) and masu salmon and Biwa salmon (*Oncorhynchus rhodurus*) perform more courtship displays towards females who had recently ovulated (Honda 1982). Aside from the study of De Gaudemar et al. (2000) showing that female Atlantic salmon prefer males based on intensity of courtship, there do not appear to be any studies that investigate how female preference for males varies according to duration and quality of courtship displays performed.

A genetic basis of courtship behaviour has recently been identified in *Drosophila* (e.g. Yamamoto and Koganezawa 2013). An understanding of the genetic basis of pre-mating behaviours and courtship in salmonids including differences in genetic makeup and gene expression could provide important insight into variation in reproductive success and mate choice.

(h) Social factors

While the majority of research on mate choice and reproductive success has focused on morphological traits such as body size and coloration, there is growing evidence that one's social environment (e.g. individuals within signaling and receiving distance), and interactions with others, aside from prospective mates, can affect mate choice, sexual competition and thus reproductive success (e.g. Gröning and Hochkirch 2008). Extensive evidence that social factors are important to mate choice exists in amphibians (e.g. Hettyey and Pearman 2003), birds (e.g. White and Galef 1999), fish (e.g. Oliveira et al. 2002; Hesse et al. 2016), and mammals (e.g. Perret 1992). Because in most instances salmon spawn in the presence of multiple individuals and will compete directly with others for access to breeding locations and high quality mates, the social environment is likely relevant to mate choice in salmonids. One's social environment also provides opportunity for individuals to learn about prospective mates and competitors from observing the behaviour and interactions of others (Valone

and Templeton 2002; Witte 2006; Grosenick et al. 2007).

In natural social networks fish are able to eavesdrop on the interactions of others when their own personally acquired information may not be reliable or it is too expensive to adequately sample all potential resources. One social phenomenon that may be especially interesting in relation to salmon mate choice is mate choice copying. There is a large body of evidence that female insects, birds, fish, and mammals will use social information to assess the quality of potential mates and copy the mate choice of other females (see Vakirtzis 2011 for a review). An increasing number of studies also demonstrate mate choice copying by males (e.g. Schlupp and Ryan 1997; Auld and Godin 2015). Copying the mate choice of another male increases sperm competition for both males, but that cost may be offset for the copier by reduced costs of sampling females. To avoid being copied and the subsequent increase in sperm competition males can either alter their mate choice, change their behaviour to conceal their true mate choice or avoid competition (e.g. Schlupp and Ryan 1997; Auld and Godin 2015). In Trinidadian guppies, this change in mating behaviour is strongest in the presence of larger, more competitive rivals (Auld et al. 2017). In salmonids, chemicals released that can influence spawning behaviour in the opposite sex could also provide information to intrasexual competitors (e.g. Arctic charr, Sveinsson and Hara 1995; rainbow trout, Yambe and Yamazaki 2001).

In other species, familiarity with potential mates can also affect mate choice with individuals preferentially mating with or avoiding familiar individuals (reviewed in Cheetham et al. 2008). Avoidance of mating with familiar individuals is evident in insects (e.g. fruit flies, *Drosophila melanogaster*, Ödeen and Moray 2008), reptiles (brown anole, *Anolis sagrei*, Tokarz 1992), and live-bearing fish (guppies, Hughes et al. 1999). Conversely, medaka fish (Okuyama et al. 2014) and giant kangaroo rats (*Dipodomys ingens*) (Randall et al. 2002) preferentially mate with familiar individuals. Familiarity with potential mates allows individuals to make mate choice decisions based on accumulated personally acquired information while mating with unfamiliar individuals may reduce risk of inbreeding and/or introduce novel genes into the population. However, aside from studies on the effect of density in coho (Fleming and Gross 1994) and

Atlantic salmon (Weir et al. 2012), and the effect of social environment in rainbow trout (Rouger and Liley 1993; Liley et al. 2002) (see Table 1) we are not aware of any studies that examined the effect of the social environment on salmonid mating behaviour even though in other contexts salmonid behaviour can be affected by social environment. For example, Arctic charr learn anti-predator behaviours from conspecifics (Vilhunen et al. 2005). Given this ability of salmonids to use social information, we should explore potential use of social information in a mating context including possibilities of mate choice copying and audience induced changes in mating behaviour of salmonids.

Mechanisms and trends

There are pros and cons to the different methodologies used in the studies discussed in this review. Many studies did not actually test behavioural mate choice, but rather inferred mate choice from genotypes of offspring (e.g. Landry et al. 2001; Forsberg et al. 2007). While the ultimate production of viable offspring is important, and survival offspring to sexual maturity is the true measure of an individual's fitness, it provides little insight to the mechanisms leading to the production of those offspring. For instance, it is possible that individuals made other mate choice decisions that did not result in successful fertilizations or survival of offspring. Studies that used natural spawning events in river systems and inferred mate choice from the genotypes of juvenile offspring produced have the advantage of most closely mimicking conditions in the wild. However, this method makes it difficult to determine whether the observed mate pairs are the result of inter- or intra-sexual competition and whether selection is happening before or after spawning.

Some new insights into the mechanism of selection can be gained from controlled mate choice experiments in artificial stream channels. Using artificial stream channels allows for more control of potentially confounding factors and facilitates behavioural observations, but at the expensive of a less natural environment. Finally, stripping gametes for artificial fertilizations allows for very controlled studies of sperm competition and gamete choice, but has the disadvantage of gametes being damaged in the process (e.g. Campbell et al. 1992). It is important to pursue questions related to mate choice in salmonids and

polyploids in general, using traditional methodologies, such as behavioural studies together with novel methodologies, including the incorporation of genetic techniques, transcriptomics and proteomics (Makiguchi et al. 2016b; Gombar et al. 2017) within the same system. The complementary use of methodologies within a single system may allow researchers to answer questions related to mating behaviour and reproductive success that would not be possible with traditional behavioural studies (Archie and Chiyo 2011). The use of these techniques together with behavioural studies may shed light on the mechanisms driving patterns of mate choice in polyploids observed in nature.

Mate choice decisions can be plastic and context-dependent (e.g. Gauthey et al. 2016), being influenced by the environment including abiotic and biotic conditions such as predation and the social environment. It is therefore important to not just consider current mate choice decisions in one scenario or point in time, but to identify trends and understand how they vary across time and environments. This understanding is particularly important because environmental change of today is demonstrating striking extremes and rates of flux across habitats. Sustainable practices, therefore, needs to learn more about the interface of these variable phenomena (mate choice and climate), including new response to unprecedented states, in order that our futures remain resilient. Determining trends in salmon mate choice and how mate choice varies with environmental conditions should be a priority. Among salmonids, certain groups are under-represented in the current body of literature on salmonid mate choice and reproductive success (e.g. taimen, long-fin charr, round whitefish (*Prosopium cylindraceum*), lenoks). Further study on these species/populations could provide greater insight into patterns of reproductive success. The use of meta-analyses and comparative studies to determine underlying patterns that contribute to the variation of mate choice and reproductive success in salmonids, including finer scale differences within populations will be useful to determining the underlying mechanisms that are driving the different mate choice patterns seen in different species, populations, and studies.

Finally, many of the aforementioned studies used the production and/or survival of juvenile offspring, as a proxy of mate choice and/or RRS, which, while informative and an important measure, does not

provide information regarding the survival of those offspring to sexual reproduction themselves (i.e. fitness). In instances where studies of mate choice are being undertaken to improve conservation and/or hatchery practices, it is useful to know whether the offspring produced survive to reproduce themselves. Given that salmonids do not reach sexual maturity for several years, this would require investment into the implementation of multi-year studies.

Additional complexities owing to ploidy

Extensive literature on the evolutionary significance of polyploidy among plants holds that (1) polyploids have higher levels of heterozygosity, (2) are less inbred and (3) experience genome rearrangements more commonly than their diploid counterparts (Soltis and Soltis 2000). This raises a number of interesting questions for mate choice. However, mate-choice studies in plants are rare and the few existing studies focus largely on pre-zygotic mechanisms among gametes and associated reproductive organs rather than behaviour (Wilson and Burley 1983; Marshall and Ellstrand 1988). Other research notes that polyploidy is less prevalent in the animal kingdom; notable exceptions include amphibians and fish where complete lineages, including salmonids are of relatively recent polyploid origin (Zhou et al. 2002; Le Comber and Smith 2004; Mable et al. 2011). Indeed, some have pointed to the notion that a ploidy shift may have provided genomic innovations that enabled development of anadromous life histories expressed among salmonids (Allendorf and Thorgaard 1984; Mable et al. 2011). Intriguing research exploring whether ploidy variance among insects may indeed provide innovation for evolution of highly social honeybees (Chau and Goodisman 2017) has yet to be fully explored.

Studies such as these raise question as to whether ploidy shifts observed among salmonids may have opened new doors for the development of socially based aspects in this group, including those related to mate choice mentioned above. Returning to more basic considerations, salmonid tetrasomy raises a pressing question for mate choice: genetic variation is potentially doubled among mates, yet only an unknown fraction of this variation is actually expressed. How is this unknown ‘boon’ of heritance accounted for as partners make choices? While, this

issue occurs among diploid species to some extent because of dominance, and partners always risk the gamble of which actual allele will occur in the gametes they and their partner(s) contribute to fertilized zygotes they share, in tetraploid species, gametes may contain two alleles for paralogous loci. Given greater chances of genomic rearrangement noted above, how do mate choice decisions account for these increasing aspects of variability? Some studies have provided evidence for use of sound and/or odors as means of attaining ploidy-specific assortative mating in amphibians (Keller and Gerhardt 2001; Mable et al. 2011) and note that it would be interesting to determine whether mate choice by ploidy exists among fish and underlying mechanisms. We, however, are not aware of any literature that has broached our question about how to account for, or gamble with increasing levels of variability, likely among polyploid mate choice scenarios. Development of mate choice models that incorporate increased levels of ploidy and the use emergent experimental gene silencing using CRISPR-Cas9 technologies in empirical studies may illuminate some of these issues. Resolving these questions in salmonids could further shed light on mate choice in other polyploid fishes such as sturgeon (Acipenseridae) and some carp (Cyprinidae) (Leggatt and Iwama 2003).

Application and importance for salmonid aquaculture, conservation, and management

There is a growing body of evidence that mate choice is important for offspring production in captive contexts, with greater offspring production for individuals who were able to choose their own mates compared to individuals who could not (see Martin-Wintle et al. 2018 for a review). In salmon aquaculture, individuals are not given the opportunity to select their mates and in many instances, there is little to opportunity for post-copulatory sexual selection (e.g. cryptic female choice or sperm competition between potential sires). A more complete understanding of salmon mate choice and how this varies across context (species, climate and space) will better inform decisions related to mate pairings in a hatchery context. This and other improved hatchery practices that provide climate sustainable fitness to offspring will contribute to conservation and management strategies for more resilient futures.

Conclusions

There is strong evidence of mutual mate choice in many salmonids; however, unresolved questions remain surrounding traits that affect mate choice and how those traits are affected by external factors such as changing environments, how they differ between populations and over time, and how those preferences affect reproductive success. Combining emerging technologies, including genetic techniques, with traditional behavioural studies can improve our insight into the mechanisms and maintenance of variation in behaviours including those related to mate choice. Answering these questions will propel forward our current knowledge about salmonid populations and help inform future fisheries management decisions. Moreover, it will shed light on the different inheritance patterns in tetraploids and the selective forces that drive speciation of salmonids.

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