Dispersal and gene flow in anadromous salmonids: a systematic review

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Abstract

Dispersal is a ubiquitous ecological process that has been extensively studied in most groups of organisms. Despite several evidence and earlier reviews, dispersal and its implications are still overlooked in salmonids, where homing is the predominant strategy. We provide a systematic and updated review of dispersal and gene flow among several species of anadromous salmonids. The 372 reviewed studies were unevenly distributed among species, with Atlantic salmon and sea trout being the most studied. A significant proportion of studies focused on the genetic differentiation between populations without estimating dispersal, while others examined straying from hatchery fish. Few studies investigated dispersal on wild populations and a few modelling approaches were developped on the topic. We highlight various facets of dispersal, including the terminology, metrics, methods, and spatio-temporal scales used. We showcase a strong variability in estimated rates within and between studies, which is likely related to methodologies, species propensity, and spatial systems. We also investigated the relationship between dispersal metrics and distance. Finally, we emphasize a lack of knowledge on the drivers of dispersal and that still few studies consider, and even fewer assess, the implications of dispersal for the conservation and management of salmonids.

Keywords: salmonids, dispersal, gene flow, metapopulation.

Introduction

Dispersal, i.e. the movement of individuals between populations with potential consequences for gene flow (Ronce, 2007), is a ubiquitous ecological process. It has been extensively studied in most groups of organisms (Clobert et al., 2012; Bonte and Dahirel, 2017), with a focus on its causes and consequences (Fronhofer et al., 2023). Indeed, the proximate and ultimate causes of dispersal have been largely described, with dispersal being selected as it may reduce competition, kin interactions, inbreeding as well as buffer against habitat stochasticity (Bowler and Benton, 2005). Ultimately, dispersal has several consequences for the eco-evolutionary dynamics of populations. It can limit the risk of extinction and aid in colonization, but it can also influence the local dynamics, stability, and adaptation of a set of populations (Garant et al., 2007; Benton and Bowler, 2012; Webster et al., 2017; Lamarins et al., 2022). To better understand the dynamics of a local population, it is then necessary to identify its metapopulation context.

Anadromous salmonid species, such as Atlantic salmon (*Salmo salar*), Chinook salmon (*Oncorhynchus tshawytscha*), or Rainbow/Steelhead trout (*Oncorhynchus mykiss*), are well-known for their philopatric behaviour, commonly referred to as 'homing' (Salmenkova, 2017). Despite long oceanic migrations, anadromous salmonids have a remarkable ability to return to their natal river to breed. As a result, salmonids often exhibit significant local adaptation and genetic differentiation between populations (Fraser et al., 2011), which may explain why dispersal has been less studied in salmonids than in organisms (Birnie-Gauvin et al., 2019). Additionally, the three phases of dispersal (i.e. emigration, transfer and settlement, Bonte et al., 2012) lack clear identification in the case of anadromous salmonids, which limits our ability to comprehend the process of dispersal and identify its drivers. However, salmonids may be considered from a metapopulation perspective (Rieman and Dunham, 2000) as defined by Schtickzelle and Quinn (2007). This is because salmonids have i) discrete spawning habitats, ii) asynchronous population dynamics and iii) dispersal behaviour.

Several reviews on the dispersal of salmonids already exist, each with a particular focus

summarized in Table 1. First, Quinn (1993) compared dispersal from wild populations to that from hatcheries, while Altukhov and Salmenkova (1994) reviewed straying intensity and genetic differentiation in several salmonid species. Then, Rieman and Dunham (2000) wrote an opinion paper on metapopulation dynamics in inland salmonids, while Schtickzelle and Quinn (2007) extended this approach for anadromous salmonids and their conservation. Hendry et al. (2004) also devoted a chapter of their book providing an evolutionary perspective on homing and straying among salmonids. More recently, Keefer and Caudill (2014) reviewed dispersal mechanisms and rates in several species, while Bett et al. (2017) reviewed the main factors potentially influencing dispersal rates. Each of these reviews has made a significant contribution to our understanding of dispersal in salmonids.

However, none of them carried out a systematic review, i.e. by using a query with identified keywords to enable reproducibility and quantification of studies. Additionally, they did not differentiate between dispersal from wild populations to hatcheries. Yet, there are several evidence that dispersal may be higher in hatcheries compared to wild populations (Labelle, 1992; Quinn, 1993; Ford et al., 2015). Methods and metrics used to estimate dispersal have not been thoroughly reviewed, despite their potential to strongly influence estimations and our understanding of dispersal. Estimated rates have been examined by Altukhov and Salmenkova (1994), Hendry et al. (2004), and Keefer and Caudill (2014), but an update based on recent literature and focusing solely on wild populations is needed. In addition to empirical dispersal estimations, we included modelling approaches of salmonid dispersal (either statistical or simulation models such as Bowlby and Gibson, 2020) because they can enhance our understanding of this process and its consequences. Finally, the implications of dispersal for salmonid conservation have not been reviewed.

Our study proposes a systematic review of dispersal and gene flow among several species of anadromous salmonids, including facultative anadromous species such as sea trout (*Salmo trutta*) and Steelhead trout (*Oncorhynchus mykiss*). First, we used a keyworded search to ensure reproducibility and quantifiability. We present an updated review of the methods and metrics

Table 1: Similarities and differences between existing reviews. For each study we indicate whether it is a systematic review, the number of species reviewed, whether they differentiate wild *vs* hatchery fish, whether they reviewed the methods and metrics to estimate dispersal, the factors that might influence its propensity, the estimated rates, but also whether they reviewed modelling studies of dispersal (statistical or simulation models) and implications for conservation. Discuss.= discussed.

Review	Quinn (1993)	Altukhov and Salmenkova (1994)	Hendry (2004)	Schtickzelle and Quinn (2007)	Keefer and Caudill (2014)	Bett et al. (2017)
Systematic	No	No	No	No	No	No
Number species	6	8	8-20	-	7	7
Wild *vs* hatchery	Yes	No	No	No	No	No
Methods	No	Yes	Yes	No	No	No
Metrics	No	No	No	No	Yes	No
Factors	Yes	No	Yes	No	Yes	Yes
Rates estimates	No	Yes	Yes	No	Yes	No
Models	No	No	No	No	No	No
Conserv. implic.	Discuss.	Discuss.	No	Yes	No	Discuss.

employed, factors identified as drivers of dispersal, and estimated rates among several species, with a focus on wild populations exclusively. Additionally, we examined the spatial and temporal scales of estimations. Finally, this review aims to assess the consideration of dispersal implications for conservation and management, including modelling approaches, among studies.

Method for the literature review

To evaluate to which extent dispersal is measured and considered in salmonids, we performed a literature review on the Web of science (WOS) advanced research query using the following keywords: "Species (see below) *AND* (dispersal *OR* straying *OR* gene flow *OR* metapopulation *OR* homing) *NOT* (juvenile *OR* lice)". Note that this literature research is limited from 1955 to 24th January 2023 and to articles reported in WOS, including grey literature (e.g., technical reports).

The search focused on the following species: Atlantic salmon (*Salmo salar*), Coho salmon (*Oncorhynchus kisutch*), Chum salmon (*Oncorhynchus keta*), Pink salmon (*Oncorhynchus gorbuscha*), Sockeye salmon (*Oncorhynchus nerka*), Chinook salmon (*Oncorhynchus tshawytscha*), Steelhead trout (*Oncorhynchus mykiss*), and Brown trout (*Salmo trutta*). Each of these species present one anadromous life history form. Because it appeared in several queries, it is important to note that one study on several species was considered as several studies (i.e. one per species).

From this query, studies based on resident life histories forms, landlocked populations, reviews, not found studies, and others focusing on other topics or species (e.g. parasites, introgression impacts, physiology) were classified as non relevant (73% of studies overall). The 358 relevant studies retrieved from the query focus on populations that are at least partly anadromous. We included 14 additional references to the database using a snowball approach: we only kept studies cited in previous reviews which estimated or suggested dispersal in wild populations (i.e., studies based on hatchery or transportation experiments, as well as studies limited to genetic differentiation were not included).

Box 1: Glossary of studies categories and dispersal metrics

- *Juvenile*: studies investigating dispersal of juveniles.
- *Hatchery*: studies providing estimations or observations of dispersal of fish coming from hatcheries or hatched during a certain period of time.
- *Wild genetics*: genetic analysis (e.g., genetic differentiation among populations) suggesting dispersal and gene flow without estimating it.
- *Model*: modelling approach (statistical or simulation models) including a dispersal process.
- *Wild observation*: studies showing evidence of dispersal among wild populations but not providing estimates (e.g. low sample size).
- *Wild estimate*: studies providing estimates of dispersal (either gene flow, donor rate or immigration rate) in wild populations (*via* genetic or tagging methods).
- *Emigration rate*: proportion of a focal population, after migration to sea, that does not return to its original population, but instead returns to another population.
- *Immigration rate*: proportion of the focal population which is not originating from it.
- *Gene flow*: transfer of genetic material between populations, which is measured as a number of migrants per generation incoming to populations (Nm) or a migration rate (m).

We classified every study according to several categories (see Box 1 and Figure 1) and species (Supplementary Material 1). We evaluated whether the implications of dispersal for population conservation and management were discussed or investigated in empirical studies of wild populations and modelling studies. We also reported the frequency of different terms referring to dispersal within the manuscripts. Then, focusing only on studies that provide

estimates of dispersal, we identified the method used (e.g. genetic or tagging approaches) as well as the spatial and temporal scales of measurements. We collected the estimated rates from these studies and classified them into three metrics: *emigration rate*, *immigration rate*, and *gene flow* (see Box 1; Supplementary Material 2). We did not analyze estimates of the number of migrants per generation for gene flow because they were not comparable between studies. Only migration rates were considered. Additionally, we reported the distance between populations. If distance measurement was not specified in the study, we measured the "swimming" distance, which is the distance separating two populations along the coastline or the river system. Finally, we reported whether studies investigated the influence of individual and population factors (e.g. sex, age, density), or environmental factors (e.g. water temperature, discharge) as potential drivers of dispersal.

Query overview

Species representation

The 372 retained studies were unevenly distributed among species (Figure 1 A). Atlantic salmon was the most represented (33% of studies), followed by sea trout (19%), steelhead trout (15%), Chinook salmon (13%), Sockeye salmon (8%), Coho salmon (5%), Chum salmon (5%), and pink salmon (2%). Keefer and Caudill (2014) also reported a higher number of studies for Atlantic salmon, Steelhead, Chinook salmon, compared to Coho, Sockeye, Pink and Chum salmon. At first glance, it is surprising that Pacific salmon and particularly Pink salmon, an iconic species of spatial dispersal, are under-represented. It may be explained by the broader historical and current interests in other species such as Atlantic salmon and trouts. Additionally, the restricted spatial distribution of Pacific salmon, although expanding for Pink salmon, may also contribute to this phenomenon.

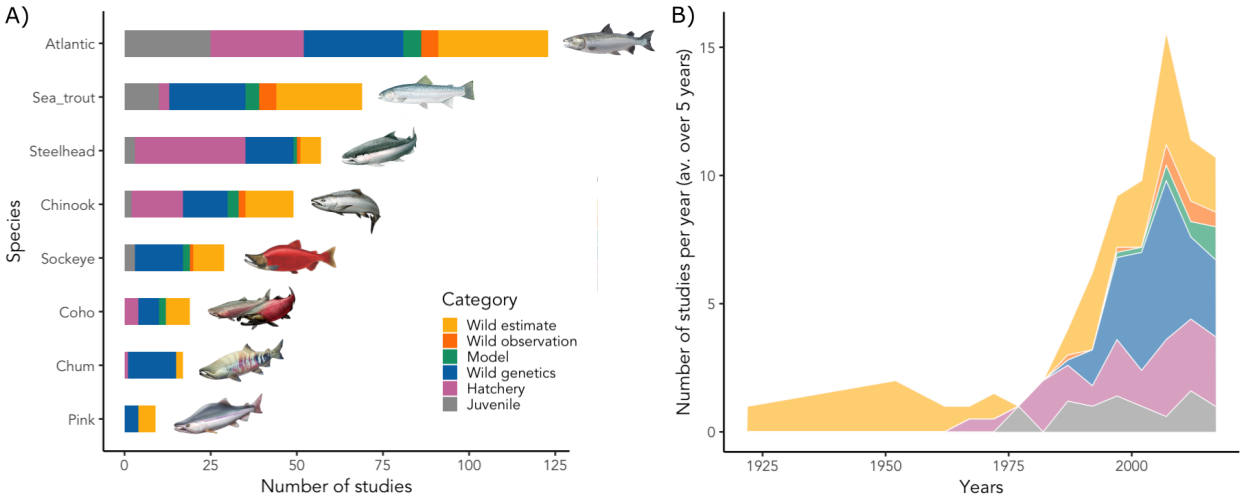

Figure 1: A) Number of studies of each category per species. B) Temporal evolution of the number of studies per year per category, averaged over periods of 5 years, over all species.

Genetic structure

Overall, 31% of studies focused on evolutionary history or genetic structure of populations, indicating gene flow and dispersal. This study type gained popularity in the 2000s due to advancements in genetic tools (”Wild genetics” category, Figure 1 A-B). However, as these studies do not provide estimates, we did not analyze them any further in this review.

Juvenile dispersal

Eleven percent of the studies investigated dispersal behaviour in juveniles rather than in anadromous adults (”Juvenile” category, Figure 1 A-B). This finding raises questions about the use of the term ”dispersal” for two distinct behavioral processes occurring at different life stages (i.e. juvenile *vs* adult stage) that likely have different consequences. Indeed, dispersal is defined as the movement of individuals with potential for gene flow. But the studies from the query report juvenile movement over very short distances, typically less than 1km (with the exception of Westley et al., 2008).

Hatchery

A large proportion of studies focus on the dispersal of hatchery fish, farm escapees, or transplanted fish (22% as ”Hatchery” category, Figure 1 A-B). This is particularly evident for Atlantic salmon, Steelhead trout and Chinook salmon. This focus has primarily been driven by hatchery management’s perspective and the issue of efficiency loss in stocking programs. These programs aim to maximize return rates of a target population without affecting others but straying behavior hampers these efforts. This interest appears to persist over time. Although acknowledging the higher dispersal propensity of hatchery fish compared to wild populations (Quinn, 1993; Jonsson et al., 2003), Keefer and Caudill (2014) reviewed dispersal rates without distinguishing their origin. This likely led to an overestimation of the general dispersal tendency of salmonids. Therefore, we focused solely on wild populations for the present study.

However, it is possible that estimated dispersal may also be affected by past or current stocking practices within these wild populations.

Dispersal in wild populations

Overall, there were few studies focusing on wild anadromous populations (31%), and even less providing estimations (27%, 100 studies, "Wild estimate" category). Studies providing evidence of dispersal without estimations ("Wild observation" category) were generally based on small sampling size and occasional observations, but they also provide important information by adding further evidence to dispersal behavior in wild populations of salmonids. For example, Perrier et al. (2010) genetically assigned Atlantic salmon to their population of origin and showed evidence of long distance dispersal. Using otolith chemistry, large immigration rate have been measured by Donohoe et al. (2021) and Mikheev et al. (2021) on steelhead and sea trout respectively, but they were based on small sample size or introduced populations. Among the 13.7% of immigrants identified in the Bidasoa river (NW Spain) using CWT tags, Leunda et al. (2013) also reported a case of long-distance dispersal of an Atlantic salmon originating from the River Tamar in SW England, more than 1000 km away. Nevertheless, dispersal in wild populations of salmonids is still overlooked compared to other species in the animal kingdom. This may be due to the prevalence of philopatry, but it is also related to the difficulty of assessing dispersal in the wild for these species with complex and relatively long life cycle. Indeed, it requires intense monitoring programs at large spatial and temporal scales, despite high mortality rates between life stages.

Modelling approaches

Modelling approaches can also be complementary to empirical approaches by addressing these challenges. They can be used to provide estimations of dispersal rates but also as virtual laboratories to evaluate the consequences of dispersal. A few modelling studies (17 overall, 5% as "Model" category, Figure 1 A-B), mainly published from 2010s, have been developed on

salmonids, most of them for Atlantic salmon, brown trout and Chinook salmon, and a few developed for Coho, Sockeye salmon and Steelhead trout. No models reviewed here were developed for Pink and Chum salmon. Most of these models were developed to better understand the metapopulation dynamics of a population network, including identifying source and sink populations (e.g. Fullerton et al., 2011), evaluating the viability of populations in a metapopulation context (e.g. Bowlby and Gibson, 2020), and exploring management strategies such as exploitation (e.g. Hindar et al., 2004) or barrier mitigation (e.g. Ioannidou and O'Hanley, 2019).

Various facets of dispersal

Terms used in studies

The diversity of terms used by studies to describe dispersal among populations illustrates the various facets of dispersal. Among studies providing estimates and observations of dispersal in wild populations, as well as modelling studies, the terms most frequently used are *migration* (-migra-, 39% of studies), *straying* (stray-, 31%), *gene flow* (12%), *dispersal* (dispers-, 10%) and *metapopulation* (metapop-, 5%). Each of them has a specific significance. For instance, genetic studies frequently used the term *migration* to refer to migration rate, immigration, or number of migrants. However, this term is imprecise as it could also refer to reversible migration or migration at sea. *Straying* was also prevalent, but it has a negative connotation. It suggests an unintentional error and thus disqualifying dispersal as a life history strategy with significant implications. *Gene flow* and *dispersal* are less common. But the choice between these two terms is crucial because they do not necessarily carry the same meaning. Dispersal (or straying) is not systematically followed by reproduction, whereas gene flow (or effective dispersal) requires dispersal and reproduction. Note that gene flow may be lower than the dispersal rate due to reduced reproductive success of immigrants. Conversely, gene flow may be higher if immigrants have higher reproductive success, possibly due to sexual selection favouring immigrants and/or

higher survival of their offspring. Finally, *metapopulation* is the less frequent term and it was exclusively used in modelling studies.

Metrics and methods for dispersal rate estimation

Several metrics and methods are used by the studies to measure dispersal among wild populations. Most studies measured gene flow (effective dispersal) and emigration rates (36% each), closely followed by immigration rate (28% of studies, Figure 2). This result differs from Keefer and Caudill (2014) who showed "disproportionate" reports on straying rates from donor populations (i.e. emigration rate) while straying into receiving populations (i.e. immigration rate) was "under-reported". The difference between our findings and Keefer's can be attributed to the fact that we only considered studies on wild populations, whereas Keefer and Caudill (2014) included studies based on hatcheries, as well as the updated literature.

Emigration rates are often measured but they do not indicate the full extent of the impact that the emigrants have on other populations. For example, even a small emigration rate from a large population can have a substantial impact on neighbouring smaller population. Therefore, immigration rates may be more relevant for evaluating the consequences of dispersal (Bett et al., 2017). However, immigration does not necessarily have genetic consequences - gene flow may thus extend our understanding, but is often not representative of contemporary dispersal. Using a combination of metrics may allow to counteract the limits of each one and provide a global appreciation of dispersal within a system. In this review, 16% of studies used two or more metrics. For example, Mortensen et al. (2002) measured an emigration rate of 1.4% in a population of pink salmon but higher immigration rates (from 2.1 to 7.6%) in receiving populations. Both high emigration rates and immigration rates were measured by Tallman and Healey (1994), but low levels of gene flow suggest low reproductive success of immigrants in chum salmon. Similarly, Masson et al. (2018) measured lower levels of gene flow compared to immigration rates of sea trout.

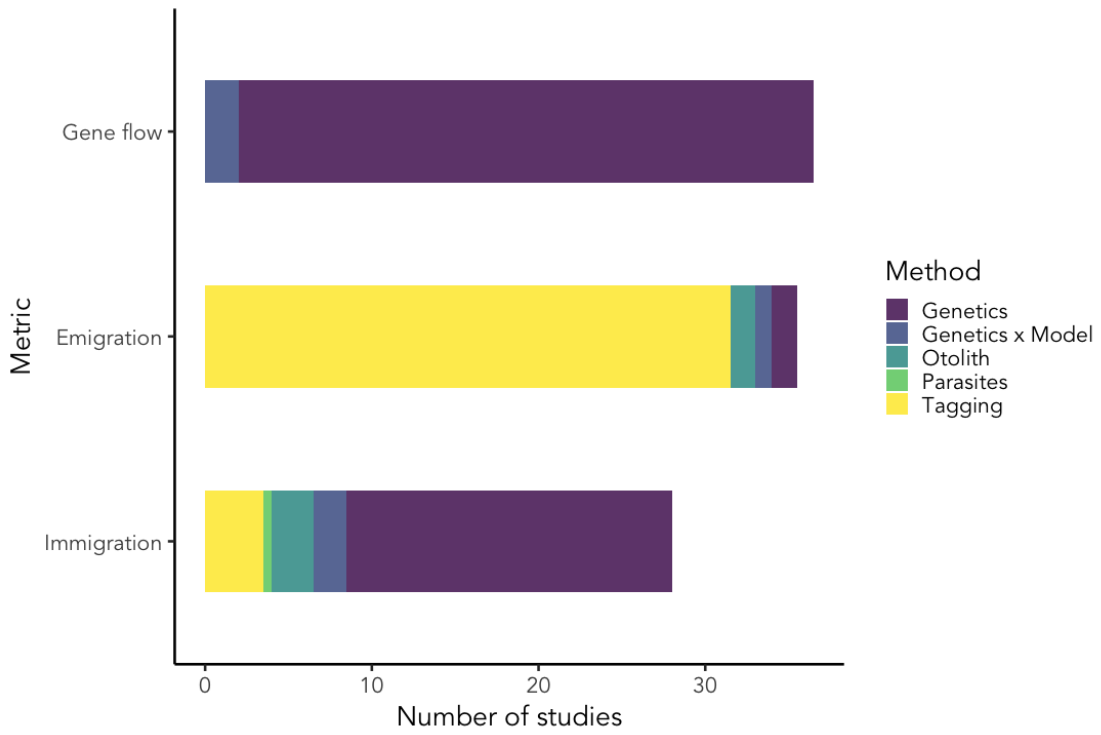

Figure 2: Number of studies providing estimates on wild populations per metric (emigration rate, immigration rate and gene flow) and per method (e.g. genetic, tagging).

To estimate these metrics, a diversity of methods are used, either alone or in combination (11% of studies use a combination of approaches). Genetic approaches represent a high proportion of study methods, accounting for around half of the studies conducted on most of species, and even more for sea trout. They were primarily used to estimate gene flow (e.g. F statistics, Wright (1951); allelic frequencies, Wang and Whitlock (2003); Wilson and Rannala (2003)) and immigration rate (e.g. genetic assignment, parentage analysis). Tagging methods (e.g. Carlin tags, fin clips, Coded Wire Tags) also represent a significant proportion of study methods (35%). They are mainly used to estimate emigration rates, with a small proportion used for immigration. While Hendry et al. (2004) reported more studies using genetics than tagging methods, Keefer and Caudill (2014) found the opposite, but this was only from emigration and immigration rates, not gene flow. Alternative methods, although less common, may also provide estimations of dispersal rates. Otoliths are used by a few studies (4%) for emigration and immigration rates

estimations, through micro-chemistry (e.g. Hamann and Kennedy, 2012; Turcotte and Shrimpton, 2020) or thermal marking analysis (e.g. Mortensen et al., 2002). One study also used parasitic prevalence to estimate immigration (Quinn et al., 1987). Modelling approaches are also used in combination with genetic methods to estimate all three metrics (Bekkevold et al., 2004; Lin et al., 2011; Perrier et al., 2013).

Other studies already discussed the benefits and limits of the different direct and indirect methods of estimation provided by genetic and tagging approaches (Koenig et al., 1996; Bossart and Pashley Prowell, 1998; Bullock et al., 2006). For example, the limits of estimating gene flow via the *Fst* estimators of genetic differentiation are well recognized (Whitlock and Mccauley, 1999). Also, the diversity of genetic methods which can give different estimations for the same system (e.g. Palstra and Ruzzante, 2010) makes between-studies comparisons difficult. For estimates of emigration and immigration rates, a common challenge between genetic and tagging methods that may lead to underestimation is the non exhaustive survey of possible locations where dispersers may go / come from, as already suggested by Keefer and Caudill (2014). In conclusion, it is recommended to use a combination of methods and metrics to obtain a comprehensive and accurate understanding of dispersal.

Spatial and temporal scale of dispersal

Finally, there is a lot of variation among studies in the spatial and temporal scales at which dispersal is measured. This may be of particularly importance for estimations. First, spatial dispersal in anadromous species can both occur between basins (i.e. different estuaries) and within basins (i.e. same estuary). We reviewed the spatial scale of studies to determine whether the extent of dispersal between and within basins is similar. 54% of the studies investigated dispersal between basins, 33% within basins, and 11% both. Also, 72% of studies reported estimated rates on individual populations, while 20% reported rates over several populations pooled together, and 5% having both.

Second, dispersal may strongly vary over time, so the temporal scale at which studies

measured rates has been reviewed. 59% of the studies reported rates that were pooled over several years or a single rate for a time period, while 33% reported yearly estimates and 8% had both.

Variability of dispersal rates estimation - from populations to species

Overall (over species), estimates of emigration, immigration and migration rates are oscillating between 0% (importance of showing the 0 in studies) and 100%, and show strong difference between median and mean (Table 2). Using median, these results show an overall immigration rate of 20% that is greater than emigration rate (2.8%) and migration rate (i.e. gene flow, 1.1%). This could suggest an overall small proportion of dispersers from large populations to small populations, and a low reproductive success of immigrants leading to low level of gene flow.

Table 2: Summary of estimated rates over all species. Migration rates exclude estimates of number of migrants per generation (*Nm*).

Metric	Min	Max	Median	Mean	Sd
Emigration rate	0	100%	2.8%	7.57%	12.78%
Immigration rate	0	100%	20%	25.91%	24.06%
Migration rate	0	99%	1.1%	5.66%	11.8%

Estimates also show a high degree of variability (Table 2), suggesting different ability to disperse among species. Over all three metrics, there was no clear pattern among species, except sea trout which show higher immigration rates and gene flow (Figure 3 A-C). This unexpected result could be explained by the influence of the resident form of the species which limits the cost of dispersal. A few studies (n=6) provided direct comparison of dispersal rates between different species from the same river system. Shapovalov and Taft (1954) showed higher emigration rates in Coho salmon compared to steelhead trout, while similar rates have been measured between Coho and Chinook salmon by Anderson et al. (2015), and between Chum and Chinook salmon

by Lin et al. (2011). Keefer et al. (2005, 2008) reported higher rates of emigration for steelhead trout compared to Chinook salmon, while Pearsons and O'Connor (2020) did not find differences in the average rate of dispersal between these two species.

Methods used to estimate rates are also an important source of variability. But our analysis indicates that there is insufficient data to compare dispersal rates between methods. Furthermore, caution must be taken when comparing estimates provided by a method as the observational process (data collection) itself can influence dispersal measurements, being variable in time and space (between populations) and potentially selective (as a function of age or size). Ideally, different methods (e.g. genetic *vs* tagging) would need to be applied to the same system to estimate the same metric (e.g. immigration rate). Several studies used alternative genetic methods to estimate gene flow (Quinn et al., 1987; Wehrhahn and Powell, 1987; Verspoor et al., 1991; Elo, 1993; Kinnison et al., 2002; Hansen et al., 2002; Palstra et al., 2007; Hansen et al., 2009; Palstra and Ruzzante, 2010), but we only found two studies reporting differences in immigration rates by using different methods (Hess et al., 2014, genetic *vs* tagging; Kuparinen et al., 2010, tagging *vs* model). No study was found to estimate emigration rates using more than one method.

Variability in estimated rates among studies may also arise from the spatial systems studied. This can be illustrated by strong differences in dispersal propensity reported within studies between different river systems or even between populations from the same system (e.g. Labelle, 1992; Hess et al., 2014). The spatial configuration of populations, e.g. if they share a common estuary or not, can also influence dispersal behaviour and propensity. One could assume that dispersal within basin (i.e. same estuary) might be higher than between basins (i.e different estuary). This hypothesis seems supported by overall results of emigration rates, that are higher within basins compared to between basins, despite a low number of within basin estimates (Figure 3 A). It is important to note that immigration and migration rates are functions of the relative size of the populations. Therefore, comparing these metrics within basins to those measured between basins is challenging without considering the spatial context,

including the dynamics of the source populations. For a single system, estimated rates can also strongly vary depending on the spatial scale considered. This is very well described by Pearsons and O'Connor (2020) who showed emigration rates of Chinook salmon and Steelhead trout were lower at the basin scale (on average 0.23% and 0.2%, respectively) compared to sub-basin scale (2.36% and 2.38%) and tributary scale (2.42% and 4.57%). Hamann and Kennedy (2012) also showed immigration rates of Chinook salmon at two locations were higher by considering a fine scale (40% and 73%) than a coarse scale (12% and 18%), while Chat et al. (2022) showed a negative relationship between immigration rate and distance to river mouth across several river systems of sea trout.

In addition to spatial variation, temporal variation is also rarely assessed in dispersal studies. Only 29% of studies provided estimates at several years from the same system (with a maximum of 24 years), allowing appreciation of temporal dynamics and variability of dispersal. Yet, strong variation in dispersal has been measured between successive years in several studies (e.g. Labelle, 1992; Jonsson et al., 2003; Keefer et al., 2005; Fraser et al., 2007; Hess et al., 2014), highlighting that a single measure is only a temporal snapshot and one may not generalise it to the system studied more generally.

Finally, strong variability can also come from limited sampling size (e.g. Keefer et al., 2005; Jonsson and Jonsson, 2017; Turcotte and Shrimpton, 2020), recent recolonisation events (e.g. Østergaard et al., 2003; Anderson et al., 2015), and past or recent hatchery influence in stocked populations (e.g. Consuegra et al., 2005; Valiente et al., 2010; Kuparinen et al., 2010; Ford et al., 2015). These factors may explain very high rates measured in several studies.

All together, the lack of data required to conduct a comparative analysis can be explained by these different sources of variability and the complexity of monitoring dispersal in the wild. It is therefore important to consider the spatial and temporal context of the focal population when interpreting results, especially when focusing on a component of dispersal such as immigration.

Relationship with distance?

Dispersal is a behavior associated with several costs (Bonte et al., 2012), including energetic and opportunity costs, i.e. dispersers' fitness is assumed to be low if the population of destination is far from the natal river and genetically differentiated. It is thus commonly assumed that dispersal rates decrease as distance between populations increases. The relationship is commonly depicted using a dispersal kernel that considers euclidean distance as the primary factor (Nathan et al., 2012). In this review, a few studies illustrate this dispersal kernel by providing the distribution of dispersal distances among emigrants, such as Jonsson et al. (2003) and Thedinga et al. (2000) in Atlantic and Pink salmon, respectively. We attempted to explore this relationship between the three metrics (i.e emigration, immigration and migration rates) and distance (averaged distance where emigrants went or immigrants come from) reported over all studies and species.

The relationship between emigration rates and distance to receiving populations is not significant, despite a trend for a decrease of emigration strength with increasing distance (Figure 3 D), the highest rates being associated with the smallest distances. But studies also showcase long distance dispersal, up to 328 kms. Nevertheless, distance is a simple and convenient descriptor that does not capture the underlying mechanisms of the emigration process and the choice of the population of destination.

Immigration patterns also show long distance dispersal (up to 710 kms), and opposite relationships with distance from source populations between spatial scales (between and within basins; Figure 3 E). Indeed, immigration rates may be more likely influenced by the relative population size than by distance. For example, if a small population receive immigrants from a large donor population, immigration rate might be high despite a large distance separating them. Attractivity of populations may also influence this pattern (i.e. collective behaviour, Berdahl et al., 2016), with large populations attracting dispersers. Estimation method such as genetic assignment might also face some limitations in accuracy and influence the pattern. Finally, some systems specificities might also influence the results. For example, the high values

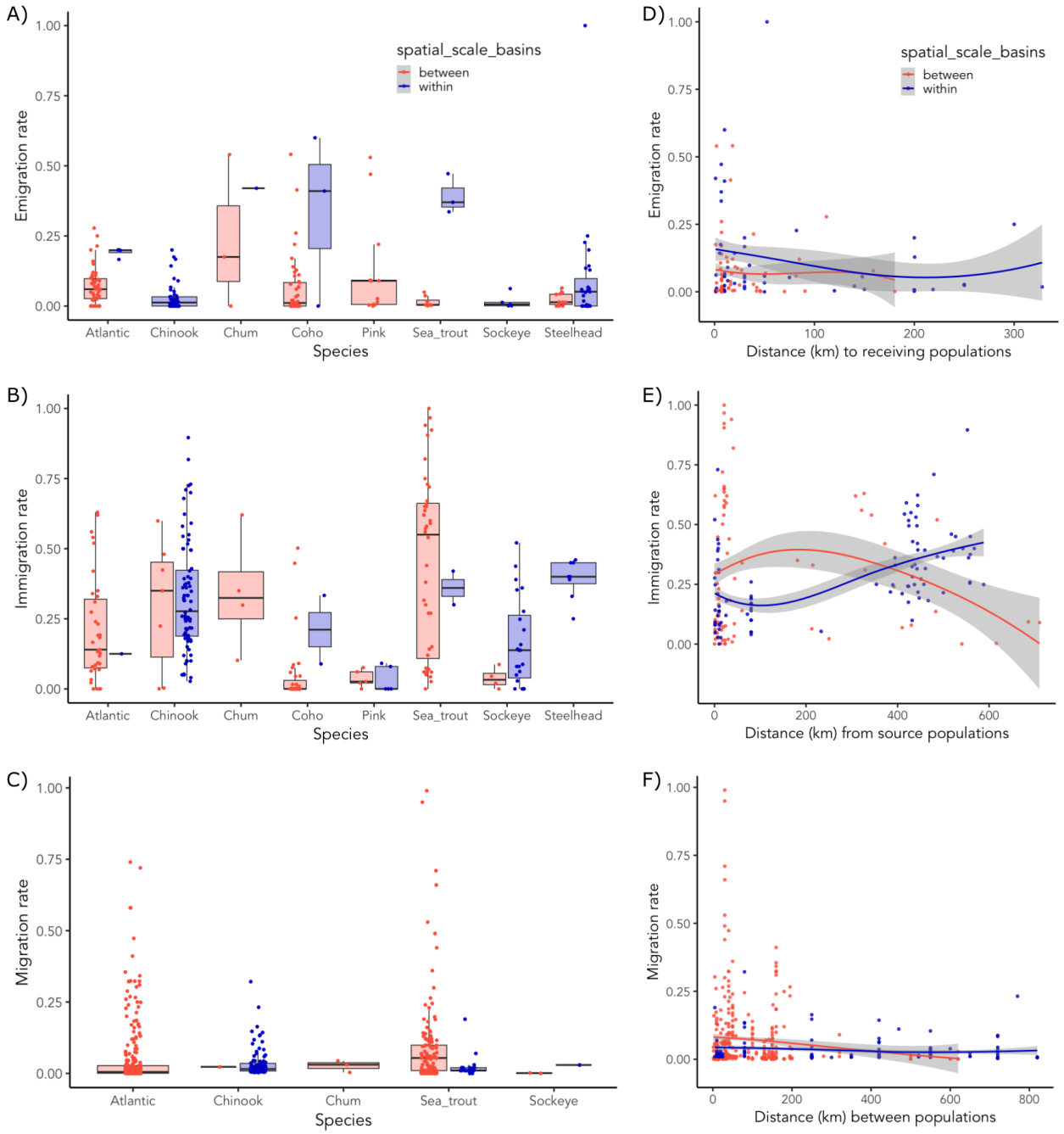

Figure 3: A-C) Distributions of estimated emigration, immigration and migration rates among species, and D-F) relationship with distance (km) by spatial scale considered (between / within basins). Points represent estimates and the line a local regression (Locally Estimated Scatterplot Smoothing). The distance is reported as the average "swimming" distance of dispersers to/from populations.

of within basin immigration rates reported for high distances all come from large river system in the US, i.e. the Fraser river and the Columbia river (Hess et al., 2014; Bett et al., 2017; Matala et al., 2017).

Gene flow, which results from immigration patterns and the relative fitness of immigrants, also slightly decreases with increasing distance among populations, the relationship being stronger for gene flow between basins than within basins (Figure 3 F). Indeed, gene flow might be more likely to be reduced with increased distance between basins because of local adaptation which may impede dispersers' reproductive success.

Drivers of dispersal

Few research studies have examined the primary factors that influence dispersal propensity in salmonids limiting our understanding of the drivers of dispersal (see Keefer and Caudill, 2014; Bett et al., 2017 for review). It is likely related to the difficulty to assess dispersal in wild populations especially over space and time. In this study, we quantified the studies that assessed the influence of one or more factors on dispersal rates. Only a small proportion (22% overall) of studies estimating rates in wild populations evaluated factors promoting dispersal, such as individual characteristics (e.g. sex), environmental conditions (e.g. temperature), or population density (Figure 4).

Studies commonly evaluated sex, body size, and sea age as potential drivers of dispersal in salmonids (Figure 4). Indeed, theoretical studies suggest that sex-biased dispersal is widespread and contingent on mating systems and kin competition (Trochet et al., 2016; Li and Kokko, 2019). From our literature review, several studies did not show evidence for sex biased dispersal (Thedinga et al., 2000; Palstra et al., 2007; Consuegra and García de Leániz, 2007; Ford et al., 2015), while others provided results consistent with male biased dispersal (Bekkevold et al., 2004; Hamann and Kennedy, 2012). Body size may also affect dispersal due to potential size-dependent costs, while sexual selection can lead to differences in body size. Size at

downstream migration was found to be negatively correlated with dispersal rate (Shapovalov and Taft, 1954) but this relationship was not significant in Jonsson and Jonsson (2014). Finally, time spent in river or at sea (sea age) can also affect the olfactory imprinting of juvenile salmon in the river and the olfactory memory of adults at sea, and therefore their ability to distinguish between water sources (Dittman and Quinn, 1996). In our study, contrasted patterns were reported regarding sea age influence on dispersal propensity. While no difference was observed in Potter and Russell (1994) and Ford et al. (2015), Källo et al. (2022) showed a negative relationship between dispersal rate and time at sea, whereas Jonsson et al. (2003) measured higher straying with sea age. However, it is difficult to disentangle the effects of these factors because they can be correlated. For example, females are likely to be older (spending more time at sea) and larger. But, the rationale for choosing these factors may simply be that they are easy to measure in wild populations.

Density also appears as influencing dispersal propensity with a negative density-dependence showed by Jonsson et al. (2003), supporting the hypothesis of collective behaviour raised by Westley et al. (2015) and Berdahl et al. (2016). Regarding environmental factors, temperature has also been studied in 2 studies from our literature review, showing a positive correlation between temperature increase, immigration rate and gene flow (Valiente et al., 2010; Horreo et al., 2011). Water flow or discharge may also influence the choice of river destination for salmon returning, i.e. higher water flow could be more attractive to them. Two studies in our review showed contrasting results. While Labelle (1992) explained the high immigration rate of a Coho population by the river's large discharge, Jonsson et al. (2003) did not find a significant relationship between water flow and stray rate in an Atlantic salmon population. Finally, the genetic basis of dispersal has been poorly studied (but see Jonsson and Jonsson, 2017) despite its evidence in many other organisms (Saastamoinen et al., 2018).

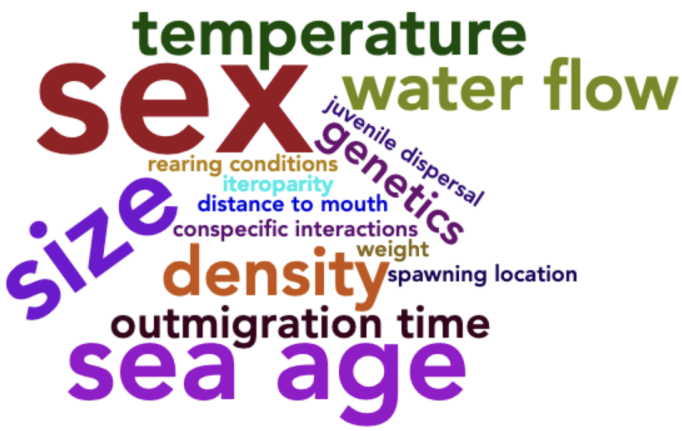

Figure 4: Wordcloud of the factors identified as potential drivers of dispersal, their size being proportional to their occurrence among studies providing estimates on wild populations.

Dispersal implications for conservation and management of salmonids

Most studies discussing dispersal implications focus on demography, genetics and conservation aspects. Demography includes the persistence, resilience, and stability of populations. Genetics involves the preservation of genetic diversity and local adaptation by limiting or promoting gene flow. Conservation aspects include recolonization and restoration potential for populations (Figure 5). But studies examining the implications of dispersal for the conservation and management of salmonids are still scarce. Only a small proportion of studies in wild populations or using models discussed this topic (26%) and even less evaluating (11%, 15 modelling studies over the 8 species) the implications of dispersal.

We caution that neglecting dispersal can affect our understanding of the focal population and the measurement of key demographic parameters used to characterise the status of the population. For instance, return rate is often used as a measure of sea survival, which is a crucial indicator of the conditions experienced at sea. It is calculated as the ratio of adults returning in a river and the number of smolts produced for a given cohort. However, return rate is a combination of survival, maturation decision and dispersal. Ignoring dispersal can lead to

biased estimates of return rates and survival if the emigration and immigration rates are unbalanced. Dispersal and the functioning of metapopulations have also implications for fisheries management in estuaries and rivers. Mixing of populations due to dispersal increases the risk of overexploitation of weaker stocks. Therefore, it is important to consider the relative importance of populations in fisheries management, including their impact on the functioning of the metapopulation as a whole. For example, in the context of source-sink dynamics, source populations can help maintain small populations (sinks). By fishing source populations, which are often the largest and most focused on, fisheries can affect not only the targeted source populations, but also the sink populations that depend on them. Surprisingly, few studies of this review assessed or discussed these potential effects (but see Hindar et al., 2004).

As studying dispersal and its effects on salmonid populations in their natural environment is challenging, modelling approaches provide a convenient way to simulate sets of interconnected populations and investigate the eco-evolutionary consequences of dispersal, fisheries and management measures over short and medium term. Few studies used mathematical and statistical models (e.g. PVA model, graph theory, SPOM) to investigate the demographic consequences of dispersal and source-sink dynamics within salmonids metapopulations (Fullerton et al., 2011; Bowlby and Gibson, 2020; Bradford and Braun, 2021). However, they did not explore genetic consequences (e.g. on local adaptation) and their potential interplay with demography (i.e., eco-evolutionary feedback loops). Lin et al. (2017) and Lamarins et al. (2022) used simulation models (Demo-Genetic Agent Based Model, DG-ABM) of sockeye and Atlantic salmon metapopulations respectively, to evaluate the consequences of dispersal both at demographic, phenotypic and genotypic levels. Castellani et al. (2015) also used a DG-ABM to evaluate the role of immigration on introgression buffering. Metapopulation models have also been developped to evaluate applied management strategies, such as harvesting strategies (Hindar et al., 2004), barrier removal (Schick and Lindley, 2007; Ioannidou and O'Hanley, 2019; Rodeles et al., 2021), or invasive species regulation (Minett et al., 2023; Healy et al., 2023). Modelling approaches can be useful in demonstrating the dangers of

ignoring metapopulation functioning (Cooper and Mangel, 1999) and explore novel management strategies in this context. However, more empirical information is ultimately necessary to design appropriate management measures.

Figure 5: Wordcloud of the different implications of dispersal for conservation and management that were discussed or evaluated. Words size is proportional to their occurrence among empirical studies on wild populations and modelling studies.

Conclusion and perspectives

Our review highlights that dispersal in wild populations of anadromous salmonids continues to be overlooked, with the term 'straying' often used with a negative connotation. The benefits of using different approaches, methods and metrics are evident in the large variability in estimates between studies, but quantitative analysis is hampered by pooling strategies and lack of

replication. Moreover, our study reveals it is still difficult to establish a clear relationship between dispersal metrics and drivers. Importantly, the lack of knowledge prevents us from understanding the full implications of dispersal for management and fisheries. The incorporation of modelling approaches holds promise, particularly for investigating challenging issues such as the effects of fisheries on metapopulation and the eco-evolutionary consequences of dispersal. The integration of empirical knowledge into models and vice versa creates a symbiotic relationship that highlights gaps in understanding and motivates further empirical investigation.

There is no single approach or method to fully grasp the process of dispersal in wild populations. Instead, it is necessary to combine multiple approaches and develop methods. For example, more precise genetic assignment analysis can be used by employing large numbers of single nucleotide polymorphisms (SNPs). Additionally, microchemical analysis of calcified structures such as otoliths and ray fins can be used. We also encourage that the databases of tagging programs from monitored populations should be made available to facilitate the identification of dispersers. These advances offer exciting opportunities for future research and have the potential to reveal the causes and consequences of dispersal in anadromous salmonids that are difficult to assess directly from a limited number of populations. In summary, embracing methodological diversity, promoting consistency and incorporating cutting-edge approaches will be crucial to advancing our understanding of dispersal in wild populations of anadromous salmonids.

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Data availability

The databases used for this review are provided as supplementary materials and will also be made available on a data repository held by INRAE.

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