

Propagule pressure and initial dispersal as determinants of establishment success of brook trout (*Salvelinus fontinalis* Mitchill 1814)

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Abstract

Establishment success of invasive species depends largely on the size of the initial source population because small populations are more likely to fail due to stochastic or inverse density-dependent Allee effects. However, there are difficulties involved in using propagule pressure as an explanatory variable to account for establishment success because records concerning the size of initial source populations are typically (i) non-existent, (ii) only rough estimates and/or (iii) based on indirect measurements. The focus of this study was the establishment success of a deliberately introduced non-native salmonid, *Salvelinus fontinalis* as a function of actual site-specific propagule pressure. Additionally, we investigated whether newly released fish located suitable habitat patches, potentially facilitating the spread of the invader across Finnish stream systems. We found that the propagule pressure leading to highly successful establishment amounted to approximately 8000 released individuals. Additionally we also noted that one fourth of the newly introduced fish rapidly located suitable habitat patches (small tributaries) during initial dispersal, thus potentially increasing establishment success and the spread of the invader. The results suggest that by considering both propagule pressure and initial dispersal it will be possible to understand the latter stages of the invasion process, eventually leading to an improved capability in predicting successful invaders and sites that will be invaded.

Key words: introduction, invasion success, mark-recapture, non-native species, salmonid

Introduction

The invasion process constitutes a series of stages through which invaders should pass in order to become established in recipient systems (Kolar and Lodge 2001; Heger and Trepl 2003; Williamson 2006). The probability of passing through a stage is highly variable and case-specific, with only a minor proportion of invaders completing the invasion sequence from initial colonization to the establishment of a self-sustaining population eventually spreading on the habitats of native species and causing severe impacts. Kolar and Lodge (2001) suggested that in order to overcome constraints set by the filters, invading species must possess certain characteristics enabling them to complete each stage of the invasion successfully. In this case some species may be more efficient invaders than others, making it easier to predict which

invading species is most likely to become established in a given region.

Recently however, the significance of species' characteristics in explaining successful invasions have been questioned (McKinney and Lockwood 1999; Colautti et al. 2006; Hayes and Barry 2008) and purely trait-based explanations may be confounded by anthropogenic factors. For example, it is possible to envisage the large size of invasive organisms as an important biological trait facilitating invasions. However, this surmise could be misleading, because intentionally introduced species can be selected for their large body size (Miller et al. 2002). An alternative factor explaining invasion success is propagule pressure (number of individuals released and introduction events), which appears to be a powerful factor for various taxa. The logic behind the idea of propagule pressure is relatively simple: increasing the number of

invaders should increase the probability of their establishment (Lockwood et al. 2005; Von Holle and Simberloff 2005; Colautti et al. 2006). The size of the initial source population is important because small populations are more likely to become extinct due to stochastic or inverse density-dependent Allee effects (Lockwood et al. 2005; Taylor and Hastings 2005). However, there are also difficulties involved in using propagule pressure as an explanatory variable to account for establishment success because records concerning the size of initial source populations are typically (i) non-existent, (ii) only rough estimates and/or (iii) based on indirect measurement (Marchetti et al. 2004; Mikheyev et al. 2008). Such a lack of reliable information may stem from the fact that many invaders enter recipient systems unintentionally (e.g. via ballast water tanks, Gollasch and Leppäkoski 2007). Failed invasions remain frequently unrecorded, resulting in a serious bias of findings towards successful invasions (Simons 2003; Puth and Post 2005). Understanding propagule pressure is therefore considered an important new frontier in invasion ecology (Richardson and Pyšek 2008).

Propagule pressure is only a relevant explanatory factor for sites with suitable environmental conditions facilitating potential invasion. In the past, suitable areas for invaders have been determined by matching niche requirements of non-native species with the environmental characteristics of recipient ecosystems (Peterson and Vieglais 2001; Korsu et al. 2007, 2008). It has been suggested that a close match between niche requirements and recipient ecosystem, as well as low biological and environmental resistance, could enhance invader establishment, whereas propagule pressure has frequently been ignored in such analyses (e.g. Fausch et al. 2001; Korsu et al. 2007). Therefore, it should be noted that the interplay between propagule pressure and the environmental characteristics of recipient ecosystems potentially modify invasion success (Herborg et al. 2007; Leung and Mandrak 2007; Hayes and Barry 2008).

In order to better understand invasions, their early stages, such as propagule pressure and dispersal of newcomer individuals (initial dispersal), should be further investigated because they act as the crucial first filters that affect later stages of the invasion process (Lockwood et al. 2005; Jeschke and Strayer 2005; Puth and Post 2005). However, it may be possible to overcome the major limitation (lack of data on source

population sizes) involved in studying the role of propagule pressure by examining deliberately introduced species for which release events have been recorded by government agencies amongst others. In this study, we investigated the roles of propagule pressure and an invader's initial dispersal in an attempt to explain the establishment success of a deliberately introduced North American fish species (brook trout, *Salvelinus fontinalis* Mitchill 1814) in Finnish streams and lakes. *S. fontinalis* is a globally distributed, highly mobile invader that has spread extensively in stream ecosystems in many parts of the world (Simon and Townsend 2003; Peterson and Fausch 2003; Korsu et al. 2007). In Finland, *S. fontinalis* has been introduced since the 1960s, with both failed and successful establishment reported. An exceptional opportunity to consider in detail the effects of propagule pressure at site scale has been provided by Finnish fishery administrators, who have kept a register of the majority of such introductions. We combined data from the fish stocking register and field surveys to examine the establishment success and dispersal of *S. fontinalis* in streams and lakes affected by a wide range of propagule pressure. The aims of the study were to (i) determine the propagule number of *S. fontinalis* needed to produce an established population, and to (ii) investigate the ability of the newly released fish in locating suitable habitats for reproduction. We expected establishment success of *S. fontinalis* to be positively related to propagule pressure and that success would be further facilitated through the active initial dispersal of newly released fish.

Material and Methods

Propagule pressure

In order to determine the range and extent of propagule pressure, we searched the official fish stocking register updated by the Fisheries Sector of the Employment and Economic Development Centre of Finland (<http://www.te-keskus.fi>). We identified the streams and lakes where *S. fontinalis* had been released and registered the site-specific numbers of released fish. We consulted the staff of the regional Environmental Centres, the Finnish Game and Fisheries Institute, the Ministry of Agriculture and Forestry, Water and Environment Associations, universities, several fisheries organizations (<http://www.ahven.net>), and local fishermen to gain information on both established *S. fontinalis*

populations and failed introductions. We further supplemented the data by results from fish sampling by electrofishing (Bohlin et al. 1989) stream sites close to the known introduction sites in summer-autumn 2007. Sampling was carried out by several field workers to confirm the presence or absence of established *S. fontinalis* populations at the sites where brook trout had initially been introduced, though lacking previously collected data on fish populations. If fish had been released in a lake, nearby streams were also sampled because *S. fontinalis* is known to spawn mainly in flowing water (Wiztel and MacCrimmon 1983). We recorded a failed introduction if *S. fontinalis* was not located after sampling several stream sites and adjacent tributaries (minimum area sampled was 200 m² per site). Sampling started from the downstream end of a site, and it was performed by two persons, one operating the backpack electroshocker, the other using a dip net to catch stunned fish. For logistic reasons and because propagule pressure is only a relevant explanatory variable for invulnerable sites (see Herborg et al. 2007), sampling was targeted at sites with the highest potential to sustain naturally reproducing populations of *S. fontinalis* in terms of habitat quality. These sites were mainly in small tributaries and headwaters as described in Korsu et al. (2007) and Korsu et al. (2009). We did not include suboptimal sites in the sampling program, thus potentially slightly biasing the results. Yet, based on our knowledge on the habitat use of *S. fontinalis*, we consider that the sampling program covered a major part of the stream area most suitable for *S. fontinalis* in each studied system, and that the non-sampled sites were mainly population sinks.

We combined the results of previous samples (originating from sources listed earlier) with data collected during this field study (Annex 1) to form the final data set, which comprised presence - absence information (establishment success) of *S. fontinalis* supplemented by fish stocking information within 54 catchments across Finland (located between 61°N and 67°N). Due to inappropriate documentation of the stocking history, we could not use several stream systems although they were introduced by *S. fontinalis*. Most of the 54 catchments we included to the data set were close to aquaculture stations that had provided *S. fontinalis* to the local fisheries organizations. The decision to introduce *S. fontinalis* to a specific site is unknown but probably the sites were selected to

meet the environmental requirements of the species. Thus, the 54 catchments can not be considered as randomly selected, affecting the generality of our results.

We used logistic regression analysis to demonstrate the relationship between three measures of propagule pressure and the establishment success of *S. fontinalis*. The variables that we entered to the analysis were (i) the total site-specific number of individuals released (ln transformed), (ii) the number of introduction events, and (iii) the number of years since the last introduction event which was selected to account for potential time lags typically involved in the population growth of newly introduced species (Crooks 2005). We used the forward selection of variables and measured total variance explained using the Nagelkerke method (Nagelkerke 1991). All analyses were carried out by SPSS 10.0 software using site-specific data.

Initial dispersal

We based our analysis on previously unpublished recapture data concerning reared *S. fontinalis* (mainly age-2 and c. 20 cm in length) that had been tagged below the dorsal fin with individually coded Carlin tags (Carlin 1955) and released by the Finnish Game and Fisheries Research Institute (FGFRI) between 1970 and 1994. Fish were released in mainstream sites of six rivers (Table 1). The term initial dispersal refers to the movement distances of the newly released fish mainly within the first and second year after the release events (see results). Local fishermen were offered a reward as an incentive to recover and return the tags of the released groups and to inform us of the local sites where the fish had been recaptured. After catching a marked fish, local fishermen did not release them to the stream, i.e. we had only one datum per fish.

We categorized the individual recapture data into spatial groupings. First, we divided the fish into *Stayers* that did not migrate farther than 5 km beyond the release site and into *Movers* that were captured ≥ 5 km from the release site. We categorized a fish also as a *Mover* if it ascended a tributary stream < 5 km from the release site (nearby tributaries) because this would also indicate behaviour involving active movement towards habitats most suitable for the species (Rahel and Nibbelink 1999; Korsu et al. 2007, 2009). Secondly, we categorized *Movers* on the basis of whether they had been captured from

Table 1. The rivers where Carlin-tagged *Salvelinus fontinalis* were released

River	No. fish released	Year of release	Location coordinates
Kostonjoki	1000	1972	65°30'N, 28°50'E
Livojoki	199 and 500	1970 and 1972	65°30'N, 27°00'E
Ounasjoki	1500	1972	67°10'N, 27°00'E
Piehinginjoki	100	1994	65°40'N, 24°20'E
Parjanjoki	200	1972	65°40'N, 27°50'E
Siuruanjoki	500	1972	65°30'N, 26°20'E

mainstream or remote tributaries (≥ 5 km from the release site). We set the rather rough distance threshold of 5 km because the spatial grain of the recapture site information was relatively large (typically the name of the river reach or the tributary stream). We calculated the distance moved by fish by measuring the shortest distance along the streams between the release site and the midpoint of the recapture location using 1:16000 maps.

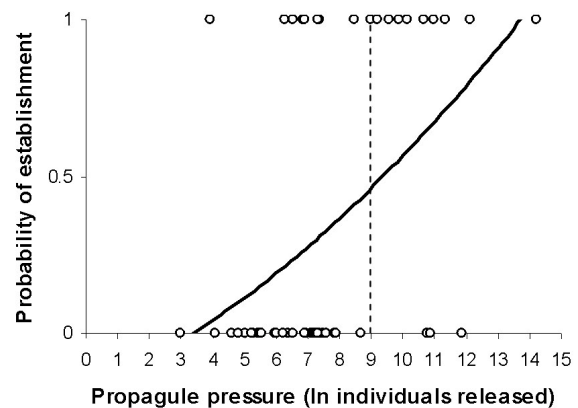
Results

Propagule pressure

The site-specific establishment success of *S. fontinalis* was significantly related to the number of individuals released ($P = 0.003$), whereas (i) the number of introduction events and (ii) the number of years since the last introduction event were both insignificant (total variance explained: Nagelkerke $r^2 = 0.28$, Table 2). Median propagule pressure in successfully established sites was c. 8000 individuals (ln 9, see Figure 1).

Table 2. Key parameters for logistic regression analysis exploring the factors affecting establishment success of *Salvelinus fontinalis*. Although included in the initial model, (i) the number of introduction events ($P = 0.949$) and (ii) the number of years since the last introduction event ($P = 0.100$) were insignificant and thus dropped

	B	S.E.	Wald	df	P
ln individuals released	0.493	0.165	8.974	1	0.003
Constant	-4.493	1.326	11.499	1	0.001

**Figure 1.** Site-specific probability of establishment (0 = failed, 1 = successful) as a function of propagule pressure (ln individuals released) for non-native *Salvelinus fontinalis*. A logistic curve indicates the relationship between propagule pressure and establishment success. Vertical line indicates median propagule pressure in successfully established sites (c. 8000 released individuals)

Initial dispersal

In total, 221 (6 %) fish were recaptured with information also provided on the recapture site. Of these fish, 75 % were captured during the release year and 18 % during the next year. Approximately half (51 %) of the recaptured fish were *Movers* which dispersed at least 5 km from the release site or had ascended small (1-3 order) tributary streams close to the mainstream release sites. The rest of the recaptured fish (49 %) were *Stayers* that moved less than 5 km within the streams they had been released. The importance of tributary streams as a habitat for *S. fontinalis* was demonstrated since 55 % of *Movers* were recaptured in such small streams (nearby and remote tributaries combined). The rest of the *Movers* (45 %) dispersed along the mainstream (migration distance ≥ 5 km). The mean distance travelled by the *Movers* was 14.1 km (SE 5.6) with the highest observed distance being 80 km.

Discussion

Our results indicated that *S. fontinalis* have frequently become established in sites where propagule pressure was the highest: median propagule pressure in successfully established sites was 8000 individuals. We also found that newly introduced *S. fontinalis* were successful in finding suitable habitat patches via initial dispersal: one fourth of the marked fish

introduced to suboptimal habitats (rivers) were recaptured in small tributaries that are known to be the core habitat of the species both within its native and introduced ranges (Rahel and Nibbelink 1999; Korsu et al. 2007). *S. fontinalis* was also capable of moving long-distances within the river systems since the most remote recapture site was 80 km from the release site. The dispersal distances of the introduced fish were far higher than found among natural populations of *S. fontinalis* (e.g. Peterson and Fausch 2003), underlining the active dispersal behaviour of newly introduced hatchery fish. We conclude that by considering both propagule pressure and initial dispersal, invasion success can be better understood: when a high number of individuals are released, it helps to ensure that a sufficient number of them find suitable establishment locations.

Our results are important because there are not enough studies that focus on the initial stages of invasion. Subsequently, researchers have been forced to use theoretical models to understand the crucial first stages of the invasion process (Puth and Post 2005). In consequence, such a lack of empirical results makes it more difficult to evaluate the propagule pressure threshold required to facilitate invader establishment, for example during risk evaluation projects concerning non-native species (Lockwood et al. 2005). Based on meta-analysis, Traill et al. (2007) indicated that the average minimum viable population size (MVP) for various taxa consists of a few thousand (95 % CI = 3577 - 5129) individuals. Although our study animals were targeted to active sport fishing, MVP values of Traill et al. (2007) match our findings rather well and might indicate that our results could also be applied to other invading species and invaded systems. However, there is growing evidence that successful invasions could be based on very few propagules: for example, Moyle and Marchetti (2006) suggested that 100 individual fish released in the freshwater systems of California could be used as a threshold above which invasion success begins to increase (see also Soule 1980; Marchetti et al. 2004). Moreover, Roman and Darling (2007) underlined the high ability of invasive species to overcome the negative impacts of severe population bottlenecks.

Apparently, the rough threshold value (8000 individuals) presented here may not be the same in all situations because of variable biotic and environmental resistance in different systems

(Lockwood et al. 2005; Drake and Lodge 2006). If suitable breeding habitats are patchily distributed and/or remote, or if there is a lack of interconnecting migration routes, more propagules will be needed to establish a population compared to recipient systems where suitable habitats are abundant. Moreover, species with a poor ability to find suitable habitats may be unable to fully compensate for mortality during dispersal (Barlow and Kean 2004). It is therefore obvious that the threshold can also be species-specific. Indeed, Pascual and Cianto (2007) indicated in their literature review that the establishment success rates of introduced species with complex life histories and genetically driven migratory behaviours were lower than among resident, non-migratory species. Our focal species was a deliberately introduced freshwater-resident game fish and, to account for environmental resistance, we only included sites that contained suitable habitat patches close to release sites. Moreover, to improve probability of establishment the fish were probably introduced to sites known to be suitable for the species. Therefore, our results indicating the propagule pressure required to facilitate the establishment of *S. fontinalis* should be considered as a minimum estimate. It is also possible that recreational fishing pressure varied among the 54 watersheds. However, according to mark-recapture data, the local fishermen were rather ineffective, potentially leading to only a minor bias in results. Another potential biasing factor is that fishing pressure probably decreases as the distance from the introduction site increases. Therefore, the proportion of Movers should also be considered as a minimum estimate.

Recently, it has been understood that trait-based explanations of invasion success can be biased due to the fact that non-native species are a non-random sample of the global species pool, affected by anthropogenic and various dispersal vectors (McKinney and Lockwood 1999; Colautti et al. 2006; Hayes and Barry 2008). This may challenge the current paradigms of invasion biology and impair the prediction of high-risk invaders solely based on the characteristics of invaders or invaded systems. As our results indicate, propagule pressure can be applied as a simple yet powerful null-model with the potential to predict invasions (see also Colautti 2005; Colautti et al. 2006). In this study, the highly variable invasion success of *S. fontinalis* within suitable habitats would have remained largely unexplained without knowledge of site-

specific propagule pressure. More generally, our results indicate that in order to understand the latter stages of invasion it is also necessary to focus studies on the crucial early stages of the invasion process (Korsu et al. 2007). Therefore, data on the initial stages of the invasion process should be considered a part of any research project or modelling attempt designed to explain the success of a non-native species in recipient systems.

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Annex 1. Results of fish sampling during summer-autumn 2007

Location	Geographic coordinates		Presence/absence of <i>Salvelinus fontinalis</i>
	Latitude, N	Longitude, E	
Hännättämönjoki	62°20'	24°30'	+
Jaaskamonjoki	65°50'	27°30'	+
Ossauskoski, sivupuro	66°20'	25°10'	+
Salmijärvenpuro	62°20'	25°00'	+
Sikopuro	62°30'	25°50'	+
Iso-Kuorikka, puro	61°50'	24°50'	-
Juponoja	66°40'	25°50'	-
Kaijanpuro	62°20'	24°50'	-
Keskinenjärven puro	61°20'	22°40'	-
Kupanjoki	62°20'	24°30'	-
Kylmäoja	65°20'	25°30'	-
Lanajoki	61°30'	23°00'	-
Martimojoki	65°20'	25°30'	-
Matalajoki	65°10'	29°30'	-
Multianjoki, sivupuro	62°20'	24°50'	-
Mustalampi, puro	62°20'	24°50'	-
Naistenjärvi, puro	61°20'	22°40'	-
Niemisjärvet, purot	61°20'	25°00'	-
Pesäpuro	62°30'	24°30'	-
Piehinginjoki	64°30'	24°20'	-
Pietilänjoki	62°30'	25°10'	-
Pulkajärvi, puro	61°20'	22°40'	-
Ropsajoki	66°20'	25°40'	-
Sanginjoki	65°00'	25°50'	-
Ternujoki	66°20'	25°10'	-
Utosjoki	64°40'	26°30'	-
Vepsänjoki	65°00'	26°20'	-
Vieremäjoki	65°10'	29°30'	-
Vähäjärvi, puro	61°20'	22°40'	-
Vähälamminoja	65°20'	25°10'	-
Ylinenjärvi, puro	61°20'	22°40'	-
Ängeslevänjoki	64°30'	25°50'	-