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Overland Spread of Aquatic Invasive Species among Freshwater Ecosystems due to Recreational Boating in Canada

Drake, D. Andrew R.

Department of Biological Sciences
University of Toronto Scarborough
1265 Military Trail
Toronto, Ontario M1C1A4

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Foreword

This series documents the scientific basis for the evaluation of aquatic resources and ecosystems in Canada. As such, it addresses the issues of the day in the time frames required and the documents it contains are not intended as definitive statements on the subjects addressed but rather as progress reports on ongoing investigations.

Research documents are produced in the official language in which they are provided to the Secretariat.

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ABSTRACT

A literature review was conducted to summarize the overland spread of aquatic invasive species (AIS) among freshwater ecosystems due to recreational boating in Canada. Based on a review of 57 primary publications, factors contributing to overland spread involved heterogeneity in individual boater behaviour, such as differences in trip-taking frequency, the timing between trips, and the spatial distribution of boating locations relative to source populations of AIS. These factors, in addition to measures taken by boaters to remove AIS from boats and related equipment (such as picking visible material from anchors or cleaning hulls) dictate the variety, density, and viability of transported AIS between source and recipient ecosystems, ultimately determining the likelihood of overland spread. Therefore, as with other pathways of AIS introduction and spread within Canada, a subset of human-mediated events pose the majority of invasion risk due to context-dependent environmental and behavioural factors.

Contamination of boats and equipment with AIS can be classified based on the functional fouling characteristics of species, such as:

1) plankton and organisms with planktonic stages, transported in live wells, bilge water, and other whole-water niche spaces;
2) organisms with direct attachment potential (i.e., freshwater molluscs), transported by direct attachment on hulls and trailers; and,
3) organisms with indirect fouling potential, commonly entangled on trailers and related equipment such as anchor lines (i.e., aquatic macrophytes, benthic invertebrates).

The overland movement of recreational boats has led to the spread of several high-profile AIS in Canada, such as Spiny Waterflea (*Bythotrephes longimanus*), Fishhook Waterflea (*Cercopagis pengoi*), and *Dreissenid* spp. (predominantly transported as veligers), and is suspected in the transport of Eurasian watermilfoil (*Myriophyllum spicatum*) and Bloody-red Mysid (*Hemimysis anomola*). Future AIS having functional characteristics similar to these species are expected to undergo boater-mediated overland spread in Canada. Moreover, because the spatial distribution of several high-profile AIS correlates strongly with overland boat movements, future spread appears to be predictable with relatively high fidelity. A first-order estimate of the number of inland boaters (1.5 million) and inland boating trips (24.7 million/y) likely underestimates the scale of the pathway among freshwater ecosystems in Canada. Based on a simulated range of per-boating-trip probabilities of AIS introduction, even infrequent rates of overland AIS transfer (e.g., 1 in 1,000, 1 in 10,000, or 1 in 100,000 boating trips) will lead to at least 10, 100, or 1,000 nationwide AIS introduction events per year. Results of this assessment support the management of AIS in Canada by documenting the scale of the pathway, identifying species and functional groups of regional and national concern, and informing the development of offensive and defensive AIS management programs.

Propagation par voie terrestre d'espèces aquatiques envahissantes entre des écosystèmes d'eau douce par l'intermédiaire de la navigation de plaisance au Canada

RÉSUMÉ

Une analyse documentaire a été réalisée dans le but de faire le point sur la propagation par voie terrestre d'espèces aquatiques envahissantes (EAE) dans les écosystèmes d'eau douce causée par la navigation de plaisance au Canada. Après avoir dépouillé 57 publications primaires, on a constaté que les facteurs qui contribuent à la propagation par voie terrestre comprennent l'hétérogénéité des comportements des plaisanciers, notamment les différences dans la fréquence des voyages, l'intervalle entre les voyages et la répartition spatiale des installations de navigation par rapport aux populations sources des EAE. Ces facteurs, outre les mesures prises par les plaisanciers pour retirer les EAE de leurs embarcations et de leur équipement de navigation (par exemple, enlever les matériaux visibles de l'ancre ou nettoyer la coque du bateau), dictent la variété, la densité et la viabilité des EAE transportées entre les écosystèmes d'origine et d'accueil et déterminent en fin de compte la probabilité d'une propagation par voie terrestre. Ainsi, comme c'est le cas pour les autres voies d'introduction et de propagation des EAE au Canada, un sous-groupe d'événements d'origine anthropique présente le plus grand risque d'invasion en raison de facteurs dépendant du contexte environnemental et comportemental.

La contamination des embarcations et de l'équipement par des EAE peut être classée selon les caractéristiques fonctionnelles de salissure causée par des espèces tels que :

1) Plancton et organismes ayant une forme planctonique à un certain stade de leur cycle de vie, transportés dans des viviers, l'eau de cale et d'autres espaces où ils peuvent vivre dans de l'eau non filtrée;

2) Organismes présentant un potentiel de fixation directe (p. ex., mollusques d'eau douce), transportés par fixation directe sur la coque ou la remorque;

3) Organismes présentant un potentiel de salissure indirecte, souvent enchevêtrés dans les remorques et d'autre équipement, comme les lignes de mouillage (c.-à-d. macrophytes aquatiques, invertébrés benthiques).

Le déplacement des embarcations de plaisance par voie terrestre a entraîné la propagation de plusieurs EAE bien connues au Canada, telles que le cladocère épineux (*Bythotrephes longimanus*), le cladocère pêcheur (*Cercopagis pengoi*) et la moule dreissénidée (surtout transportée sous forme de véligère) et est probablement responsable du transport du myriophylle en épi (*Myriophyllum spicatum*) et du mysidacé tacheté (*Hemimysis anomola*). D'autres EAE présentant des caractéristiques fonctionnelles de salissure semblables à celles des espèces susmentionnées se propageront probablement par voie terrestre par l'intermédiaire du transport de bateaux de plaisance. En outre, du fait de la forte corrélation entre la répartition spatiale de nombreuses EAE bien connues et le déplacement des bateaux par voie terrestre, il semble qu'il soit possible de prédire avec assez de certitude les propagations futures. Il est très probable que l'estimation de premier ordre du nombre de plaisanciers sur les plans d'eau intérieurs (1,5 million) et de sorties nautiques sur les plans d'eau intérieurs (24,7 millions par année) sous-estime la portée des voies d'introduction entre les écosystèmes d'eau douce au Canada. Selon la portée simulée de la probabilité d'introduction d'EAE par sortie de navigation, même de faibles taux de transfert d'EAE par voie terrestre (p. ex., 1 transfert par 1 000, 10 000 ou 100 000 voyages nautiques) entraîneront au moins 10, 100 ou 1 000 événements d'introduction d'EAE au pays chaque année. Les résultats

de la présente évaluation appuient la gestion des EAE au Canada en documentant la portée des voies d'introduction, en identifiant les espèces et les groupes fonctionnels préoccupants à l'échelle régionale ou nationale, et en éclairant l'élaboration de programmes de gestion des EAE fondés sur les principes d'attaque et de défense.

1.0 INTRODUCTION

Canada has numerous pathways known or suspected of transporting aquatic invasive species (AIS), often classified as those intentionally importing species, such as for commerce or trade (e.g., water garden, aquarium, and live food industries; Marson et al. 2009a, 2009b), and those unintentionally transporting species as an unintended consequence of operational activities (e.g., the ballast water pathway; Casas-Monroy et al. 2014, 2015; hull fouling of commercial vessels; Chan et al. 2015; and, the movement of invasive fishes through live baitfish pathways; Drake et al. 2014a, b; Nathan et al. 2015). Pathways operate at a variety of spatial scales and involve primary species introductions to Canada resulting from international movement of AIS, plus secondary spread within Canada due to domestic movement. Assessing the ecological risk posed by invasion pathways is the cornerstone of an aquatic invasive species program (Mandrak and Cudmore 2015; e.g., Casas-Monroy et al. 2014; Drake et al. 2014a) and research to better understand mechanisms of AIS introduction and spread is a priority under Canada's Invasive Alien Species Strategy (Environment Canada 2004). Given efforts to inventory pathways of AIS globally (Hulme 2009), gaining a better understanding of the mechanisms for AIS introduction and spread within Canada remains a core research and management issue.

The use of recreational boats, defined as 'small-craft' vessels not commercially operated and less than 12.2 M in length (definition similar to Rothlisberger et al. 2010) has been implicated in the introduction and spread of native, non-indigenous, and invasive species throughout North America for over twenty years (Schneider et al. 1998, Buchan and Padilla 1999, Bossenbroek et al. 2001, Johnson et al. 2001, Muirhead and MacIsaac 2005, 2011, Leung et al. 2006, Jacobs and MacIsaac 2007, 2009, Drake et al. 2017). Concerns about recreational boating as a pathway for the introduction and spread of AIS initially developed following the invasion of Zebra Mussel (*Dreissena polymorpha*) within the Laurentian Great Lakes basin (GLB). Due to frequent fouling of boat and trailer surfaces and the ability of transient organisms to survive overland (i.e., trailered) movements (Johnson et al. 2001), boater-mediated secondary spread occurred rapidly from points of introduction within the GLB to suitable habitat across North America, including boater-mediated movement across the U.S. continental divide, a distance greater than 1,500 km overland from nearest source populations (see spread projections from Bossenbroek et al. 2007).

The continued expansion of Zebra Mussel within and beyond Canada, plus the expansion of other AIS believed to be boater-mediated, has led to broader concerns about the overland spread of a variety of current and future AIS. Given the association of numerous non-indigenous plankton (Muirhead and MacIsaac 2005, 2011; Koops et al. 2010), aquatic macrophytes (Jacobs and MacIsaac 2009; Rothlisberger and Lodge 2011; Wittmann et al. 2015), and molluscs (Bossenbroek et al. 2001; Leung et al. 2006) with recreational boating, developing a better understanding of the characteristics of this pathway will help to inform AIS management in Canada.

A related Canadian Science Advisory Secretariat research document has been published to assess the ecological risk of recreational boating for the secondary spread of aquatic invasive species *within* large lakes in Canada as a function of on-water boating activity (Drake et al. 2017). The purpose of this document, however, is to review primary literature involving the spread of aquatic invasive species through the overland (i.e., trailered) movement of recreational vessels *among* Canada's freshwater ecosystems. Although information presented in this review has been summarized from publications across North America, the focus of this research document is to review science of, and management implications for, the inland recreational boating pathway in Canada.

2.0 SCOPE OF LITERATURE REVIEW

This document has been prepared to summarize primary literature about the overland spread of AIS among freshwater ecosystems due to recreational boating in Canada. Ecological concerns about among-lake spread are relevant when AIS have been introduced to Canada's freshwaters through primary or secondary mechanisms (e.g., ballast water, baitfish activity, water gardens, natural dispersal) and overland spread from these source locations may occur through recreational boating activity. Thus, as with the spread of AIS *within* navigable waters, the among-lake pathway is a mechanism for the introduction and spread of AIS at the scale of road-accessible waters within Canada. Recreational boats are defined as vessels < 12.2 meters in length used strictly for recreational purposes. This assessment covers overland (i.e., trailered or car-topped) movements of recreational vessels, encompassing:

1) power-driven vessels, such as recreational fishing boats, bow-riders, houseboats, and other related classes of power-driven vessels;
2) sail-driven vessels, such as small and large sailboats; and,
3) manually-driven vessels, such as kayaks and canoes. This assessment excludes small commercially operated vessels such as barges, tour boats, and commercial fishing boats.

In this document, the term spread is used broadly to reflect the uptake (fouling or infestation) of AIS, the movement and introduction of fouled species to locations within Canada not currently invaded, and the overall potential for survival and establishment as a result of boater-mediated movement. As with baitfish pathways (Drake and Mandrak 2014b), the risk of secondary spread due to recreational boating is dynamic as AIS ranges expand in relation to factors like natural dispersal and contract in relation to control efforts.

Several provincial research initiatives have evaluated (Ontario, through the Canadian Aquatic Invasive Species Network) or are currently evaluating (British Columbia, Alberta) location- and species-specific risks associated with the overland movement of recreational vessels (L.-M. Herborg, Province of British Columbia, pers. comm.; K. Wilson, Province of Alberta, pers. comm.). To avoid duplicating research effort, this document will not explicitly quantify the ecological risk of overland recreational boating as a pathway for aquatic invasive species in Canada. Instead, the goal is to complement current research initiatives by summarizing primary literature involving the potential for AIS introduction through among-lake movement, including the potential for AIS survival during overland transport. The final section of this document presents a first-order estimate of the number of inland recreational boating trips among freshwater ecosystems in Canada and the overall probability of AIS introduction associated with this pathway.

To conduct the literature review, a search of primary scientific literature was conducted between February and September 2015. Web of Science and Google Scholar were used with the search terms "boating + aquatic invasive species", "secondary spread", "vector", and "human-mediated" to compile articles that were directly or indirectly related to recreational boating as a pathway for the spread of AIS. The initial search revealed over 250 articles, of which many were only marginally related to understanding the scope and scale of the pathway in Canada. A second set of search terms were used, incorporating "recreational boating + aquatic invasive species", "secondary spread", and "human-mediated". A subset of articles from the second search (57 articles) was selected as relevant for summarizing the pathway in Canada. Publications were loosely categorized into the following research themes:

1) Studies documenting the contamination of vessels with native, non-native, or invasive fauna (Table A1: 10 publications, 18% of total; e.g., Johnson et al. 2001; Minchin et al. 2003; Jacobs and MacIsaac 2007; Rothlisberger et al. 2010; Kelly et al. 2013);
2) Studies quantifying the survival of aquatic species during overland transport through field or laboratory methods (Table A2: 16 publications, 28% of total; e.g., Wood et al. 2011; Jerde et al. 2012; Barnes et al. 2013; Havel et al. 2014), including the assessment of decontamination strategies such as power washing (e.g., Comeau et al. 2011);
3) Studies forecasting the location of freshwater ecosystems at greatest risk of invasion due to overland boating, often conducted with gravity-type models and tailored to the spread of individual species, such as Zebra Mussel and Spiny Water Flea (Table A3, 21 publications, 37% of total; e.g., MacIsaac et al. 2004; Timar and Phaneuf 2009; Muirhead and MacIsaac 2011; Potapov 2011a; Gertzen and Leung 2011; Chivers et al. 2012; Wittmann et al. 2015); and,
4) Studies describing the role of inspection stations, the link between boater behaviour and educational campaigns, and other factors involved in spread management (Table A4, 10 publications, 18% of total; e.g., Jensen 2010; Shaw and Howell 2014; Lee et al. 2015; Pradhananga et al. 2015).

The loosely defined categories were not necessarily mutually exclusive and publications were assigned to categories of best fit. The focus of the literature review involved primary publications; however, grey literature was also reviewed where relevant. Studies were summarized within the body of the research document and a list of each paper, including key findings, is presented within Appendix 1.

This document also presents a first-order estimate of the number of inland trips across freshwater ecosystems in Canada (section 3.4) and the overall probability of AIS introduction associated with these trips (section 3.5).

3.0 CHARACTERIZING PROPAGULE PRESSURE FROM RECREATIONAL BOATING

The potential for recreational boats to transport viable AIS propagules overland, to uninvaded ecosystems, is a combination of factors related to the scale of recreational boating activity, boater behaviour, and fouling and survival characteristics of AIS. Section 3.0 reviews these factors and how they lead to propagule pressure within the recreational boater pathway, including the role of boater behaviour (section 3.1), the infestation of boats with functional groups of AIS, their survivorship during fouling, and the effect of boat cleaning (section 3.2), models describing the potential for boater-mediated spread (section 3.3), and a first-order estimate of the number of inland recreational boat trips within Canada (section 3.4), including the overall probability of AIS introduction (section 3.5).

3.1 RECREATIONAL BOATER BEHAVIOUR

The potential for overland boat movements to introduce and spread AIS will vary based on the scale of the pathway (e.g., number of trips per year; first-order estimate given in section 3.4), the timing between trips, the spatial distribution of trips in relation to source populations of AIS (e.g., Muirhead and MacIsaac 2005; 2011; Leung et al. 2006; Potapov 2011a, b; Drake and Mandrak 2010), and steps taken to reduce the infestation of boats with AIS. These factors interact with AIS populations to determine the scale and frequency of boater-mediated spread across the freshwater landscape (MacIsaac et al. 2004; Muirhead and MacIsaac 2005; Rothlisberger and Lodge 2011).

3.1.1 Trip-taking Frequency

Data from Ontario indicate that certain boaters have the potential to introduce AIS as a function of their trip-taking frequency (data in Drake et al. 2017). For example, the potential for an individual boater to take more than 100 trips per year (Figure 1) indicates that certain trips during the boating season will occur in relatively quick succession, potentially leading to insufficient drying of boat and trailer components and promoting survival of contaminated AIS on boats, trailers, and related components (see section 3.2 for estimates of AIS survival on boats transported out of water). Should a subset of these trips visit multiple waterbodies within a relatively short period, the potential for AIS introduction exists when surviving propagules are released inadvertently to a destination waterbody.

In Alberta, Papenfuss et al. (2015) found 1,246 instances during a roughly three year period where anglers visited two different lakes in a seven day window (many of these movements involved the use of recreational boats; P. Venturelli, University of Minnesota, pers. comm.). Rothlisberger et al. (2010) found that fishing guides in Wisconsin transported their trailered boats overland to visit an average of 5.4 waterbodies within a two week span, while non-guide boaters would visit an average 2.72 waterbodies within a two-week period. In both studies, a boater visiting multiple waterbodies within a short period was relatively rare compared with the overall boating population (e.g., in Rothlisberger et al. 2010, guides represented 23% of the surveyed population and in Papenfuss et al. 2015, multi-lake visits within a seven day window occurred only 10% of the time). In a survey of boaters and other recreationalists at boat launches in New York, Muirhead (2007) found that 71% of respondents reported 7 or fewer days since their equipment was last used. In Ontario, nearly 40% of Great Lakes basin (GLB) boaters indicated also using their boats within inland waters, while 3.4% of GLB boaters would use their boats in waters outside of Ontario (Drake et al. 2017). Therefore, a subset of boaters have trip timing and movement patterns that could promote the dispersal of viable propagules among waterbodies. Given the absolute number of trips across the boating population in Canada, the subset of trips with the potential to transfer aquatic species among freshwater ecosystems can be quite large (see section 3.4 for calculations illustrating how boating events can lead to a large number of AIS introductions).

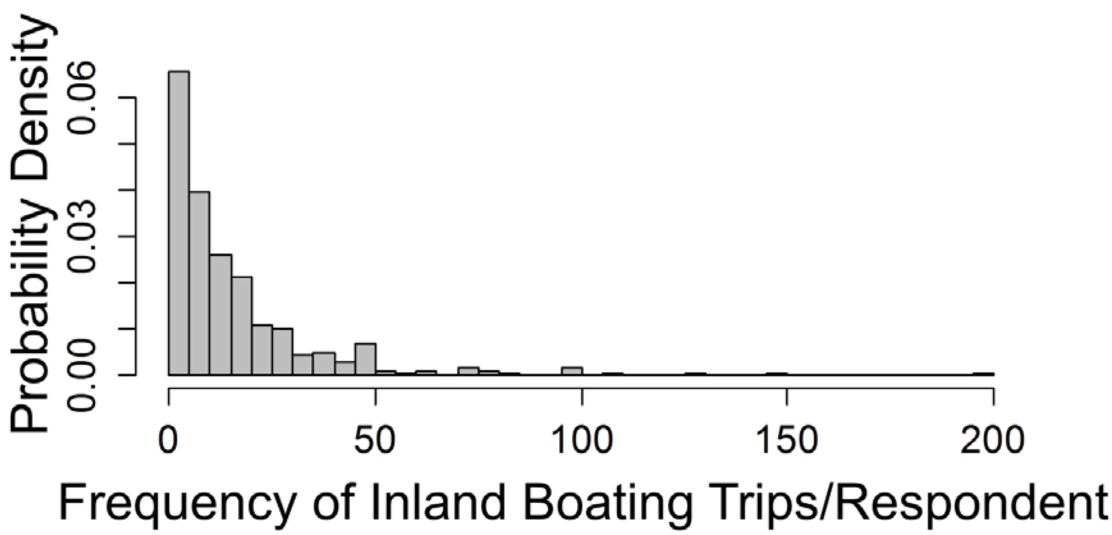

Figure 1. Probability distribution of the number of inland recreational boating trips per year per respondent, based on surveyed populations in Ontario (Drake et al. 2017).The probability distribution was best described as Negative Binomial with μ = 16.42 and k = 1.

3.1.2 Overland Travel Distance

The overland movement of trailered recreational boats often follows a geometric or exponential probability distribution, in which the probability of moving declines strongly as distance becomes large (e.g., Figure 3 in MacIsaac et al. 2004). This pattern indicates that most trailered movements will be relatively short, but some will be substantially longer (Figure 2). Compared to on-water travel distances (based on the exponential rate parameter of 0.09 derived from the Great Lakes basin in Drake et al. 2017), overland (i.e., trailered) movements in Ontario occur at far lengthier distances (Figure 2; rate parameter of 0.00323 from Drake and Mandrak 2010, see also Muirhead 2007, with rate parameter of 0.005). These findings suggest that the overland distance of AIS moved via trailering is, on average, far greater than movement that occurs during in-water boating.

In the Alberta study, Papenfuss et al. (2015) found that of 1,246 overland movements occurring within a seven day window, 80% of trips occurred over Euclidean distances less than 150 km but as many as 4.3% were greater than 300 km. Drake and Mandrak (2010) identified a strongly right-skewed movement kernel of live bait anglers in Ontario, where median travel distances were as great as 296 km, though not all of these lengthy movements involved trailered boats. In a study of recreationalists (including boaters) moving from lakes invaded with *Bythotrephes longimanus*, Muirhead (2007) found that approximately 40% of respondents traveled 100 km or less to their next destination lake, but 2% would travel distances greater than 800 km.

Patterns of recreational boater movements captured through gravity models also support the finding that the longest movements of trailered boats are relatively infrequent compared to shorter movements. However, in a gravity model framework, large destination lakes can be visited at lengthy overland travel distances, especially when a large number of trips leave a given origin (Bossenbroek et al. 2001, 2007; Leung et al. 2006; Muirhead and MacIsaac 2011; Muirhead et al. 2011). Based on a production-constrained gravity model, MacIsaac et al. (2004) found that boater-mediated invasions of *B. longimanus* in central Ontario occurred at distances of 107 and 200 km overland, confirming the transport of viable propagules via recreational boats over substantial distances. Bossenbroek et al. (2007) predicted that the overland transport of a boat infested with Zebra Mussel from central states to the southwestern United States would occur with high probability, an overland distance of approximately 1500 km. A review of gravity models is given in Section 3.3 and Table A3.

As with the frequency of trips taken in a given year (section 3.1.1), the longest overland travel distances are relatively rare in a given boater population, but empirical and modelling results indicate these movements will occur with certainty each year due to the scale of the pathway in Canada (section 3.4). These findings confirm that lengthy overland trips, many of which have the potential to transport viable AIS, exist across Canada’s freshwater landscape (see section 3.5 for an overall estimate of the probability of AIS introduction).

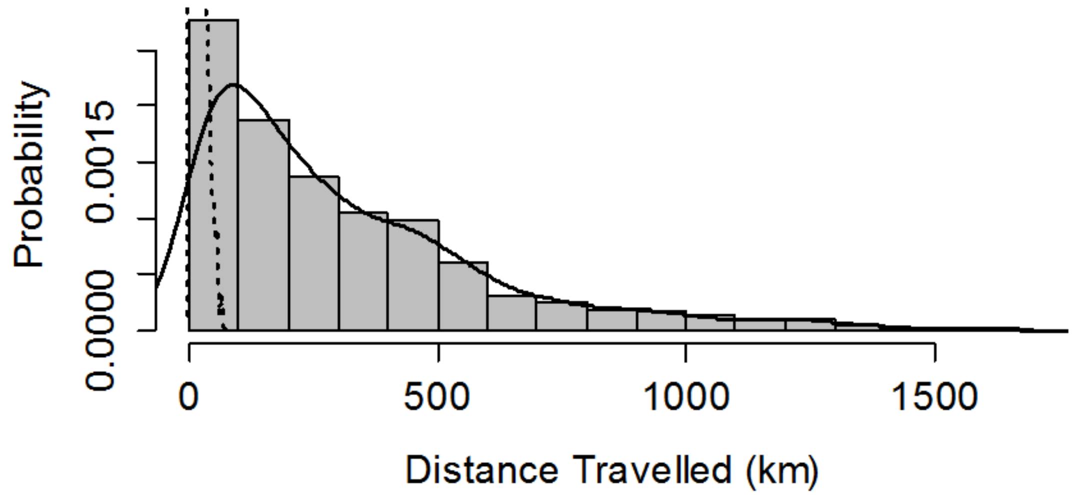

Figure 2. Comparison of exponential dispersal kernels for live bait anglers in Ontario, Canada (solid black line; Drake and Mandrak 2010) with on-water GLB travel distances undertaken by recreational boaters (inset; black dotted line; Drake et al. 2017).

3.1.3. Cleaning Behaviour

Differences in boat cleaning behaviour can lead to changes in the condition, diversity, and abundance of AIS onboard recreational boats during trailered movement (Rothlisberger et al. 2010). Steps taken to clean or remove aquatic organisms from vessels typically involve purposefully drying vessel and trailer components (especially between trips that occur in short succession), purging livewells before leaving launch ramps, scrubbing hulls, picking biological material and detritus from anchor lines and other boat components, and cleaning and flushing engine cooling systems (Kelly et al. 2013).

Multiple authors have found variation in cleaning behaviour within and among boaters. For example, in the Ontario survey (Drake et al. 2017, Table 4), 64% of inland boaters reported undertaking at least one cleaning step, but participation in any individual step was relatively low (e.g., flushing of motor intakes, proportion = 0.05; rinsing boat with hot water, proportion = 0.088; draining bilge and other areas that accumulate standing water, proportion = 0.1; Table 1). The highest rate of participation in cleaning involved drying vessels for 5 or more days, as well as rinsing boating equipment with high pressure water (proportion = 0.29). In contrast, Kelly et al. (2013) found that as few as 12.5% of boaters surveyed in Lake Simcoe, Ontario reported drying boats and related equipment for 5 or more days, though almost 68% reported cleaning anchors and anchor lines. Rothlisberger et al. (2010) found that at least 10% of boaters traveling among lakes in Wisconsin admitted they did not clean boats by rinsing, pressure washing, or drying before moving among lakes. However, in that study, cleaning boats and trailers of macrophytes was self-reported to be undertaken at least 57% of the time. Despite the high self-reported rate of macrophyte removal, 19% of boats arriving to launches contained aquatic macrophytes, as did 63% leaving launches. These results suggest that self-reported activities may have been misreported, especially given the effectiveness of visual inspection and hand removal of macrophytes in a recent study (Rothlisberger et al. 2010).

While the effectiveness of cleaning on reducing a boat’s propagule pressure is not always well understood, Rothlisberger et al. (2010) reported that visual inspection and hand removal of macrophytes can lead to high propagule reductions (88% reduction in the amount of macrophytes per boat), which was similar to the rate of removal obtained through high-pressure washing. However, high-pressure washing was most effective for removing small-bodied organisms (e.g., amphipods, gastropods, cladocerans; 91% removal rate), while low-pressure washing and hand removal were not as effective for those taxonomic groups (74% and 65% removal rate, respectively; Rothlisberger et al. 2010).

Emphasizing the role of individual behaviour when boat cleaning, Cimino and Strecker (2014) reported that although 75% of boaters indicated that they would use a boat wash station, only 38% actually used stations when they were present. Cimino and Strecker (2014) also found that 60% of boaters were aware of the clean, drain, dry campaign slogan, while Lee et al. (2015) reported that there is a cumulative effect of boat cleaning awareness as outreach programs develop. Jensen (2010) indicated that behavioural changes, including cleaning, could reduce relative propagule pressure by 51-93% among boaters. Jensen (2010) also reported that boaters who undertook cleaning reported “a sense of personal responsibility”, “desire to keep AIS out of lakes”, and “preventing damage to equipment” as motivating factors. Therefore, a large body of evidence indicates that washing practices can reduce propagule pressure for overland boat movements, but social factors will influence participation in, and effectiveness of, boat cleaning.

Table 1. Response rates from the Ontario Recreational Boater Survey distributed between April and September 2010. The survey required boaters to describe boating for the 2009 boating season. Table reproduced from Drake et al. 2017.

Surveyed Question	Overall	Great Lakes (GL) Specific
Proportion of respondents indicating boat ownership and boat use in survey year (includes both GL and inland activity; hereafter, ‘active’ users)	767/1497 respondents = 0.523	-
Proportion of boat users indicating some level of boating activity in GL, given that they were active users	-	234/767 = 0.305
Proportion of active boaters that stored boat in water at marina or in water at principal residence	173/767 = 0.225	43/234 = 0.183
Proportion of GL boaters that used their boat in inland waters	-	94/234 = 0.401
Proportion of boaters that used their boat in waters beyond Ontario and the Great Lakes	25/767 = 0.032	8/234 = 0.034
Proportion of boaters that reported always or sometimes:	-	-

Surveyed Question	Overall	Great Lakes (GL) Specific
Removing plants and animals by visual inspection	150/767 = 0.195	48/234 = 0.205
Purposefully draining boat areas that accumulate water (bilge, livewell, etc.)	77/767 = 0.100	23/234 = 0.098
Completely drying boat and related components for 5 days or more	229/767 = 0.298	88/234 = 0.376
Rinsing boats and related equipment with high pressure water	230/767 = 0.299	87/234 = 0.371
Rinsing boats and related equipment with hot water	68/767 = 0.088	24/234 = 0.102
Cleaning anchors, anchor lines, and related components	107/767 = 0.139	25/234 = 0.106
Cleaning downriggers, fishing line, and related components	61/767 = 0.079	23/234 = 0.098
Flushing motor intake (i.e., cooling system)	39/767 = 0.050	11/234 = 0.047
Conducting at least one of the cleaning steps presented above	491/767 = 0.640	161/234 = 0.68

3.1.4 Summary of Boater Behaviour and the Role of Trip Heterogeneity

The influence of trip timing, travel distance, and cleaning behaviour suggest that boaters and trips across Canada are highly heterogeneous in their risk of transporting AIS. Heterogeneity refers to the context-dependent nature of risk for a trip in which a sequential series of undesirable activities must occur for a trip to introduce viable AIS beyond their current range. For example, only a subset of boaters will undertake trips in relatively short succession, suggesting that only a subset of trips will operate within the timing window of AIS survivorship. Of these closely timed trips, only a subset will involve first visiting an infested lake and then moving to an uninfested lake. Only a subset of these infested-uninfested pairs will involve lengthy travel distances, and only a subset of these will avoid cleaning practices.

This hierarchical process implies that the majority of boating trips are relatively benign, while a smaller proportion of trips likely support the bulk of boater-mediated AIS introductions. Predicting these rare events remains a core challenge in invasion ecology (Franklin et al. 2008), as there is rarely a robust means to identify and segregate these infrequent but extremely important events from those that are benign. A complicating factor is that even though a small proportion of trips satisfy the conditions for AIS transport, these infrequent events occur with certainty each year due to the sheer volume of boating activity (see section 3.4, 3.5). This mechanism, whereby a small fraction of trips supports the bulk of AIS risk, has been well described for a variety of AIS pathways across Canada. Drake and Mandrak (2014) described similar mechanisms involving rarity and trip heterogeneity for live bait anglers, in which the per-trip probability of introducing AIS was low ($p = 0.00088$, or 1 in 1,136 live bait trips), but the sheer magnitude of live bait angling activity as a whole would likely lead to over 3,000 introduction events of AIS each year. While it is very likely that certain classes of boaters (e.g., professional fishing guides; Rothlisberger et al. 2010) pose a relatively higher risk of spreading AIS based on their boating and cleaning habits, a great deal of uncertainty about the risk-release relationship (Wonham et al. 2013) makes drawing conclusions about the absolute risk among sub-populations of boaters difficult.

3.2 BOAT CONTAMINATION, SURVIVORSHIP OF AIS, AND EFFECTIVENESS OF DECONTAMINATION TECHNIQUES

A review of the diversity of aquatic species fouled on recreational boats and related equipment is useful to understand the characteristics of current and future AIS likely to be spread overland (Table A1). The general characteristics of boater-mediated AIS are reviewed in Drake et al. (2017). Three main functional groups (a term used here as it relates to fouling characteristics) described below are known to be transported overland in viable condition:

3.2.1 Plankton and aquatic organisms with planktonic life stages

Plankton (phytoplankton, zooplankton) and aquatic organisms with planktonic life stages, such as *Dreissenid* spp., including current AIS of national concern such as Spiny Waterflea (*Bythotrephes longimanus*; Muirhead and MacIsaac 2005, 2011); Fishhook Waterflea (*Cercopagis pengoi*; Jacobs and MacIsaac 2007, Muirhead et al. 2011); Bloody Red Shrimp (*Hemimysis anomola*; suspected, Koops et al. 2010); Zebra and Quagga Mussel veligers (*Dreissena polymorpha* and *D. bugensis*; Johnson et al. 2001, Dalton and Cottrell 2013, Kelly et al. 2013); and, Killer Shrimp (*Dikerogammarus villosus*) in Europe, Bacela-Spychalska et al. (2013), have been transported on recreational boats. Many native species of zooplankton are also transported on recreational boats (Rothlisberger et al. 2010, Kelly et al. 2013) and the number of native zooplankton present on a boat has been weakly correlated with its volume of standing water (Kelly et al. 2013).

The density of plankton on transported boats is highly variable (Johnson et al. 2001, MacIsaac et al. 2004, Kelly et al. 2013), but plankton densities are generally highest in compartments that pool water from below the water's surface, such as livewells, bait buckets, engine cooling water, and wakeboat ballast tanks, while lower densities are found in bilge water or other small collection points (Johnson et al. 2001). Some planktonic species have strong affinity for certain structures due to morphological features. For example, MacIsaac et al. (2004) found that fouling of Spiny Waterflea was greatest on fishing line but lowest in livewells and float plane pontoons, while Jacobs and MacIsaac (2007) found that Fishhook Waterflea preferentially attached to fishing line and a positive relationship was observed between distance trolled and the rate of accumulation (these findings likely also apply to *Bythotrephes sp.*). The average maximum concentration of transported plankton appears to be at, or slightly below, the density of plankton in source waters (Drake et al. 2017), and these groups may be transported overland in viable condition when intake structures have been used in a manner to promote containment and survivorship of hitchhiking species (e.g., failing to completely drain livewells).

The survival of plankton on boats and trailers during overland travel is difficult to observe directly, but laboratory studies provide guidance about desiccation tolerance, temperature effects, and variation of survival among species and seasons. Choi et al. (2013) found that planktonic Zebra Mussel veligers could survive in simulated transport conditions (submerged, but exposed to high ambient temperatures) for five days during summer conditions, but survival would be much longer, up to 28 days, during cooler weather. Horvath and Crane (2010) found that veliger survival was strongly related to the extent of hydrodynamic forces applied to plankton, with implications for the effectiveness of high-pressure washing.

3.2.2 Species (usually molluscs) with direct attachment potential

Species (usually molluscs) with direct attachment potential, such as Zebra Mussel (*D. polymorpha*; Johnson et al. 2001, Minchin et al. 2003), Quagga Mussel (*D. bugensis* transported in GLB and suspected of overland transport near Lake Mead, USA; Comeau 2011, Comeau et al. 2011, Choi et al. 2013); and, New Zealand Mud Snail (*Potamopyrgus antipodarum,* suspected, Therriault et al. 2011) have been transported on recreational boats. Other invasive aquatic snails in central North America, such as *Bithynia tentaculata*, *Cipangopaludina chinensis*, and *Viviparus georgianus* (suspected; Wood et al. 2011, Havel et al. 2014) have been transported on boats and equipment, with apparently good survivorship. For example, *B. tentaculata, V. georgianus, and C. chinensis* exhibited survival after 42 days of experimental drying conditions, indicating strong potential for surviving lengthy overland distances. A variety of native aquatic snails (Rothlisberger et al. 2010) have also been found on recreational boats. Generally, boats stored on land are infrequently fouled with adult molluscs (Johnson et al. 2001). Johnson et al. (2001) indicated that an average of 2.3 adult Zebra Mussel were found on macrophytes entangled in boat trailers leaving Lake St. Clair boat launches, and estimated that 5% of trailers, and 0.9% of anchors would transport adult Zebra Mussel away from invaded launch sites. Also illustrating the role of boat storage conditions, Minchin et al. (2003) found average fouled densities of up to 44,000 Zebra Mussel per m^2 for boats that were stored in water, moved infrequently, and not cleaned. For smaller boats used frequently and stored in-water, average densities were usually lower than 10,000 adult Zebra Mussel per m^2 when fouling occurred.

3.2.3 Aquatic macrophytes and other species with potential for indirect attachment

Aquatic macrophytes and other species with potential for indirect attachment include Eurasian watermilfoil (*Myriophyllum spicatum*; suspected, Buchan and Padilla 2000, Rothlisberger and Lodge 2011), Fanwort (*Cabomba caroliniana;* Jacobs and MacIsaac 2009), plus native macrophytes (e.g., *M. heterophyllum*; Rothlisberger et al. 2011, other native macrophyte species; Kelly et al. 2013, Johnson et al. 2001) and are known to be transported. Typically plants are transported as viable fragments in livewells, bait buckets, and in other niche areas, and as clumps on trailers (Johnson et al. 2001), anchors, and anchor lines (Kelly et al. 2013). A variety of benthic species, namely scuds and isopoda, may be inadvertently transported in anchor sediments (L. Chadderton, The Nature Conservancy, pers. comm.), but the range of species associated with this transport mechanism is poorly known.

Macrophyte survival during overland transport is highly variable, as indicated by species-specific differences in desiccation rate (Barnes et al. 2013). Bruckerhoff et al. (2015) found that *M. spicatum* and *P. crispus* were viable for up to 18 and 12 hours, respectively, during simulated transport. Physical coiling of *M. spicatum* extended the period of viability to 48 hours due to humidity effects, indicating strong potential for overland survivorship when clumps, as opposed to single strands, are transported. The significance of clumping also extends to other species. For example, individual *Cabomba* spp. fragments survived up to 3 hours if exposed to wind, but clumps remained viable for up to 42 hours. Jerde et al. (2012) found that survival of non-clumped aquatic macrophytes was rare beyond a 24 hour period, but clumped individuals, often found in livewells or on trailers, could be viable for up to two weeks in certain environmental conditions.

Numerous decontamination techniques are effective in reducing the fouling of recreational boats with functional group of AIS (Table A2). Beyer et al. 2011 found that immersion of juvenile *B. longimanus* in hot (> 45 °C) water for 10 minutes would lead to complete mortality, but only 5 minutes of immersion was necessary for complete mortality of adult Zebra and Quagga Mussels. For Killer Shrimp, Bloody Red Mysid, and several other AIS, immersion in 45 °C water caused complete mortality within 1 hour (Anderson et al. 2015). For *Didymo* sp., a native fouling species in Canada, hot water decontamination techniques were extremely effective (Kilroy et al. 2006), as were bleach, a commercial solution of the Virkon brand, and salt (Root and O'Reilly 2012), suggesting that these techniques may be useful in the decontamination of invasive macrophytes or algae.

3.3 POTENTIAL FOR AIS SPREAD THROUGH RECREATIONAL BOATING

Numerous landscape-scale models, known as 'gravity models', have been used to quantify the spread and establishment of AIS associated with overland recreational boat movements in North America (Table A3). The term gravity model encompasses a class of spatial models that describe the movement of humans based on the relative attractiveness of destinations, the relative push of origins, and their distance separation (Thomas and Huggett 1980). When applied to the movement of recreational boats (and AIS as hitchhiking species), overland boat movements are modeled as a function of travel distance between an origin cell and a destination lake, the number of outbound boat movements from a given origin cell, and measures of lake attractiveness (e.g., lake surface area; see Bossenbroek et al. 2001 and Leung et al. 2006 for examples). In some cases, model terms are added to reflect the habitat suitability of AIS for destination lakes. In addition to describing patterns of boater-mediated AIS spread (Bossenbroek et al. 2001), gravity models have also been used to directly estimate boater movements across the landscape (Leung et al. 2006; Drake and Mandrak 2010).

Correspondence between gravity model predictions and patterns of AIS establishment provide strong evidence for the boater-mediated spread of AIS in Canada. Gravity models have been developed by MacIsaac et al. (2004), Muirhead and MacIsaac (2005, 2011), Gertzen and Leung (2011), and Potapov et al. (2011a, b) to forecast Spiny Waterflea establishment in south-central Ontario lakes. Additional models by Drake and Mandrak (2010, 2014b) and Chivers and Leung (2012) have been developed for Ontario that are species neutral. Several models in North America have predicted the overland spread of Zebra Mussel, encompassing multiple spatial scales (e.g., Bossenbroek et al. 2001, 2007, Leung et al. 2006). While each model differs in its assumptions and goals, in most cases gravity models have explained a large portion of the occurrence and spread of AIS (e.g., Muirhead and MacIsaac 2011 reported that a production-constrained gravity model resulted in an Area Under the Curve (AUC) value of 0.647, signifying that the model performed better than random at predicting the spread of *Bythotrephes*, while a doubly-constrained gravity model resulted in an AUC of 0.810, performing far better than random and representing good model fit with observed spread data; an AUC value of 1.0 represents perfect model fit; see Table A3 for other characteristics of gravity models). Jacobs and MacIsaac (2009) reported an AUC of 0.838 for predicting the spread of *Cabomba caroliniana* in Kawartha Lakes, and Muirhead et al. (2011) reported an AUC of 0.984 when forecasting the spread of Fishhook Waterflea in New York State. The AUC values of both models signified strong correspondence between the models and observed invasion data, confirming that predictions performed significantly better than random. While the probability of establishment associated with an individual boating trip is unknown, Bossenbroek et al. 2001 estimated a per-trip probability of introduction, survival and establishment of $p = 0.000041$ for

Zebra Mussel in the Great Lakes basin based on the relationship between a lake's invaded status and the model forecast of boating trips.

In some cases, gravity models perform poorly when predicting the distribution of AIS that are believed to be boater-mediated. Buchan and Padilla (2000) found that habitat-based variables, rather than measures of boating activity, provided the most suitable forecast of Eurasian watermilfoil in inland lakes in Wisconsin. Olden et al. (2011) found that lake morphology was a key predictor of Rusty Crayfish (*Orconectes rusticus*) when combined with indices of boater accessibility, and Rothlisberger and Lodge (2011) found that gravity model scores were not correlated with the presence of Eurasian watermilfoil in Wisconsin. These findings indicate that species and site-specific factors, as well as model specification, can influence the predictive success of gravity models. However, given the high AUC values of numerous gravity models reviewed in Table A3, the boater-mediated overland spread of many AIS is likely to be predicted with relatively high fidelity when gravity model approaches are applied to Canada's freshwater ecosystems.

3.4 FIRST ORDER ESTIMATE OF THE NUMBER OF FRESHWATER RECREATIONAL BOATING TRIPS IN CANADA

A key challenge for estimating the overall probability of AIS introduction through the recreational boating pathway is uncertainty around the absolute number of boats, boaters, and yearly boating trips in Canada. This uncertainty makes it difficult to understand the scope of AIS transfer potential relative to other pathways. Because boaters in Canada are generally not required to register vessels below a given motor size (10 hp), a national database of boaters and boats is lacking, which makes estimating the scale of the pathway difficult.

To address this uncertainty, a first-order calculation was used to estimate the absolute number of boaters and boating trips across Canada's freshwater ecosystems. The estimate was based on data from Ontario that were extrapolated across Canada as a whole. Ontario data were assumed to be representative of a national average and were chosen because of the lack of data for each province and territory regarding the number of active resident boaters. The effect of incorporating Ontario data was explored through sensitivity analysis. In addition to estimating the scale of the pathway, the purpose of the calculation was to estimate the overall probability of AIS introduction by joining the national trip estimate with a range of hypothetical per-boater-trip probabilities of AIS introduction (section 3.5).

To conduct the first-order estimate of the number of trips per year by Canadian resident boaters in freshwater ecosystems, the calculation involved:

1) obtaining the 2015 Canadian population estimate from Statistics Canada;
2) multiplying the population estimate by the proportion of the population believed to boat in a given year ('active boaters'); and,
3) multiplying the number of active boaters by the average number of trips taken each year by an individual boater.

The ratio between population size and the number of active boaters, as well as the number of trips taken by an individual boater, were obtained from Ontario populations.

In Ontario, 1.2 M boats are believed to exist (Thorp and Stone 2000; likely an underestimate when manually powered vessels such as canoes and kayaks are considered). This value of boats exceeds the number of boaters because some boaters own multiple boats. An Ontario-specific estimate of the number of boats owned per boater was established based on survey data (Figure 3; see Drake et al. 2017 for a description of the Ontario survey).

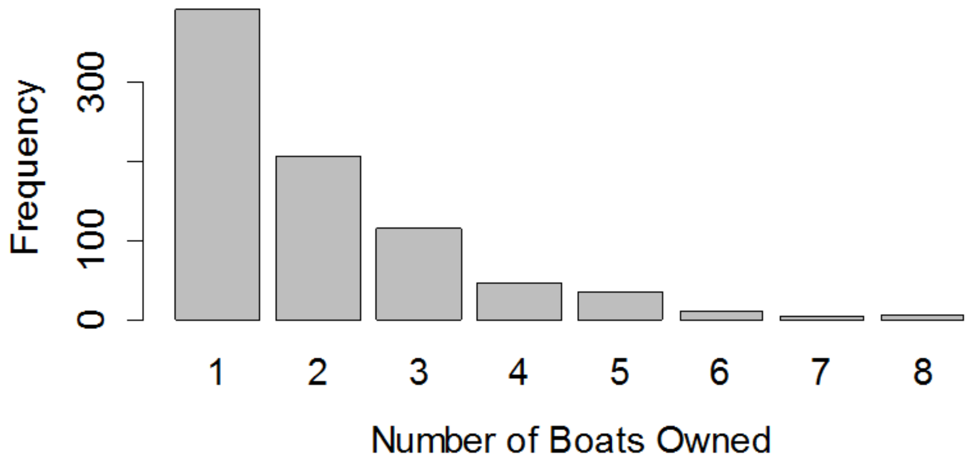

Figure 3. Distribution of recreational boats owned by active boaters in Ontario, 2009. See Drake et al. 2017 for surveying methods.

The number of boats per boater was used to estimate the number of active boaters in the Ontario population as:

Total number of boat owners in Ontario = (Proportion of Ontario sample owning 1,2,3…*n* boats * 1.2 M total boats) / Number of boats 1,2,3…*n* for each proportion.

The result of this calculation was an estimated 585,600 boat owners in Ontario (Table 2). For comparison, Ontario has approximately 650,000 resident licenced anglers, of which some are believed to own recreational boats (Drake and Mandrak 2010). The number of boat owners (585,600) was divided by the Ontario resident population size (13,792,100, Statistics Canada 2015) to determine the overall proportion of Ontario residents owning at least one recreational boat (value of 0.042), termed 'active boaters'. This proportion provides a conversion between resident population size and the subset of individuals owning and using at least one boat within freshwater ecosystems. The proportion of 0.042 was assumed to reflect the nationwide proportion of boat ownership, with the total number of active boaters in Canada calculated as:

Number of Canadian residents (35,852,500) * Proportion boat owners (0.042) = 1,505,763 active boaters in Canada assumed to take at least one trip within freshwater ecosystems in a given year.

Table 2. Relationship between the number of recreational boats owned and the estimated number of boaters (Ontario residents) in each class.

Number of Boats Owned	Proportion of Surveyed Individuals (Active Boaters in Ontario)	Estimated Number of Boaters (Calculation Based on 1.2 M Boats in Ontario; Thorp and Stone 2000)
1	0.235	282,000
2	0.124	148,800
3	0.069	82,800
4	0.027	32,400
5	0.021	25,200
6	0.006	7,200
7	0.003	3,600
8	0.003	3,600
Total	1.0	585,600

Data from the Ontario survey describing the number of yearly trips taken by an individual inland boater (Figure 1; probability distribution of best fit is negative binomial with μ = 16.42 and k = 1 based on maximum likelihood and Akaike's Information Criterion) were used to estimate the total number of trips within freshwater ecosystems in Canada. By applying Ontario-specific trip frequencies, this approach assumes that Ontario trip frequencies are reflective of the national average.

A resampling framework was used to generate a probability distribution of the total freshwater trips per year in Canada. To conduct the estimate, the number of inland boaters across Canada (1,505,763) was randomly sampled from the negative binomial trip frequency distribution (μ = 16.42, k = 1), reflecting 1,505,763 individual trip frequencies in a given year. The sum of n random samples provided a point estimate of the yearly total number of freshwater trips across Canada and the process was repeated 100 times to generate a probability distribution. While this is, at best, a first order estimation because Ontario data are assumed to be reflective of the rate of ownership and the frequency of boat use across Canada, this calculation is helpful to determine the scale of pathway activity across the Canadian landscape when bounded by a series of simplifying assumptions (see sensitivity analysis below). The resulting estimate of the mean number of yearly trips in freshwater ecosystems in Canada was 24,725,253 (95% CI 24,692,478 to 24,765,383; Figure 4).

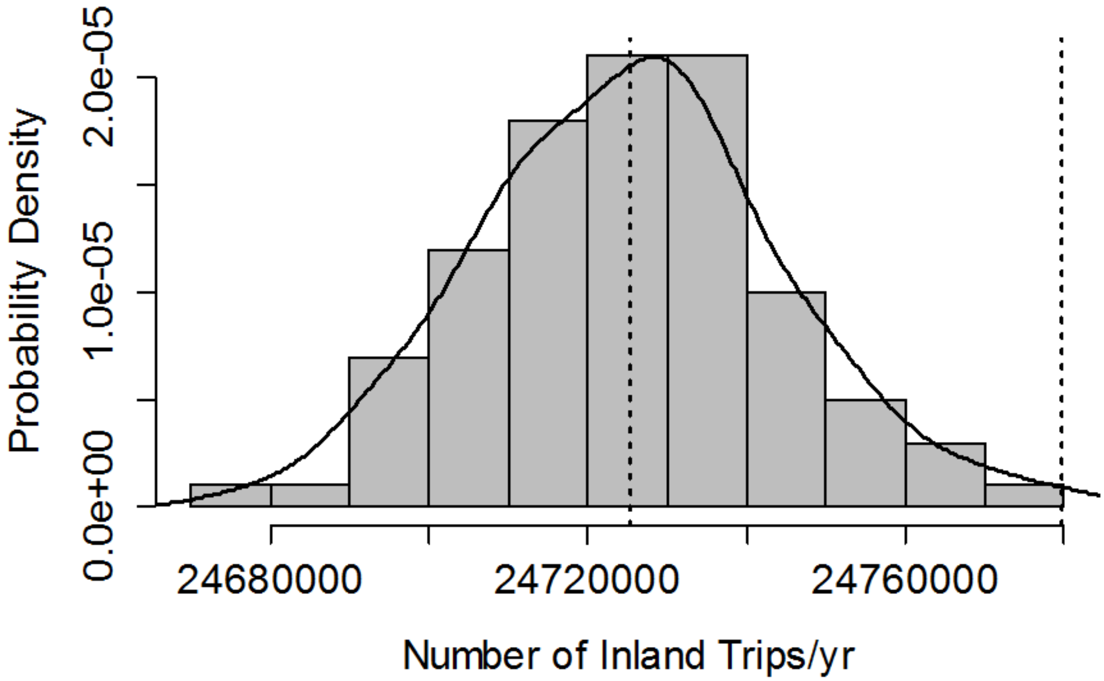

Figure 4. Probability distribution of the total number of freshwater recreational boating trips in Canada, based on data extrapolated from Ontario. Vertical dotted lines represent mean and maximum values.

To determine how sensitive the first-order estimate was to Ontario input data, the proportion of the population actively boating and the mean number of trips per boater (μ from the negative binomial distribution) were shifted ± 25% from their original values and the response in the first-order estimate observed. The goal of sensitivity analysis was to understand whether changes in the values obtained from the Ontario survey, reflecting potential differences in underlying national values, would lead to changes in the first-order estimate.

There are several reasons why Ontario data may overestimate freshwater boating trips at a national scale. For example, some residents in coastal provinces may prefer boating in marine ecosystems, leading to an overestimate of freshwater trips at the national scale when Ontario proportions have been used. Alternatively, underestimation may also occur, as would be expected if Ontario’s large urban population leads to a lower rate of boat ownership and a lower frequency of trip-taking relative to provinces that have greater rural populations.

Sensitivity analysis revealed that the annual number of boating trips per year was generally sensitive to changes in input parameters. Increases or decreases in the proportion of the population deemed to boat actively would lead to changes of similar magnitude to the first-order estimate, signifying a relationship was close to 1:1 (Table 3). For example, a 25% increase in the proportion of the Ontario population deemed to boat actively would increase the nationwide estimate of boating trips by 24.9% (Table 3). When both parameter values (proportion active and mean trip number) were shifted simultaneously, the first-order estimate shifted from a low of -43% to a high of 56%, signifying greater sensitivity when both parameters are considered jointly (Table 3). These results indicate that the first order estimate is generally sensitive to the use of Ontario data to establish a national estimate of boating trips in freshwater ecosystems. Future research to obtain more complete information about the number of active boaters residing in each province and territory would reduce uncertainty and provide a more reflective national estimate.

Table 3. Sensitivity of the number of freshwater trips per year based on changes to the proportion of active boaters and the mean number of trips per year by active boaters. All increases and decreases involved 25% shifts in input parameter values.

Sensitivity Perturbation	Mean Number of Trips per Year	Percent Change from Baseline (mean of 24,725,253 trips/y)
Increased proportion of active boaters	30,906,297	24.9%
Decreased proportion of active boaters	18,542,994	-25.0%
Increased mean number of trips/y	30,907,060	25.0%
Decreased mean number of trips/y	18,543,688	-25.0%
Joint increases in the proportion of active boaters and mean number of trips/y	38,635,477	56.26%
Joint decreases in the proportion of active boaters and mean number of trips/y	13,909,688	-43.74%

3.5 ESTIMATE OF THE OVERALL PROBABILITY OF RECREATIONAL BOATING INTRODUCTION OF AIS TO FRESHWATERS

The ability of AIS to foul recreational boats and survive overland transport conditions, combined with millions of boating trips across freshwater ecosystems, suggests strong potential for AIS to be introduced when even a small subset of trips involve repeated boater movements between invaded and uninvaded ecosystems. To better understand the overall probability of introduction, Table 4 presents the relationship between a range of per-trip probabilities of AIS introduction (true values are unknown, but a range of hypothetical values were chosen to illustrate their influence on the overall number of introduction events each year) and the overall probability that at least n AIS introduction events will occur in a given year. The binomial probability formula is: P (K successes in N trials) = $\binom{n}{k}$ $p^k(1\text{-}p)^{n\text{-}k}$,

where P is the overall probability that at least 100, 1,000, or 10,000 events/y will involve the overland transport of AIS to beyond their current range, given p, the per-trip probability of AIS introduction by a recreational boater (true rate unknown; p will be species-specific based on current AIS ranges and the interactions with boater behaviour and trip heterogeneity), k, the number of successes (100, 1,000, or 10,000 introduction events each year), and n, the overall number of probability trials (24.7 M freshwater boating events, estimated from the baseline mean value in Table 3).

Results of this estimation procedure suggest that even low per-trip probabilities of introduction (i.e., a low chance that an individual trip will satisfy all conditions to transport viable AIS) can result in a relatively large absolute number of AIS introduction events each year (Table 4). For example, if the per-trip probability of introduction by a recreational boater is 1 in 100,000 and 24.7 M boater events occur each year, there is certainty (p = 1.0) that at least 100 AIS introduction events will occur in Canada, but it is extremely unlikely that at least 1,000 or 10,000 events will occur. If a higher per-trip probability of introduction is assumed (e.g., 1 in 1,000), then there is certainty that at least 100, 1,000, or 10,000 AIS introduction events will occur. While the nationwide per-trip probability of introduction is unknown and will vary based on the

AIS of interest and interactions with regional boater activity, Koops et al. (2010) estimated that a recreational boater in the Great Lakes region would transport *Hemimysis anomola* to an inland lake with $p = 1.15 \times 10^{-5}$, or 1 in 86,956 boating events.

The binomial probability calculations were also performed on intentionally different estimates of nationwide annual boating trips, with the goal of exploring how sensitive the probability of introduction calculations were to the number of boating trips obtained via extrapolation with Ontario data (section 3.4). To explore these sensitivities, alternate values of 13.9 M and 38.6 M trips per year were chosen, which represent the number of trips expected following joint 25% decreases and increases in the extrapolated values from the Ontario survey. Results indicated that although the number of yearly boating trips was sensitive to the Ontario input data (see section 3.4), the overall probability of AIS introduction was generally insensitive to the assumed number of trips, because binomial calculations on both the lower and upper number of yearly trips led to overall probability of introduction values that were very similar to baseline (Table 4). Therefore, obtaining a better understanding of whether Ontario data are reflective of the national average will help to reduce uncertainty in the total number of freshwater trips per year, but will not necessarily lead to greater resolution of the overall probability of AIS introduction among freshwater ecosystems at a national scale.

Results in Table 4 confirm that rare individual boating events can lead to a collectively large number of AIS introduction events when a large number of probability trials (boating events) exist. Similar mechanisms have been found for live bait anglers in Ontario (Drake and Mandrak 2014a, b) and for the spread of AIS through on-water recreational boating (Drake et al. 2017). While the per-boating-trip probability of invasion (e.g., the joint introduction, survival, and establishment of AIS) remains unknown and will vary based on species of interest, these estimates provide a baseline measure against which to test species-specific levels of introduction against their expected survival and establishment.

Table 4. Hypothetical relationship between the number of AIS introduction events, the per-boating-trip probability of AIS introduction, and the overall probability that at least N AIS introduction events occur in a given year, based on 24.7 M inland recreational boating trips (also shown are results when 38.6 and 13.6 M trips are assumed). Note that per-boating-trip probabilities of introduction are unknown, but this table illustrates the effect of different per-trip values on the overall probability of introduction.

Number of AIS Introduction Events of Interest	Per-trip Probability of AIS Introduction	Overall Probability that at Least *N* AIS Introduction Events Will Occur (24.7 M trips assumed)	Overall Probability that at least *N* AIS Introduction Events Will Occur (38.6 M trips assumed)	Overall Probability that at least *N* AIS Introduction Events Will Occur (13.6 M trips assumed)
100	0.1 (1 in 10)	1.0	1.0	1.0
100	0.01 (1 in 100)	1.0	1.0	1.0
100	0.001 (1 in 1,000)	1.0	1.0	1.0
100	0.0001 (1 in 10,000)	1.0	1.0	1.0
100	0.00001 (1 in 100,000)	1.0	1.0	0.9997

Number of AIS Introduction Events of Interest	Per-trip Probability of AIS Introduction	Overall Probability that at Least *N* AIS Introduction Events Will Occur (24.7 M trips assumed)	Overall Probability that at least *N* AIS Introduction Events Will Occur (38.6 M trips assumed)	Overall Probability that at least *N* AIS Introduction Events Will Occur (13.6 M trips assumed)
100	0.000001 (1 in 1,000,000)	1.29e-30	5.46e-17	3.33e-51
1,000	0.1 (1 in 10)	1.0	1.0	1.0
1,000	0.01 (1 in 100)	1.0	1.0	1.0
1,000	0.001 (1 in 1,000)	1.0	1.0	1.0
1,000	0.0001 (1 in 10,000)	1.0	1.0	1.0
1,000	0.00001 (1 in 100,000)	4.45e-283	2.43e-149	0
1,000	0.000001 (1 in 1,000,000)	0	0	0
10,000	0.1 (1 in 10)	1.0	1.0	1.0
10,000	0.01 (1 in 100)	1.0	1.0	1.0
10,000	0.001 (1 in 1,000)	1.0	1.0	1.0
10,000	0.0001 (1 in 10,000)	0	0	0
10,000	0.00001 (1 in 100,000)	0	0	0
10,000	0.000001 (1 in 1,000,000)	0	0	0

4.0 MANAGEMENT IMPLICATIONS

This review has identified several overarching factors contributing to the overland spread of AIS among freshwater ecosystems due to recreational boating in Canada. Primary focus has been given to the variety and density of fouling species on recreational boats (Table A1), survival of AIS during overland transport and opportunities to reduce survivorship through cleaning and other treatment technology (Table A2), aspects of boater behaviour and models to forecast future spread (Table A3), and other factors related to management of the pathway (e.g., offensive vs defensive management, the role of outreach campaigns; Table A4).

Based on a review of primary literature and analysis of supplementary data from Ontario, most overland recreational boating trips in Canada appear to be relatively benign due to context-specific factors. For example, a large proportion of boating events will have low potential to transport AIS because boaters are recreating entirely within waters lacking AIS, are boating entirely within waters infested with AIS or, if moving between infested and uninfested localities, are doing so over a sufficiently long number of days as to discourage AIS survivorship, or undertake cleaning practices that effectively remove AIS. However, the sheer volume of the pathway indicates that a non-negligible fraction of trips will involve the movement of viable propagules between infested and uninfested locations within a short period. Moreover, due to environmental stochasticity and imperfect cleaning participation and effectiveness, at least some of these events will be fouled with densities of propagules to promote AIS establishment (see the role of propagule pressure: Lockwood et al. 2005). As shown in section 3.5, the conditional sequence of events for an individual boating trip to spread AIS is rare, with actual values dependent on the AIS of interest (geographic range, likelihood of uptake) and regional boater behaviour (travel patterns, access to uninvaded sites, cleaning behaviour). However, even when per-trip probabilities of AIS introduction are as low as 1 in 10,000, it is certain that at least 1,000 introduction events will occur each year based on the millions of boating events in freshwater ecosystems in Canada. The important role of the magnitude of pathway activity is similar to many other AIS pathways (e.g., the live baitfish pathway, Drake and Mandrak 2014b; within-lake recreational boating, Drake et al. 2017; boater-mediated spread of AIS within marine ecosystems; Simard et al. 2017). Given the analysis in section 3.5, overland boating remains an effective mechanism for the spread of invasive plankton, molluscs, and macrophytes across Canada’s freshwater ecosystems.

Compared to within-lake recreational boating, overland movements of recreational boaters have greater potential to move AIS over long distances. Although the viability of AIS during the lengthiest overland trips will be offset by desiccation, even a 50% reduction in effective travel distance would be sufficient to overcome projected on-water rates of boater-mediated spread derived from the GLB (Drake et al. 2017). Therefore, increased management focus on overland vessel movements is warranted to reduce the rate of AIS spread in Canada.

Although this summary has led to a better characterization of overland boating activity in spreading AIS among freshwater ecosystems, several key uncertainties and considerations exist. The first uncertainty involves the frequency of cross-border trailering into Canada (calculations in this document focus on domestic movement only). Although cross-border trips occur infrequently compared to domestic movements, a large number of overland trips pass through Canada’s borders each year from infested regions in the United States (K. Wilson, pers. comm., Province of Alberta). The importance of cross-border movement warrants further investigation given the likelihood for certain AIS from the United States to survive Canadian freshwaters and given the ability of boaters to spread species overland across substantial distances (Bossenbroek et al. 2007).

The second uncertainty relates to the lack of detailed information regarding patterns of boater-mediated AIS spread among provinces and territories in Canada. For example, estimating the likelihood of boater-mediated spread from Ontario to New Brunswick, Nova Scotia, or PEI is difficult as these long-distance movements are usually not adequately captured by social surveys. In some provinces, survey data have not been collected to capture these or other boating behaviours. However, preventing the spread of AIS among provinces is a current management priority considering the potential for boating activity to establish founder populations in primary watersheds that would otherwise be inaccessible through natural dispersal (e.g., boater-mediated spread of Zebra Mussel from eastern Canada to Nelson River or Mackenzie River drainages). To address these concerns, western provinces (BC, AB, SK, and MB) are currently managing against boater-mediated introductions of Zebra Mussel and other AIS from eastern provinces and the United States. Management activities involve mandatory boater roadside inspections, including over 23,000 spot checks in Alberta and 4,300 roadside inspections in British Columbia in 2015 (L.-M. Herborg, Province of British Columbia,

K. Wilson, Province of Alberta, pers. comm.). Spot checks involve inspecting boat and trailers for fouled AIS, as well as educating boaters about the need for washing, draining, and drying their equipment prior to moving among waterbodies. Understanding the frequency and extent of domestic and international overland movement by boaters remains a strong research priority for quantifying the scale and timing of primary and secondary introductions associated with this pathway.

The third uncertainty relates to the extent of boater-mediated spread of native species beyond their native range in Canada. Although this review focused on the spread of non-native species with known impacts, it is also very likely that native species fitting functional categories are currently are being spread via the overland boating pathway in Canada.

Finally, as this review focused on the potential for overland movement among freshwater ecosystems, the fourth uncertainty relates to overland movement among marine ecosystems. While the majority of marine vessels are not trailered (but rather stored and used in-water within Canada; Simard et al. 2017), the likelihood and potential consequences of trailering within and among marine ecozones has yet to be explored at the national scale.

To guide future management of the pathway, several papers identified common themes involving landscape-level management of AIS as they relate to overland movement. Drury and Rothlisberger (2008) and Rothlisberger and Lodge (2011) found that offensive invasive species management, where infested lakes have mandatory cleaning protocols during outbound trips, was most effective at preventing spread early in the invasion process. However, as the invasion proceeds, defensive invasive species management (cleaning stations at uninvaded lakes to target inbound trips) was most effective. Muirhead and MacIsaac (2005) found that certain invaded lake ‘hubs’ lose their influence as the invasion process proceeds, because outbound connections and fringe sites eventually act as secondary sources once invaded. These studies provide important considerations for future management of the overland pathway.

This paper has summarized primary literature involving the overland spread of AIS among freshwater ecosystems due to recreational boating in Canada. The document and appendices provide information to scientists and managers to conceptualize recreational boating as a pathway for the overland spread of AIS in Canada; to identify groups of AIS likely to be boater-mediated based on their functional fouling characteristics; to support the development of AIS prevention management programs; and, to continue to better understand the role of pathways in the introduction and establishment of AIS in Canada.

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APPENDIX 1. LITERATURE REVIEW

Table A1. Summary of primary literature describing the infestation of recreational boats in freshwaters with native, non-native, or invasive fauna.

Organism	Propagule Density (Mean organisms/m^3 or m^2, unless noted)	Key Findings	Geographic Scope	Study
Zebra Mussel veligers (*Dreissena polymorpha*)	16/L or 16,000/m^3 in engine cooling water, 5.9/L or 5900/m^3 in bilge, 19/L or 19,000/m^3 in livewell, 7.9/L or 7,900/m^3 in bait bucket	Livewells and engine cooling water had greatest veliger densities (unknown survival of veligers in cooling water)	Returning to Lake St. Clair boat launches, USA following on-water boating	Johnson et al. (2001)
Zebra Mussel adults entangled in macrophytes (*Dreissena polymorpha*)	2.3 adults per trailer through entanglement with macrophytes; authors estimated that 5% of trailers and 0.9% of anchors leaving infested locations contained adult Zebra Mussel	Most adult Zebra Mussels transported as hitch-hikers on macrophyte fragments carried by boats and trailers	Departing overland from Lake St. Clair, USA boat launches	Johnson et al. (2001)
Macrophytes (species not provided)	Absent on 64% of boat trailers departing launch, present on 36% of trailers departing launch (24% of trailers had few strands of macrophytes, 10% had many strands, and 2% had macrophytes)	Macrophytes provided suitable substrate for adult Zebra Mussel attachment	Departing overland from Lake St. Clair boat launches	Johnson et al. (2001)
Zebra Mussel veligers (*Dreissena polymorpha*)	19/0.47L or 40,280/m^3 in engine cooling systems	Transport of veligers possible in livewells, wakeboat tanks, bilge water, and engine cooling water; wakeboat ballast tanks had greatest absolute abundance of propagules	Lake Mead and Lake Powell, USA	Dalton and Cottrell (2013)
Fish Hook Water Flea adult (*Cercopagis pengoi*)	Mean of 59, 9, 50, 46 individuals per fishing line trolled at 10 m depth; mean of 381, 30, 149, 259 per line trolled at 20 m depth. Maximum number per line was 1,024 individuals.	Significant, positive relationship between distance trolled and accumulation of *Cercopagis*. Certain brands of fishing line led to differences in fouling. Results likely have relevance to fouling of *Bythotrephes*.	Western end of Lake Ontario, Canada	Jacobs and MacIsaac 2007

Organism	Propagule Density (Mean organisms/m^3 or m^2, unless noted)	Key Findings	Geographic Scope	Study
Zebra Mussel veligers (*Dreissena polymorpha*), plus several native zooplankton species	Pelagic zooplankton spp. = 2,700/m^3; littoral zoo spp. = 100/m^3; benthic zoo spp. = 100/m^3; Zebra Mussel = 200/m^3 sampled from bilge (n = 19), anchor bracket (n = 1), small area behind engine (n = 1), and other localities containing standing water. List of native zooplankton species sampled: Cladocera: *Bosmina freyi*, *Ceriodaphnia lacustris*, *Chydorus sphaericus*, *Daphnia mendotae*, *Diaphanosoma birgei*, *Eubosmina longispina, Polyphemus pediculus* Cyclopoida: Nauplii, Copepodites, *Diacyclops bicuspidatus thomasi*, *Macrocyclops albidus*, *Mesocyclops edax*, *Paracyclops poppei*, *Tropocyclops extensus* Calanoida: Nauplii, Copepodites, L*eptodiaptomus minutus*, *Skistodiaptomus oregonensis* Harpacticoida Bivalvia: *Dreissena* sp.	Probability of finding a Zebra Mussel veliger on a boat was 4.8%, probability of finding any zooplankton (including *Dreissena veligers*) was 25%. The volume of standing water on a boat was significantly (although weakly) related to the number of zooplankton collected.	Lake Simcoe, Ontario, Canada	Kelly et al. 2013
Macrophyte fragments (species identity not provided)	Based on macrophyte fouling score/index. 7 of 63 boats had score of 1 (lowest level of fouling; proportion = 0.11), and 1 or 63 boats had score of 3 (highest = 0.015). All exterior surfaces sampled.	Most fragments found on anchor lines, but these fragments were generally in poor condition.	Lake Simcoe, Ontario, Canada	Kelly et al. 2013
Zebra Mussel (adult)	44,000/m^2 on barge hulls, 15,000/m^2 on tugs, 5,000/m^2 on other vessel classes, 4,500/m^2 on private cruisers, 3,000/m^2 on canal boats, 1,000/m^2 on lake boats, 1,000/m^2 on yachts, 500/m^2 on dinghies	Up to three mussel size classes have been found on multiple boat types (exterior hull surfaces) and in different densities.	Inland lakes in Ireland, UK	Minchin et al. 2003

Organism	Propagule Density (Mean organisms/m^3 or m^2, unless noted)	Key Findings	Geographic Scope	Study
Macrophyte fragments (13 native species, including *Myriophylum heterophyllum*, but not *M. spicatum*)	31 of 49 boats had macrophyte fragments, but 2 of 49 boats had fragments above weight threshold for 'viability' (35 g). Average biomass attached to a boat was 6.4 g.	Boats leaving lakes three times as likely to contain macrophytes as those arriving to lakes. Roughly two-thirds of boaters did not take steps to clean vessels or trailers. Visual inspection and hand removal can reduce macrophyte abundance on boats by 88%; high pressure washing equally effective, and low-pressure washing less effective (62% removal).	Big St. Germain Lake, northern Wisconsin and Lake Gogebic, upper Peninsula of Michigan, U.S.A.	Rothlisberger et al. 2010
Misc. aquatic species (28 in total; amphipods, gastropods, cladocerans; see Table 3 in Rothlisberger et al. 2010, for full set of species)	NA: midge larvae, aquatic snails, and water mites most abundant.	Crustaceans (esp. zooplankton) were not abundant, except for amphipods. High pressure washing had most effective removal rate (91%), low pressure washing (74%) and hand removal (65%) less effective.	Big St. Germain Lake, northern Wisconsin and Lake Gogebic, upper Peninsula of Michigan, U.S.A.	Rothlisberger et al. 2010

Table A2. Summary of primary literature describing the survival of freshwater species during overland (or simulated) transport based on field or laboratory studies.

Goal of Study	Organisms	Key Finding	Geographic Region	Study
Determine relative effectiveness of hot water application vs drying vs 'do nothing' for survival of 7 AIS	Zebra Mussel (*D. polymorpha*), Killer Shrimp (*D. villosus*), Bloody-red Mysid (*Hemimysis anomala*), Floating Pennywort (*Hydrocotyle ranunculoides*), Curly Water-thyme (*Lagarosiphon major*), New Zealand Pigmyweed (*Crassula helmsii*), and Parrot's Feather (*Myriophyllum aquaticum*).	Hot water (45 °C) caused 99% mortality within 1 h of treatment; hot water application was more effective than drying. Drying caused far greater mortality than a do-nothing approach from day 4 of the experiment onwards.	United Kingdom	Anderson et al. 2015

Goal of Study	Organisms	Key Finding	Geographic Region	Study
Quantify factors involved in the overland transport of Killer Shrimp in the Alps region; sample species from boat components	Killer Shrimp (*Dikerogammarus villosus*)	Occurrence of species more likely in low elevation lakes with prominent recreational boating activity. Species tends to attach effectively to boats compared with native amphipods.	Alps region in Europe	Bacela-Spychalska et al. 2013
Quantify the change in viability of aquatic macrophytes following desiccation experiments	*Cabomba caroliniana, Ceratophyllum demersum, Elodea canadensis, Egeria densa, Myriophyllum aquaticum, Myriophyllum heterophyllum, Myriophyllum spicatum, Potamogeton crispus, Potamogeton richardsonii, and Hydrilla verticillata*	Desiccation varied strongly among macrophyte species. Most plants experienced strong mass loss initially, with decelerating mass loss thereafter. *M. heterophyllum* had slowest desiccation rate, while *H. verticillata* was the quickest, losing 9.9 g/h. Some species exhibited complete mortality after 3 h of effective desiccation. Developed model of viability based on desiccation rate, with species-specific findings.	Generic, but study conducted in central USA.	Barnes et al. 2013
Determine effectiveness of hot water application in mortality of boater-mediated AIS	Zebra Mussel, (*Dreissena polymorpha*) Quagga Mussel (*Dreissena bugensis*), planktonic stage of Spiny Water Flea (*Bythotrephes longimanus*)	Immersion in 45 °C water for 5 minutes produced complete mortality for all three species, but 10 minute submersion preferred for *Bythotrephes*.	Wisconsin, USA	Beyer et al. 2011
Understand resistance of *Cabomba caroliniana* to dessication using laboratory experiments	'Green Cabomba' (*Cabomba caroliniana*)	*Cabomba* can survive up to 3 h if exposed to wind, but clumping increased survivorship during transport due to humidity effects. Certain clumps remained viable for up to 42 hours of desiccation time.	Queensland, Australia	Bickel 2015
Quantify the viability of Eurasian watermilfoil and Curly-leaf pondweed during simulated overland travel conditions	Eurasian watermilfoil (*Myriophyllum spicatum*) and Curly leaf pondweed (*Potamogeton crispus*)	Stems of *M. spicatum* and *P. crispus* were viable for up to 18 and 12 hours during simulated transport with air exposure. Physical coils of *M. spicatum* extended viability to 48 hours. Turions of *P. cricups* sprouted after 28 days of drying.	Wisconsin, USA	Bruckerhoff et al. 2015

Goal of Study	Organisms	Key Finding	Geographic Region	Study
Quantify survival of Quagga Mussel veligers under simulated overland, standing water (i.e., bilge) conditions to reflect warm (summer) and cool (fall) transport	Quagga Mussel (*Dreissena rostriformis bugensis*) veligers	Simulated summer thermal conditions of standing water led to 5 day survival of veligers, but cooler summer conditions led to survival of up to 28 days.	Generic, but study conducted in Lake Mead area of USA.	Choi et al. 2013
Quantify effectiveness of hot water application to induce mortality of adult Quagga Mussel	Quagga Mussel (*Dreissena rostriformis bugensis*) veligers	Water > 60°C was 100% lethal, as were spray temperatures of 54°C for 10 seconds, 50°C for 20 seconds, and 40°C for 40 seconds.	Lake Mead, USA	Comeau 2011; Comeau et al. 2011
Characteristics of desiccation of *M. spicatum*, including potential to regrow and develop rootlets following desiccation. Investigated using laboratory experiments.	Eurasian watermilfoil (*Myriophyllum spicatum*)	Observed 87%, 96%, and 100% desiccation at 3, 6, and 13 hours during simulated transport conditions (lab based). A small proportion (2%) of completely dried fragments were still viable, as demonstrated through rootlet formations.	Laboratory conditions; study conducted in New York, USA	Evans et al. 2011
Quantify the viability of three invasive aquatic snails in Wisconsin during simulated overland transport conditions (e.g., drying)	*Bithynia tentaculata, Cipangopaludina chinensis,* and *Viviparus georgianus*	Each species showed high survivorship during simulated overland transport. The species *B. tentaculata* and *V. georgianus* exhibited survival after 42 days of experimental drying. *C. chinensis* was viable after 63 days, including releasing young after 54 days of air exposure.	Wisconsin, USA	Havel et al. 2014
Understand the sensitivity of Zebra Mussel veligers to hydrodynamic forces	Zebra Mussel (*Dreissena polymorpha*)	Veliger survival significantly influenced by the length and intensity of hydrodynamic force applied	Laboratory study; veligers collected from Canadarago Lake in New York, USA	Horvath and Crane 2010
Estimate survival of Eurasian watermilfoil due to desiccation, reflecting overland conditions	Eurasian watermilfoil (*M. spicatum*)	Highest survival occurred during 1 h air exposure trials. Coiled fragments were generally viable for less than two weeks. Individual fragments desiccated for more than 24 hours had low probability of surviving. Greatest risk due to macrophyte transport via overland boats likely occurs during same-day boating periods among lakes.	Laboratory study; macrophytes collected from the St. Joseph River, Indiana, USA	Jerde et al. 2012

Goal of Study	Organisms	Key Finding	Geographic Region	Study
Evaluate the effect of temperature, light, and moisture conditions on the survival of *Didymo* sp.	Didymo (*Didymosphenia germinata*)	Hot water immersion successful at inducing complete mortality.	New Zealand	Kilroy et al. 2006
Evaluate tolerance of Zebra Mussel and Quagga Mussel to desiccation during simulated overland transport	Zebra Mussel (*Dreissena polymorpha*) and Quagga Mussel (*Dreissena rostriformis bugensis*)	Based on laboratory experiments, both species estimated to be capable of surviving overland transport in temperate conditions at a range of 3-5 days' travel from the infested locality.	St. Lawrence River, Quebec, Canada	Ricciardi et al. 1995
Determine effectiveness of decontamination strategies on *Dydymosphenia geminata* (Didymo).	Didymo (*Didymosphenia germinata*)	Dish liquid most effective decontamination tool, followed by bleach, Virkon, and salt. Decontaminant techniques were most effective if cells of *Didympsphenia* sp. were not attached to stalks.	New York, USA	Root and O'Reilly 2012
Determine the response of the invasive aquatic snail, *Bithynia tentaculata*, and the native aquatic snail, *Physa gyrina*, to desiccation trials	*Bithynia tentaculata* and *Physa gyrina*	Adult survival of *B. tentaculata* was much higher than the native snail (*P. gyrina)* after a 1 week dessication trial, though juvenile survival of *B. tentaculata* was substantially lower. May indicate strategic advantage of the invasive snail to resist drying during period of maturity.	Upper Mississippi Region, USA	Wood et al. 2011

Table A3. Summary of primary literature forecasting the sites at greatest risk of invasion due to overland boating activity. Most studies were conducted with gravity-type models and tailored to reflect introduction, spread, and establishment of individual species.

Goal of Study	Location	Organism	Principal Finding(s)	Study
Explain distribution of AIS (Zebra Mussel) with production-constrained gravity model and measures of habitat suitability	Inland lakes in Indiana, Illinois, Michigan, Wisconsin	Zebra Mussel (*Dreissena polymorpha*)	Best model to explain Zebra Mussel distribution involved distance coefficient of 1.9, a colonization threshold of 850 boats, and attractiveness value of 55,000 ha for GL boat ramps. Model estimated that an infested boat has probability of $p = 0.000041$ of leading to an invasion. Model was most sensitive to changes in distance coefficient, and least sensitive to changes in colonization probability. Model successful at predicting landscape patterns of Zebra Mussel colonization based on boater movement and habitat suitability of Zebra Mussel.	Bossenbroek et al. 2001
1. Forecast potential distribution of Zebra Mussel west of continental divide in the USA; 2. Predict the abundance of Zebra Mussel in western USA reservoirs based on water chemistry	Inland lakes of United States, with focus on Western USA reservoirs as recipient locations	Zebra Mussel (*Dreissena polymorpha*)	Best model parameters involved distance coefficient of 2.57. Model most sensitive to changes in distance coefficient. 82% of boaters traveling from infested watersheds also travelled to infested watersheds. Travelling across continental divide from invaded to uninvaded watershed was relatively rare (<0.05%). Larger reservoirs were more attractive as destinations than small reservoirs (e.g., Lake Mead, NV vs Lake Perry in KS), even though larger reservoirs were further away. Variables pH and phosphate concentration provide moderate ($r^2 = 0.43$) ability to project Zebra Mussel density in inland reservoirs.	Bossenbroek et al. 2007
Determine patterns of overland boater movements and the extent to which movements correlate with patterns of Zebra Mussel spread	Inland lakes in Wisconsin, USA	Zebra Mussel (*Dreissena polymorpha*)	Patterns of boater movement correlated with Zebra Mussel colonization in inland lakes. Boater movements exhibited strong patterns of distance decay: 90% of boaters travelled locally, 8.4% moved distances > 50 km, and 0.8% moved extremely long distances of > 261 km. The longest distances were associated with a greater number of large lakes in destination counties.	Buchan and Padilla 1999
Determine which factors, including measures of recreational boating activity, explain distribution of Eurasian watermilfoil	Inland lakes in Wisconsin, USA	Eurasian watermilfoil (*Myriophyllum spicatum*)	Habitat-related variables provided better explanatory power of Eurasian watermilfoil range than proxy variables of boater activity, such as game species presence, number and type of boat ramps, and distance from nearest road.	Buchan and Padilla 2000

Goal of Study	Location	Organism	Principal Finding(s)	Study
1. Explore differences between gravity models and random utility models 2. Understand how spread models interact with Allee effects	Inland lakes in Ontario, Canada	Species-neutral (population parameters can be applied to a range of AIS)	Landscape patterns of overland, boater-mediated invasion sensitive to model choice (gravity vs random utility). Boater-mediated invasion timelines sensitive to parameters describing population establishment (i.e., per-propagule probability of establishing and presence of Allee effects).	Chivers and Leung 2012
Explain the pattern of invasive macrophyte spread in New Zealand with boosted regression trees	Inland lakes in New Zealand	Asexual macrophytes: *Ceratophyllum demersum*, *Lagarosiphon major*, *Egeria densa* Sexually reproducing macrophytes: *Utricularia gibba*	For the three asexual species, spread was best predicted by the presence of highways and/or number of roads in close proximity, high human population density, and large lake size (55 km^2). Up-weighting of lakes at the edge of the invasion front led to better forecasts of future invasion risk.	Compton et al. 2012
Determine if road networks provide better estimate of recreational travel among inland lakes when coupled with gravity model	Inland lakes in Ontario, Canada	NA; specific to live-bait angler movements, of which subset will be trailering recreational boats	Lake size, sportfish richness, and least-cost road distance predict angler movement with ~50% deviance explained. Least-cost road networks provide advantage (albeit small) over Euclidean distance. Most trips sufficient to overcome drainage basin boundaries. Median aggregate travel distance was 292.6 km, 75th percentile was 484.6 km, 95th percentile was 775.2 km.	Drake and Mandrak 2010
Determine relationship between network structure and spread timelines for boater-mediated spread of AIS	Marinas (marine) in New Zealand	NA; generic model applied to marine boating movements	Invasions most likely at busy hubs within boater-mediated networks, but relatively unimportant locations can lead to rapid rates of spread when networked patterns of boater movement exist.	Floerl et al. 2009
Understand contribution of boater-mediated spread relative to natural dispersal of Spiny Water Flea (*Bythotrephes longimanus*) in Ontario	Inland lakes in Ontario, Canada (2EB watershed in Muskoka sampled through CAISN; 311 lakes)	Spiny Water Flea (*Bythotrephes longimanus*)	Human-mediated movement via boaters accounted for much greater variance explained compared with measures of natural dispersal for majority of inland lake invasions (99.85%). Management measures to control outbound traffic from infested lakes should be effective in reducing spread.	Gertzen and Leung 2011

Goal of Study	Location	Organism	Principal Finding(s)	Study
Forecast the secondary spread of *Cabomba caroliniana* in Ontario inland lakes using gravity models, natural dispersal, and environmental niche models	Inland lakes in Ontario, Canada	Fanwort (*Cabomba caroliniana*)	Most lakes visited by recreational boaters were within 100 km from the original invaded source lake with *Cabomba*. Sport fish richness, lake size, and distance from residence were important predictors of boater movement.	Jacobs and MacIsaac 2009
Determine advantages of joint models that formally integrate propagule pressure with invasibility (i.e., environmental suitability)	Inland lakes in Michigan, USA	Zebra Mussel (*Dreissena polymorpha*)	Measures of propagule pressure combined with measures of lake invasibility (e.g., environmental suitability for transported organisms) can lead to up to 2.5 times the number of lakes predicted to be invaded as when environmental suitability predictions are used on their own.	Leung and Mandrak 2007
Determine ability of production-constrained gravity models to forecast boater movement	Michigan, USA	NA; developed to represent boater movements as transport mechanism for Zebra Mussel	Landscape-level variables and boater registration records can predict overland boater movements fairly accurately. Registered boaters, distance travelled, and lake size were important predictor variables in gravity model, with large lakes being visited even at large distances. Non-linear modification of production-constrained gravity model led to r^2 values of 0.80. 0.35, 0.57, and 0.36 for boater traffic to lakes, distance travelled to reach a given lake, Great Lakes usage, and movement from Great Lakes to inland lakes, respectively.	Leung et al. 2006
Explain the pattern of Spiny Water Flea spread with doubly-constrained gravity models and discriminant analysis of gravity scores	Inland lakes in Ontario, Canada	Spiny Water Flea (*Bythotrephes longimanus*)	Hindcast and forecast order of lake invasion can be predicted from patterns of overland boater traffic developed through gravity models. Overland boater movements of > 100 km are rare, but will be important source of new regional lake invasions. Most boater-mediated establishment in new lakes will occur relatively locally. Relative risk of dispersal highest for fishing line and associated structures, and lowest for livewell water and float plane pontoons.	MacIsaac et al. 2004

Goal of Study	Location	Organism	Principal Finding(s)	Study
Model vector traffic from invaded to uninvaded lakes in central Ontario with production-attraction constrained gravity model	Inland lakes in Ontario, Canada	Spiny Water Flea (*Bythotrephes longimanus*)	Strong evidence for non-random patterns of boater-mediated lake invasion by *Bythotrephes*. As invasion progresses, certain lake 'hubs' lose their importance as outbound traffic is collected at predominantly invaded sites. Management effort is best applied to removing developing hubs from an inland lake-road-boater network, rather than by treating all invaded locations equally.	Muirhead and MacIsaac 2005
Evaluate unconstrained, total-flow constrained, production-constrained and doubly-constrained stochastic gravity models to assess *Bythotrephes* dispersal	Inland lakes in Ontario, Canada	Spiny Water Flea (*Bythotrephes longimanus*)	Unconstrained models provided the best estimate of boater traffic patterns, but doubly-constrained models, followed by production-constrained models, provided the best explanation of *Bythotrephes* occurrence	Muirhead and MacIsaac 2011
Predict spread of Fish Hook Waterflea based on stochastic gravity models and measures of lake physicochemistry	Inland lakes in New York, USA	Fish Hook Waterflea (*Cercopagis pengoi*)	The economic spending of recreational boaters, as well as destination lake area and population size of city nearest to the destination lake, were strong predictors of boater traffic. To predict establishment, boater traffic, lake area, specific conductance, and turbidity were most relevant. Stochastic forms of the gravity model improved predictive success.	Muirhead et al. 2011
Develop stochastic models of lake invasion and management	NA; generic model development	NA; generic model development	Neurodynamic programming can provide strong advantages for exploring effects of lake system control.	Potapov 2009
Develop a joint model based on boater-mediated propagule pressure and physical and chemical lake characteristics to explain invasion of *Bythotrephes*	Inland lakes in Ontario, Canada	Spiny Water Flea (*Bythotrephes longimanus*)	Boater-mediated lake invasions were highly predictable. Models joining boater-mediated propagule pressure and environmental conditions in lakes provided high predictive capability of inland lake invasions. Lake pH was a strong predictor given that propagule pressure existed, but phosphorus and lake elevation were also relevant. Model suggested that a significant Allee effect may exist for *Bythotrephes*.	Potapov et al. 2011a

Goal of Study	Location	Organism	Principal Finding(s)	Study
Develop stochastic gravity model for estimating lake invasion	Inland lakes in Ontario, Canada	Species-neutral	Portable stochastic gravity models can be developed to predict overland, boater-mediated spread with a few commonly available landscape variables	Potapov et al. 2011b
Develop gravity model to explain boater-mediated spread of Eurasian watermilfoil	Inland lakes in Wisconsin, USA	Eurasian watermilfoil (*Myriophyllum spicatum*)	Patterns of inland lake invasion by *M. spicatum* were not correlated with overland boater movements among lakes. Management approaches that prevent *M. spicatum* from leaving occupied lakes were more effective than protecting vacant (i.e., uninvaded) sites.	Rothlisberger and Lodge 2011
Determine relative role of within-lake recreational boater movements and habitat suitability (based on wave action) of Eurasian watermilfoil	Lake Tahoe, California and Nevada, USA	Eurasian watermilfoil (*Myriophyllum spicatum*)	Boater-mediated propagule pressure (PP) was not a significant predictor of *M. spicatum*, indicating that boater-based measures of PP may be inaccurate, or that the boater-mediated role of *M. spicatum* spread is more complex than simple delivery to nearshore sites (e.g., boaters play a role in *M. spicatum* stem breakage, subsequent fragment dispersal is by water currents)	Wittmann et al. 2015

Table A4. Summary of primary literature describing boater behaviour, inspection stations, educational campaigns, and landscape-based strategies for spread management.

Goal of Study	Organism	Key Finding	Location	Study
Determine boater awareness of AIS. Determine perceptions about boat wash stations and compare with actual use of wash stations	NA; applicable to boater behaviour	75.7% of boaters claimed they would use a boat wash station, but in a follow-up survey, only 38.5% of boaters actually used a station. 2% of surveyed boaters could not name an AIS, but around 60% were aware of the phrase ‘clean, drain, dry’.	Ten Mile Lake boat washing station, Oregon, USA	Cimino and Strecker 2014

Goal of Study	Organism	Key Finding	Location	Study
Understand the effectiveness of 'offensive' vs 'defensive' management approaches in a landscape of invaded lakes	Generic to species expected to be moved and managed among inland lakes	To reduce boater-mediated spread, offensive management is better early in invasion process, which involves placing cleaning stations at invaded lakes to target risky outbound boaters. After 1/2 of lakes in network are invaded, defensive management (targeting inbound boaters at uninvaded recipient lakes) provides greater effectiveness. To protect individual lakes having high value, defensive management provides lower per-site introduction rates.	NA: generic study	Drury and Rothlisberger 2008
Compare effectiveness of AIS outreach aimed at changing boater behaviour	NA; generic to boater behaviour involving a range of AIS	AIS outreach can lead to substantial behavioural change in boaters and can decrease relative boater-mediated propagule pressure by between 57% and 93%. Over time, outreach strategies lead to demonstrated changes in behaviour and awareness. Boaters indicated factors such as "a sense of personal responsibility", "a desire to keep AIS out of our lakes", and "prevent damage to my boat and equipment" as influencing their behaviour around AIS.	Minnesota, Vermont, Ohio, Kansas, California, USA	Jensen 2010
Summarize Michigan boater awareness of AIS spread campaigns, determine how willing boaters are to follow AIS regulations, and use information gained to design more effective strategies	NA; applied to boater behaviour and most boater-mediated AIS in Michigan	Variation exists in how boaters respond to outreach strategies. A cumulative effect of AIS awareness exists due to continued exposure to outreach material.	Michigan, USA	Lee et al. 2015
Understand interactions between management decisions and recreational boater responses to management controls designed to reduce among-lake invasions	NA; generic, but case-study applied to Eurasian watermilfoil	Management decisions to curb overland spread should consider boater behavioural responses to the presence of AIS within the lake network (e.g., avoidance). Welfare-maximizing management approaches for boaters will have different consequences for among-lake invasions than spread-minimizing management approaches.	NA; Generic model	Macpherson et al. 2006

Goal of Study	Organism	Key Finding	Location	Study
Use production-constrained gravity model to determine the effect of three different management strategies: deterring boaters from high risk lakes, targeted education at high risk lakes, and large-scale education effort	NA; generic, but case-study applied to Zebra Mussel	Preventing boaters from visiting key high-risk lakes was effective in the first 5 years following initial invasion. Targeted education more effective during later stages in the invasion. Large-scale education effective in all stages. Average reduction in the number of invaded lakes ranged from 0 to 6, depending on strategy and intensity employed.	Michigan, USA	Morandi 2013
Determine the interaction of boater behaviour with AIS management	NA; generic to boater movements	Current attitudes are good predictors for undertaking certain boating behaviours in the future	Illinois, USA	Pradhananga et al. 2015
Determine effectiveness of movie-based outreach advertising to influence boater perceptions about AIS	NA; applicable to wide range of AIS, but advertisement involved invasive macrophytes	During follow-up surveys, 18% of movie-goers were able to recall decontamination steps. Movie advertisements deemed effective to reach large number of audience members, many of whom will be boaters	Wisconsin, USA	Shaw and Howell 2014
Understand relationship between boater behaviour, policy changes, and the spread of AIS	NA; generic, but applied to Zebra Mussel	Despite best intentions during policy development, certain policies designed to reduce the overland spread can lead to increases in AIS by failing to account for different behavioural responses.	Wisconsin, USA	Timar 2008; Timar and Phaneuf 2009