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Modelling Spread, Establishment and Impact of Bighead and Silver Carps in the Great Lakes

Modélisation de la propagation, l'établissement et l'impact des carpes à grosse tête et argenté dans les Grands Lacs

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ABSTRACT

Bighead Carp (*Hypophthalmichthys nobilis*) and Silver Carp (*Hypophthalmichthys molitrix*), two species of Asian carps, have rapidly spread up the Mississippi River system after they escaped from aquaculture facilities in Louisiana and Arkansas, and could now potentially spread into the Great Lakes. Since both species are generalist planktivores, they present a unique invasion risk in that they are very large (>1m), fast-growing fishes that eat at low trophic levels. Predicting invasion probability into novel systems is often difficult because predictions must be based on a foundation of research from systems other than the one being invaded. Most existing research has been undertaken in aquaculture ponds and river systems, which are quite different from large lakes in their thermal regimes, physico-chemical dynamics and food webs. To overcome these difficulties, modelling approaches must be general enough to encompass the wide spectrum of parameters that drive them. Several modelling methodologies are presented to predict the risk of spread, establishment and ecological impact. First, an area-restricted individual-based model is used to predict spread rates and regions likely to attract carps when released from the most likely invasion sites. At even modest movement rates, carps can easily move throughout an entire lake basin within a year making it quite likely they will locate high productivity environments which have abundant food resources for survival (typically embayments such as Green Bay, Saginaw Bay, Bay of Quinte, Georgian Bay). Second, combinatoric mathematics is used to predict the number of adults needed within a basin to have a likely mating pair. The probability of mating is dependant on the number of adults and rivers. A high probability (>50%) of a successful mating requires very few adults (< 10), even if there are a large number of suitable rivers (e.g., 25). Third, an age-structured population model is used to predict the risk of establishing a population and to determine the most vulnerable stage. This approach indicates even a single release of a small number of individuals can result in an established population; the risk increases if mature adults are released or if a “leaky barrier” continually supplies a small number of new individuals. The juvenile stage is the most responsive to management/control activities and age at first maturity has the largest impact on establishment probability. Finally, the ecological impact of an established population is investigated using two mass-balanced food web models for the Lake Ontario offshore food web using high and low dreissenid mussel biomass. The predicted impacts are particularly sensitive to the degree of zooplanktivory. If the carps only eat phytoplankton and the microbial food web, then high Asian carp biomass could be sustained, even in offshore Lake Ontario, but would lead to increased risk of Alewife decline with a subsequent collapse of the Chinook Salmon fishery. Low carp biomass could be maintained with minimal food web consequences, but if zooplanktivory increases, then even small carp populations can lead to a significant decline in Alewife biomass. Thus, disruption of the pelagic food-web by Bighead and Silver carps is highly unpredictable given their extremely flexible diet. These modelling approaches predict that these Asian carps have the potential to spread rapidly through the Great Lakes, establish populations even with small initial abundances, and ultimately disrupt Great Lakes food webs.

RÉSUMÉ

La carpe à grosse tête (*Hypophthalmichthys nobilis*) et la carpe argentée (*Hypophthalmichthys molitrix*), deux espèces de carpe asiatique, ont rapidement envahi le réseau fluvial du Mississippi après s'être échappées d'installations d'aquaculture en Louisiane et en Arkansas et pourraient se propager dans les Grands Lacs. Comme les deux espèces sont des planctonophages généralistes, elles présentent un risque d'invasion particulier, en ce sens qu'elles sont très grosses (elles mesurent plus d'un mètre), ont une croissance rapide et se nourrissent d'organismes des niveaux trophiques inférieurs. Il est souvent difficile de prédire la probabilité d'invasion dans de nouveaux réseaux hydrographiques, étant donné que les prédictions doivent reposer sur des recherches réalisées dans des réseaux autres que le réseau envahi. La plupart des recherches existantes ont été entreprises dans des bassins aquacoles et des réseaux fluviaux, lesquels diffèrent passablement des lacs de grande surface en ce qui a trait à leur régime thermique, à leur dynamique physicochimique et à leur réseau trophique. Pour surmonter ces difficultés, les méthodes de modélisation adoptées doivent être suffisamment générales pour englober un large éventail de paramètres. Plusieurs méthodes de modélisation sont présentées afin de prédire le risque de propagation et d'établissement et leurs effets écologiques. Premièrement, un modèle individu-centré à zone restreinte est utilisé pour prédire les taux de propagation et les régions susceptibles d'attirer les carpes une fois échappées des sites d'invasion les plus probables. Même avec des taux de mouvement modestes, les carpes peuvent facilement envahir l'ensemble d'un bassin lacustre en moins d'un an, ce qui laisse croire qu'elles privilégieront les milieux très productifs dotés d'abondantes ressources alimentaires pour leur survie (en général des échancrures comme la baie Green, la baie Saginaw, la baie de Quinte, la baie Georgienne). Deuxièmement, les mathématiques combinatoires sont utilisées pour prédire le nombre d'adultes nécessaires dans un bassin pour obtenir un couple probable. La probabilité d'accouplement dépend du nombre d'adultes et du nombre de rivières. Une probabilité élevée (>50 %) d'accouplement réussi nécessite très peu d'adultes (< 10), même si le nombre de rivières convenables est élevé (p. ex., 25). Troisièmement, un modèle de population structuré en fonction de l'âge est utilisé pour prédire le risque d'établissement d'une population et pour déterminer le stade le plus vulnérable. Cette approche indique que même la dissémination d'un petit nombre d'individus pourra se traduire par l'établissement d'une population; le risque augmente si des adultes matures sont relâchés ou si une « barrière non étanche » laisse continuellement passer un petit nombre de nouveaux individus. Le stade juvénile est le stade qui répond le mieux aux activités de gestion ou de contrôle et l'âge de la première maturité sexuelle est le facteur qui a le plus d'incidence sur la probabilité d'établissement. Enfin, les effets écologiques d'une population établie sont étudiés à l'aide de deux modèles de réseau trophique équilibrés en fonction de la masse pour le réseau trophique au large du lac Ontario, en utilisant une forte biomasse et une faible biomasse de moules dreissénidées. Les effets prédits sont particulièrement sensibles au degré de consommation de zooplancton. Si les carpes ne mangeaient que le zooplancton et les organismes du réseau trophique microbien, une forte biomasse de carpe asiatique serait alors viable, même au large du lac Ontario, mais elle mènerait à un risque accru de déclin du gaspareau, accompagné de l'effondrement subséquent de la pêche au saumon quinnat. Une faible biomasse de carpes pourrait être maintenue avec des conséquences minimes sur le réseau trophique, mais si la consommation de zooplancton augmentait, les populations de carpes mêmes petites pourraient entraîner un déclin significatif de la biomasse des gaspareaux. Ainsi, la perturbation du réseau trophique pélagique par la carpe à grosse tête et la carpe argentée est très difficilement prévisible, étant donné leur régime extrêmement varié. Ces méthodes de modélisation permettent de prédire que ces carpes ont le potentiel d'envahir rapidement les Grands Lacs, d'établir des populations même avec une abondance initiale faible, et de perturber en bout de ligne les réseaux trophiques des Grands Lacs.

GENERAL INTRODUCTION

Bighead Carp (*Hypophthalmichthys nobilis*) and Silver Carp (*Hypophthalmichthys molitrix*), hereafter referred to as Asian carps, are two of the four species of Asian carps that were first introduced to the United States in the early 1970s and stocked into aquaculture ponds. Escape from these ponds happened quickly, and these species soon established populations in the Mississippi River basin and spread rapidly north in the Mississippi River. As this northward expansion has approached the northern limits of the Mississippi River basin, concerns have grown that they may reach the Great Lakes through man-made connections, such as the Chicago Sanitary and Ship Canal, or across weak natural watershed boundaries. Concern over the potential environmental impacts of these planktivorous Asian carps in the Great Lakes stimulated the US Asian Carp Program. Past risk assessments (Mandrak and Cudmore 2004, Kolar et al. 2007) have identified the risk associated with these species to Canada and the United States. Due to the potential for Asian carps to make it into the Great Lakes, a binational risk assessment is being conducted expressly on Bighead and Silver carps to examine their potential to establish and impact the Great Lakes ecosystem.

A non-native species risk assessment involves addressing questions around the potential for the species to arrive in the ecosystem(s) of concern, their ability to survive there, the possibility that they will establish a viable population, the potential to spread further, and the impact they may have on recipient ecosystems. The purpose of this document is to provide modelling to help address some of these questions. Specifically, we will provide models to address the following questions:

1. If Bighead or Silver carps were to escape into the Great Lakes, where will they occur?
2. What is the timeline for spread through the Great Lakes?
3. How many Bighead or Silver carps need to escape into the Great Lakes to potentially establish a viable population?
4. What is the timeline for establishment of a self-sustaining population?
5. If Bighead or Silver carps do establish in the Great Lakes, what are the likely food web impacts?

In addition to answering questions for the risk assessment, this modelling will also provide information that will help managers to design early detection monitoring programs, and if necessary, control, mitigation or eradication plans. The modelling is presented in four sections. First, by modelling Asian carp movement as a constrained random walk, we provide predictions about their potential movement in the Great Lakes (to address questions 1 and 2). Second and third, combinatorial mathematics and matrix population modelling are used to predict the number of individuals needed and timelines for establishment (questions 3 and 4). Finally, Ecopath with Ecosim (EwE) modelling is used to evaluate the potential food web impacts of an established Bighead or Silver carp population (question 5).

IDENTIFICATION OF MOST LIKELY AREAS FOR ESTABLISHMENT OF ASIAN CARPS IN THE GREAT LAKES: AN INDIVIDUAL-BASED MODEL USING AREA-RESTRICTED SEARCH

Warren J.S. Currie and Marten A. Koops

INTRODUCTION

The Silver Carp (*Hypothalmichthys molitrix*) and Bighead Carp (*Hypothalmichthys nobilis* (previously *Aristichthys nobilis*), native to Asia, have been successfully introduced worldwide as aquaculture fishes, but are considered destructive invaders outside their native range (Kolar et al. 2005). Both species of carps escaped from captivity into the Mississippi River soon after being imported in the 1970s (Kelly et al. 2011) and have now moved northward and established dense populations in the Mississippi, Illinois, Missouri and Maumee rivers (O'Connell et al. 2011). The proximity of the Asian carps to several hydrologic connections to the Great Lakes including the Chicago Ship and Sanitary Canal (Michigan) (Moy et al. 2011), Swan (Superior) and Maumee Rivers and the Erie Canal (Erie) (USACE 2010) prompted the formation of the Binational Risk Assessment on Asian Carps in the Great Lakes. Part of the justification for this study was the concern that the Laurentian Great Lakes support a multi-billion dollar sport and commercial fishery and recreational uses that could be endangered by the introduction of Asian carps.

Establishment

Models created to predict survival of Silver and Bighead carps in the Great Lakes have suggested that physiologically they are not limited anywhere in the basin (Herborg et al. 2007, Mandrak and Cudmore 2004) but initial bioenergetics and food competition models suggested few locations in the Great Lakes would support positive growth of Asian carps (Cooke and Hill 2010, Kolar and Lodge 2002) but did not include all available food resources. Given the feeding flexibility of Asian carps and the fact that several healthy specimens of Bighead Carp have been found already in Lake Erie, further research on the potential for establishment was needed.

Predicting establishment of a species into a new environment requires an understanding of its food, habitat requirements and dispersal ability. Since the native range of both carp species extends north into the Amur River watershed of Siberia, neither temperature (Herborg et al. 2007) or water hardness (Chapman and Deters 2009) are limiting to Asian carps in the Great Lakes watershed. Food limitation, however, is still unknown. While Silver Carp are considered primarily phytoplanktivorous and Bighead Carp zooplanktivorous, each show great flexibility in their diet (Kolar et al. 2005). Since both species of Asian carps are important aquaculture fishes worldwide, numerous studies investigating feeding have been undertaken in aquaria (Cooke et al. 2009, Dong and Li 1994, Rahmatullah and Beveridge 1993, Smith 1989), rivers (Irons et al. 2011, Nuevo et al. 2004, Pongruktham et al. 2010, Sampson et al. 2009, Schrank et al. 2003, Williamson and Garvey 2005), ponds (Berday et al. 2005, Cremer and Smitherman 1980, Ma et al. 2010, Opuszynski et al. 1991), lakes and reservoirs (An et al. 2010, Domaizon and Devaux 1999, Fukushima et al. 1999, Ke et al. 2007, Lu et al. 2002, Radke and Kahl 2002, Spataru and Gophen 1985, Voros et al. 1997, Xie and Yang 2000, Zhou et al. 2011, Zhou et al. 2009) indicating an extremely wide range of feeding habits. Both species of Asian carps will consume zooplankton, phytoplankton (including cyanobacteria) and detritus, with the particle sizes filtered determined primarily by gill morphology (Kolar et al. 2005). Silver Carp have spongiform gills (Jirasek et al. 1981) that utilize mucus to concentrate particles (Spataru 1977) allowing them to remove particles down to bacterial sizes (Hampl et al. 1983), while Bighead Carp can efficiently consume only larger forms of phytoplankton. Greater volumes of water are filtered with increased particle size, so larger particles are often primarily selected (Smith 1989).

Spread

Studies investigating the movement of Asian carps in natural environments are extremely rare (Degrandchamp et al. 2008, Konagaya and Cai 1989). Radio-telemetry now permits the tracking of individual fish, but equipment is expensive and requires a large investment of time and effort to collect the data. Almost all movement rates are for riverine environments, which significantly influences the behaviour of both carp species since they avoid the main channels with the highest flows (Degrandchamp et al. 2008). Most telemetry studies focus on activity or fish passage rather than movement paths since receivers are usually limited by detection distance and by numbers available for deployment (Landsman et al. 2011). Movement of fishes in pelagic or lacustrine environments are considerably different from those found in rivers (Anras et al. 1999, Zamora and Moreno-Amich 2002) primarily due to the statistical differences between 1 and 2-dimensional walk paths (Codling et al. 2008).

Trophic Dynamics

Introduction of Asian carps tends to have strong, but highly varied, trophic consequences but, when available, both carps tend to preferentially select zooplankton (Dong and Li 1994, Lu et al. 2002, Zhou et al. 2009) and zooplankton size and phytoplankton cell size tends to decrease (An et al. 2010, Fukushima et al. 1999, Lu et al. 2002, Ma et al. 2010, Radke and Kahl 2002, Spataru and Gophen 1985). Studies of the impact on other planktivorous fishes such as paddlefish and bigmouth buffalo have led to contrary findings (Irons et al. 2007, Sampson et al. 2009, Schrank et al. 2003). Few studies have investigated feeding by Asian carps on protozoa but tend to indicate that, while they are not highly preferred, they can change the composition of the microbial food web (Fukushima et al. 1999, Sun et al. 2004, Zhou et al. 2011). However, no studies have determined Asian carp feeding rates when protozoans are a dominant food source as occurs in many of the Great Lakes (Fahnenstiel et al. 1998, Munawar and Lynn 2002).

In this paper, we will present an individual-based (also known as agent-based) model of fish movement that can be used to determine dispersal under a range of movement rates including non- and auto-correlated swimming paths. Several possible introduction sites and the effect of lake current intensity on dispersal will identify regions that will attract Asian carps from increased food resources and rivers that could be used for spawning.

METHODS: MOVEMENT MODEL

The Fish Foraging and Movement model is an individual-based (DeAngelis and Gross 1992), Markov process movement model written for MatLab. The basis of the simulation model is that foragers use area-restricted search (Kareiva and Odell 1987) on 2-D food fields acquired from satellite chl-a (MODIS), and derived values for zooplankton (Shuter and Ing 1997), rotifers and microbial loop biomass (bacteria, HNF, ciliates) (Cole 1999, Munawar et al. 2010). The use of area-restricted search models (Kareiva and Odell 1987) has become common to investigate feeding behaviour and habitat use (Codling et al. 2008, Hosseini 2006, Mueller and Fagan 2008) and is particularly useful for species invading new environments (Hastings et al. 2005). Individuals using this behaviour ("prey-taxis") tend to remain in regions with higher food resources so identification of likely habitats for new invaders is particularly suited to this approach (Fig 1-1).

ARS movement was accomplished by using a threshold food field whereby the individual would move at ¼ the value of a normal steplength when food was above a specific value. Values approximating Cooke and Hill (2010) were converted to carbon units without differentiating sources from zooplankton or phytoplankton (C:Chl of 40) giving a threshold value of 320 mg C m^{-3} (Hall et al. 2003, Kasprzak et al. 2008, Russ et al. 2004, Shuter and Ing 1997, Yacobi and Zohary 2010). Each timestep, the individuals always moved in a random direction so displacement in X and Y is determined by:

$$dx = d\cdot(\sin(z\cdot 2\cdot \pi))$$
$$dy = d\cdot(\cos(z\cdot 2\cdot \pi))$$

where d is the step distance (radius of the circle) and z is a random number (0-1).

Movement was modelled using a purely random ARS where direction was always randomly selected, but paths of pelagic fishes in nature tend to be more directed (Hammerschlag et al. 2011, Hedger et al. 2008, Witt et al. 2010) so autocorrelation was added with a direction memory to the individual by averaging the newest movement with the previous one. Paths of an autocorrelated individual are more directional, exhibiting smoother arcs of longer distances than shown in non-autocorrelated movements, which tend to fill more of the available space (Fig 1-2). This autocorrelated movement tends to reduce the movement per time step, since it is averaged with the previous step which could have occurred in any direction (Table 1-1). However, overall, autocorrelated movement tends to still have the same displacement as non-autocorrelated movements because paths tend to be directional.

Four seasonally averaged values (Mar-May (JD 60-151), Jun-Aug (JD 152-243) and Sept-Nov (JD 244-305), and Dec-Mar (JD 306-59)) of Chl-a for the entire Great Lakes at 30 sec resolution (approximately 1km cell-size) were obtained from the Environment Canada, Remote Sensing Lab (Caren Binding pers. comm.) that formed the foraging grid. Extreme outlier values were corrected to values expected given previous sampling and connecting channels that might have been missed were added manually because they are below the resolution of the images. Monthly changes in chlorophyll-a were calculated by interpolation of the 2-D grids (Fig 1-3). Temperature for each lake basin was modelled using a sine wave formulation scaled to the maximum temperature found in each lake using average data from Great Lakes Surface Environmental Analysis (GLSEA) database for 2006-2011 [http://coastwatch.glerl.noaa.gov/glsea/glsea.html] (Table 1-2, Fig 1-4).

$$\text{DailyTemperature} = (\text{maxTemp}\cdot(\sin(4\cdot\text{jday}\cdot((\pi/2)/365)-0.75\cdot\pi)+1.2)/2.2)+2$$

Zooplankton biomass is notoriously patchy and variable in time so the intent of this model was to provide a general, temporally averaged zooplankton food source for the foraging carps that was reasonable and would match average values from previous studies (Barbiero et al. 2001, Carrick et al. 2001, Evans 1986, Fahnenstiel et al. 1998, Johannsson et al. 2000, Kerfoot et al. 2008, Munawar et al. 1991, Sprules and Stockwell 1995, Stockwell and Johannsson 1997, Stockwell and Sprules 1995, Yurista et al. 2006, 2009). Zooplankton biomass was determined dynamically at each timestep and each individual cell location where carps occurred using a modified temperature dependant method (Shuter and Ing 1997). The underlying relationship from Shuter and Ing (1997) is given by:

$$\text{Zooplankton P/B} = 10^{[\alpha+\beta*(\text{dailyT})]}$$

where α is taxon specific: –1.725 for cladocerans and –1.766 for cyclopoids and β is 0.044 for cladocerans and 0.040 for cyclopoids.

This relationship was scaled to a maximum of 1 and multiplied by a typical peak value for zooplankton biomass expected in early fall for each lake (Table 1-2). The increased production in nearshore and shallow sites was accounted for by adding 2ºC when the depth was less than 10m, incorporating the effects of the thermal bar and nearshore boundary circulation (Boyce et al. 1989, Rao and Schwab 2007, Ullman et al. 1998). The lower Great Lakes (Ontario, Erie and St. Clair) are dominated by cladoceran zooplankton so α and β for cladocerans only were used (Barbiero et al. 2001, Fahnenstiel et al. 1998). The α and β values were averaged for lakes Superior, Michigan, Huron and Georgian Bay since their zooplankton communities are a mixture of copepods and cladocerans. Veligers from dreissenid mussels were not explicitly modelled but are considered part of the total zooplankton biomass. Microbial plankton is even more variable and much more difficult to predict than crustacean zooplankton so a simple ratio of ¼ of the zooplankton biomass was used and added to give total zooplankton biomass (Carrick and Fahnenstiel 1990, Fahnenstiel et al. 1998, Hwang and Heath 1997, Munawar and Lynn 2002, Pace and Orcutt 1981).

Output from the model was recorded for every individual at each timestep (4 hours). Values included location, step distance, maximum displacement from start, previous locations visited, total new locations visited, which lake basin they were in, water depth, temperature, whether they were within 25 km of a spawning river (when temperatures were above 18ºC) and the phytoplankton and zooplankton biomass encountered.

To investigate the potential influence of currents in the Great Lakes on the dispersal of Asian carps, average flow conditions were taken from historical reviews and circulation models (Beletsky et al. 1999, Chen et al. 2004, Rao and Schwab 2007, Schertzer et al. 2008, Sheng and Rao 2006, Zhang et al. 2007). The intent was not to create a coupled bio-physical model, but rather to investigate how flow might intensify dispersal. The underlying current directions within the lakes were converted to the 1 km spatial grid and a mean pass 2-D smoothing filter (smooth2a) in MatLab and were not varied (Fig 1-5). Current intensity ranged from 0-0.25 km/h (0-7 cm/s) and the current vector could be added to each individual's movement using a multiplier. A value of 0.1x was a low flow influence, 0.25x was the standard flow influence and 0.5x was a high flow influence.

Scenarios involving no flow influence and very high flow influence as well as negative flow-taxis (swimming against the current) were also tested but not presented here.

RESULTS

Locations visited for 100 individuals were output every 1, 2, 5, 10 and 20 years for each run and log transformed to visualize the rare visits (Fig 1-6 to12). Rates of speed per timestep, use of autocorrelated movement or ARS, increased and decreased flow, a lowered food threshold before ARS started were all varied to determine the influence on dispersal. The rate of speed per time step was the most important predictor for dispersal (Fig 1-6). With an initial release near Chicago, a typical individual would take only 1 year to investigate most of Lake Michigan (Fig 1-13) and within 5 years is likely to have also moved throughout Lake Huron. The effect on spread and food encounter by removing ARS can be seen in Fig 1-8 and 1-14. With the “standard” movement of autocorrelation and ARS (Fig 1-6), when individuals encountered higher food conditions, the spikes were repeated or high food levels were maintained. When autocorrelation was removed, the spikes were not as repetitive when the carps encountered a region of higher food resources, even when using ARS (Fig 1-2b). If ARS was not used, the high food spikes were low in intensity and extremely short in duration (Fig 1-2c). When the mean encountered planktonic food fields for each individual were ranked, a clear pattern can be seen where individuals using ARS are twice as successful at encountering high food resources (Fig 1-14). This was particularly true for the most successful individuals (top 10-15%) that encountered very high mean food levels, above even the excessively high positive growth requirement given by Cooke and Hill (2010).

With a potential start site of the Chicago Sanitary and Shipping Canal, the most likely sites that would attract Asian carps would be Muskegon River, Traverse Bay and Green Bay within the first years of escape. Following that, Saginaw Bay in Lake Huron and the North Channel of Georgian Bay would likely attract carps during the next couple of years. Lake St. Clair, the western basin of Lake Erie and Sandusky Bay become the next potential sites for establishment, but almost every location in Lake Erie is suitable. The northern part of the Lake Erie central basin supports strong and long-lasting spring phytoplankton blooms and much of the eastern basin, especially near the Grand River plume on the Ontario side of Lake Erie has sufficiently high plankton biomass to retain carps. Only a small percentage of carps make it into Lake Ontario within 20 years, but are attracted to sites around the Genesee River and Bay of Quinte. The same is true for Lake Superior, but carps that enter and stay are attracted to the northern embayments including Black and Thunder bays and the westernmost arm near the St. Louis estuary.

Spread rates using the intermediate movement rate of 4/1 km/timestep (12 km d^{-1}) for the other four possible introduction locations (Erie, St. Clair, Montreal, Duluth) are illustrated in Fig 1-12. Two locations, in particular, are of interest for Canada since live-food trade still occurs in Montreal, and there is concern over illegal transport into Ontario and/or a trucking accident and a consequent introduction into the Thames River, which the Ontario Ministry of Natural Resources used as an emergency response training scenario. These alternative introduction locations are compared to a movement scenario for the CSSC (second column Fig 1-6), which uses a current influence of 0.25x, autocorrelated movement and area-restricted search.

Asian carps introduced at lakes St. Clair or Erie had similar results but differed in a few important ways. In both scenarios, they quickly spread through Lake Erie and, since most of the environment was above the food threshold, tended to remain there, thus reducing the spread to other lakes. When carps started in Lake Erie, some individuals ended up in Lake Ontario while in the Lake St. Clair release, approximately 5% ended up in Lake Huron or in Lake Ontario.

When carps were introduced at Montreal, it generally took more than 5 years to enter Lake Ontario. This is due to the nature of random-walks in systems that are closely 1-D. The movement path is highly restricted within the river so individuals tend to spread slower than if they were unconstrained in a 2-D system. Futhermore, the chlorophyll values within the river are reasonably high compared to Lake Ontario so the carps often encounter high food levels and slow down their rate of movement (Fig 1-15). A small percentage of individuals began to arrive in Lake Ontario by year 5 and by year 20, they were widespread throughout the lake but were not spreading yet into Lake Erie.

Asian carps introduced into western Lake Superior near Duluth tended to remain in that region since this area has higher production than many other regions of the lake. Individuals were also attracted to Black and Thunder bays and the Keweenaw Peninsula.

Due to the always-random direction nature of the movement model, individuals tend to gather near the connecting channels between lakes (southern Lake Huron, eastern Erie). This is because the connecting channel is often less than 1 km wide (the model cell size) so they repeatedly come close to entering the channel but turn back into the originating lake and return again later. This leads to highly visited sites near these locations. Even a small influence of flow is important in helping “push” individuals through these channels. This might not be an unrealistic result because Asian carps are already known to accumulate near locks on the Mississippi and Illinois rivers to pass through to the pools above (Degrandchamp et al. 2008).

Increased steplength gave the greatest increase in new sites visited with autocorrelation and flow having a lesser influence (Fig 1-13). Over the 20-year timeframe, the number of new sites visited with the 8/2 km timestep^{-1} steplength approached the value for the entire Great Lakes. Individuals using the 2/.5 timestep^{-1} steplength began to saturate at about 10 years indicating that the model grid needs to be at a greater resolution to resolve these short steps. Regardless of the scenario, under most conditions even a small population of fish explore the entire lake basin where they have been introduced within 1-2 years and, if area-restricted search is utilized, will locate areas of locally high food resources within a month of introduction.

In spite of the generally low food conditions in lakes Michigan and Superior, approximately 10% of the individuals locate much higher food resources than the average individuals (Fig 1-15). When individuals are ranked by mean food encountered, an increased tail in the distribution can be seen that is related to how often high food conditions are encountered in each lake. For instance, Lake Superior has a small tail but Lake Erie (Maumee release) has a very large tail of 25% of the individuals encountering high food conditions. There is generally a matching tail of individuals that encounter extremely poor food conditions and will most likely face serious food limitation. The food encounter graphs also illustrate the suitability to invasion for each system as indicated by the mean value likely encountered. The ranking from highest to lowest is: St. Lawrence River at Montreal, Maumee River in the Lake Erie basin, the Thames River in the Lake St. Clair basin, the Chicago Ship and Sanitary Canal in the Lake Michigan basin, and the St. Louis Estuary near Duluth in the Lake Superior basin. Approximately ½ of the individuals released in Lake Erie encountered at least 320 mgCm^{-3}, used as the moderately high behavioural foraging threshold, as their overall average. It is known that both Silver and Bighead carps will trade-off reduced flow and chlorophyll-a (Calkins et al. in press, Degrandchamp et al. 2008, DeGrandchamp et al. 2007). Given that lakes have much reduced background flow rates compared to large US rivers, the preferred value of 4 μgL^{-1} of chlorophyll shown in Silver Carp (Calkins et al. in press), with little or no zooplankton in the diet, indicates a very low food requirement for these fishes. Given that a good portion of the year has low zooplankton and phytoplankton biomass, the individuals encounter much higher food resources during the spring-early fall period.

When using area-restricted search, the fish often tend to remain nearshore or within embayments. This is not unexpected because nearshore zones, in general, have higher levels of chlorophyll-a and higher temperatures, which makes them attractive to many fishes (Murphy et al. 2011). Cladophora is not explicitly modelled, though it could be added later if food limitation was indicated for Asian carps in the nearshore of the Great Lakes. It is not known if these species would consume benthic algae, though Silver Carp have been known to pick at attached algae while in aquaria (Chapman pers. comm.). Furthermore, nearshore zones have been documented to often have extremely high levels of microbial food web members such as ciliates and flagellates, which could provide a further food source for Asian carps (Fahnenstiel et al. 1998, Munawar et al. 2010, Munawar and Lynn 2002). The foraging model can be configured to restrict the carps to within the 10m isobath, which decreases the dispersal rate of the carps but also increases the likelihood of encountering high food conditions, although it is unknown if Asian carps would exhibit this form of behaviour within lakes.

To facilitate the study of potential spawning rivers (see Mandrak et al. 2011), the foraging model was used to calculate the proximity to possible rivers when temperatures were greater than 18ºC which is the period associated with the spawning of Asian carps along with an increase in the hydrograph (Costapierce 1992, DeGrandchamp et al. 2007, Lohmeyer and Garvey 2009, Schrank and Guy 2002). If the carps entered via the CSSC in Lake Michigan, during the first 2 years, practically all of the potential spawning sites would be in Lake Michigan only (e.g. Muskegon and Fox rivers). In particular, the Muskegon River or other tributaries along the southeastern shore of Lake Michigan are the first encountered since the carps tend to be transported by alongshore currents. A similar pattern of movement was seen in a 3-D bio-physical model of larval Walleye transport, where larvae were transported from southwestern Lake Michigan to Traverse Bay in approximately 2-3 months (Beletsky et al. 2007). Under the higher movement rate scenarios (8/2 & 4/1 km timestep^{-1}), by year 5, about 25% of the rivers encountered are within Lake Huron, Georgian Bay in particular. The proximity to the Saugeen, Maitland, Saginaw and French rivers in the Lake Huron system become increasingly probable as spawning sites after year 5. Lake Erie and Lake Superior rivers begin to be proximate to a small percentage of spawners only after year 10. The model currently has no recruitment at spawning sites, which might tend to increase proximity to previous sites, but given that recruits would require 3-4 years to achieve sexual maturity, they are still very likely to disperse into high probability locations in Lake Michigan or new sites in Lake Huron. All of the scenarios produced similar results, with non-autocorrelation, reduced food limitation and no ARS changing the encounter rate with spawning rivers very little. Increased flow had some influence only during the smallest movement rates (2/.5 km timestep^{-1}) since it increased the transport of the individuals to Lake Huron.

When individuals were released from other locations, the likely spawning rivers changed accordingly. For introductions in Lake St. Clair or Lake Erie, all the rivers in Lake Erie (Maumee, Sandusky, Grand rivers) were immediately probable as spawning locations.

After 10 years, some Lake Ontario and Lake Huron tributaries had an increased possibility of becoming a spawning location. Since dispersal up the St. Lawrence River was so slow, the river itself was the dominant possible spawning location, but Lake Ontario tributaries began to become possible by year 20. In the scenario of an introduction near Duluth in Lake Superior, most of the tributaries had a small possibility of being proximate to spawners though the highest probability for spawners was indicated by the St. Louis River and increasingly the Mission and Gravel rivers after year 10. It is worth noting in Lake Superior, the period where water temperatures were greater than 18ºC was later in the summer and of shorter duration than in the lower lakes, but still occurred.

CONCLUSIONS

Given reasonable rates of daily movement for both species of Asian carps, it is likely that they can easily reach any part of a lake basin within the first year of introduction into that basin. By the second year, a small percentage of individuals (>5%) will have moved into adjacent lakes and by 10 years, more than half of the individuals will have moved into a new lake basin. If daily movement rate or the influence of current flows is increased, then the dispersal rate is also greater. The nature of the flows within the Great Lakes is such that there are strong alongshore coastal jets that can easily transport materials from the upper to lower lakes (Beletsky et al. 1999). Whether or not Asian carps will use these currents is unknown. The use of area-restricted search (ARS) concentrates individuals in regions of higher food resources, which in turn increases the possibility of mate pairings (see Cuddington et al., this report). If Asian carps are introduced into systems with higher productivity (Lake Erie, St. Lawrence River), their dispersal rates to other systems is decreased because the ARS retains them in the originating system. If however, individuals are released from low productivity systems (Lake Michigan and Superior) they tend to disperse more readily, but will remain if they encounter embayments with high food resources (Green or Traverse bays in Michigan; St. Louis Estuary, Black and Thunder bays in Superior). In particular, if escapes from the Chicago Sanitary and Ship Canal (CSSC) are expected, then St Joseph's River, Muskegon River, Traverse Bay and Green Bay are the likely systems that will attract them in that order. Given the central connectivity of Lake Huron and Georgian Bay to the other lakes and the number of long rivers this system contains, it is likely that Lake Huron may attract spawning populations of Asian carps. Lake Huron has low overall productivity, but there are several high productivity sites in the nearshore (Saginaw Bay, Parry Sound and North Channel) which have food resources to retain carps in those areas. Lake Erie was an exception where the majority of released individuals never experience limiting food conditions, so it is highly likely that Lake Erie will be a major focus of carp establishment. This condition was also true for releases into the St. Lawrence River. New studies are recommended that will examine the feeding behaviours of Asian carps using food resources expected from large lake systems. It is still unknown whether Silver Carp can be supported on diets of the plentiful protozoans available in many of the lakes. Moreover, Cladophora could be an abundant source of food in the near shore of most of the Great Lakes but no feeding studies have been done with Asian carps on these food sources. Lastly, rates of movement for Asian carps are needed from lacustrine systems to better determine the expected dispersal rates and predict arrival times in new systems.

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Table 1-1: Movement rates of carps in the model given different step-lengths for searching/feeding behaviour with or without autocorrelation. Autocorrelated movement occurs by averaging with the previous step, so the overall rate tends to be approximately ½ of non-autocorrelated movement. Location changes were calculated every 4hrs (6 timesteps/d) but can also be viewed as 6 "movement periods per day" which could occur in daytime only, crepuscular etc. Realized and average movements are values taken for a 1 year model run with 1000 individuals released into Lake Michigan.

Movement Type searching/feeding	*Potential Movement per timestep*	*Realized Movement per timestep*	*Average Movement*	
			Day^{-1}	*m/s*
8/2 autocorrelated area-restricted	8 km @ low food 2 km @ high food	4.10 km	24.6 km	0.28
4/1 autocorrelated area-restricted	4 km @ low food 1 km @ high food	2.11 km	12.7 km	0.14
2/.5 autocorrelated area-restricted	2 km @ low food .5 km @ high food	0.92 km	5.5 km	0.07
8/2 purely random area-restricted	8 km @ low food 2 km @ high food	7.86 km	47.2 km	0.55
4/1 purely random area-restricted	4 km @ low food 1 km @ high food	3.96 km	23.8 km	0.28
2/.5 purely random area-restricted	2 km @ low food .5 km @ high food	1.86 km	11.2 km	0.13

Table 1-2: Site characteristics used in the model

	Lake Michigan	Lake Superior	Lake Huron	Georgian Bay	Lake St. Clair	Lake Erie	Lake Ontario	Saint Lawrence R.
Surface Area (km^2)	180 000	82 100	23 000	15 100	420	25 700	18 960	430
Mean Depth (m)	85	147	59	43	3	19	86	4
Max Depth (m)	282	406	229	165	6	64	244	9
Mean Max Temperature (ºC)	23	18	21	22	24	24	23	23
Max Mean Zooplankton dry biomass (mg C m^{-3})	30	60	80	100	80	150	80	60
Potential Spawning Rivers	Fox, Muskegon	St. Louis, Mission, Gravel, White, Michipoten, St. Marys	Saginaw, Maitland, Saugeen	French, Spanish, Nottawasaga	Thames	Maumee, Sandusky, Grand	16 mile, Genesee, B. of Quinte	St Lawrence

Source: The Great Lakes: An Environmental Atlas and Resource Book (Canada and United States, 1995)

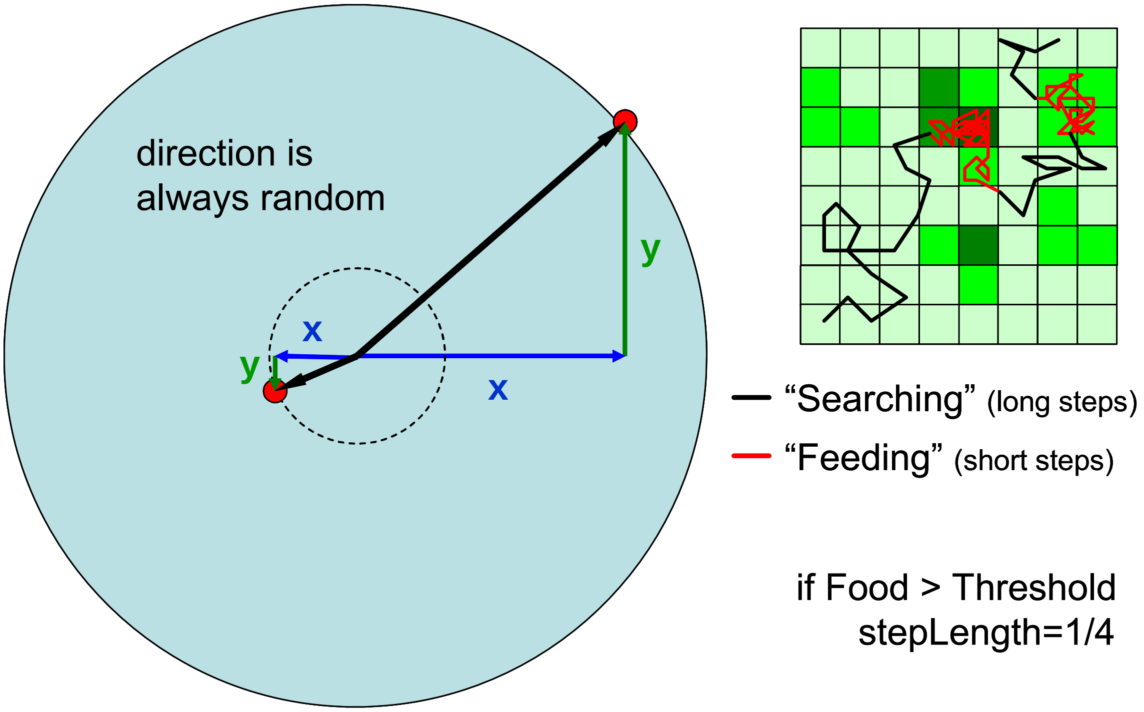

Figure 1-1: Area-restricted search (ARS). There are two behaviours. An individual moves in a random direction of a distance (steplength) in a "searching" mode. When the food value at the individual's location is greater than a threshold value (320 mgCm^{-3}), then the distance is ¼ of steplength but direction is still random in a "feeding" mode. Using this movement form, individuals tend to remain in areas of increased food resources.

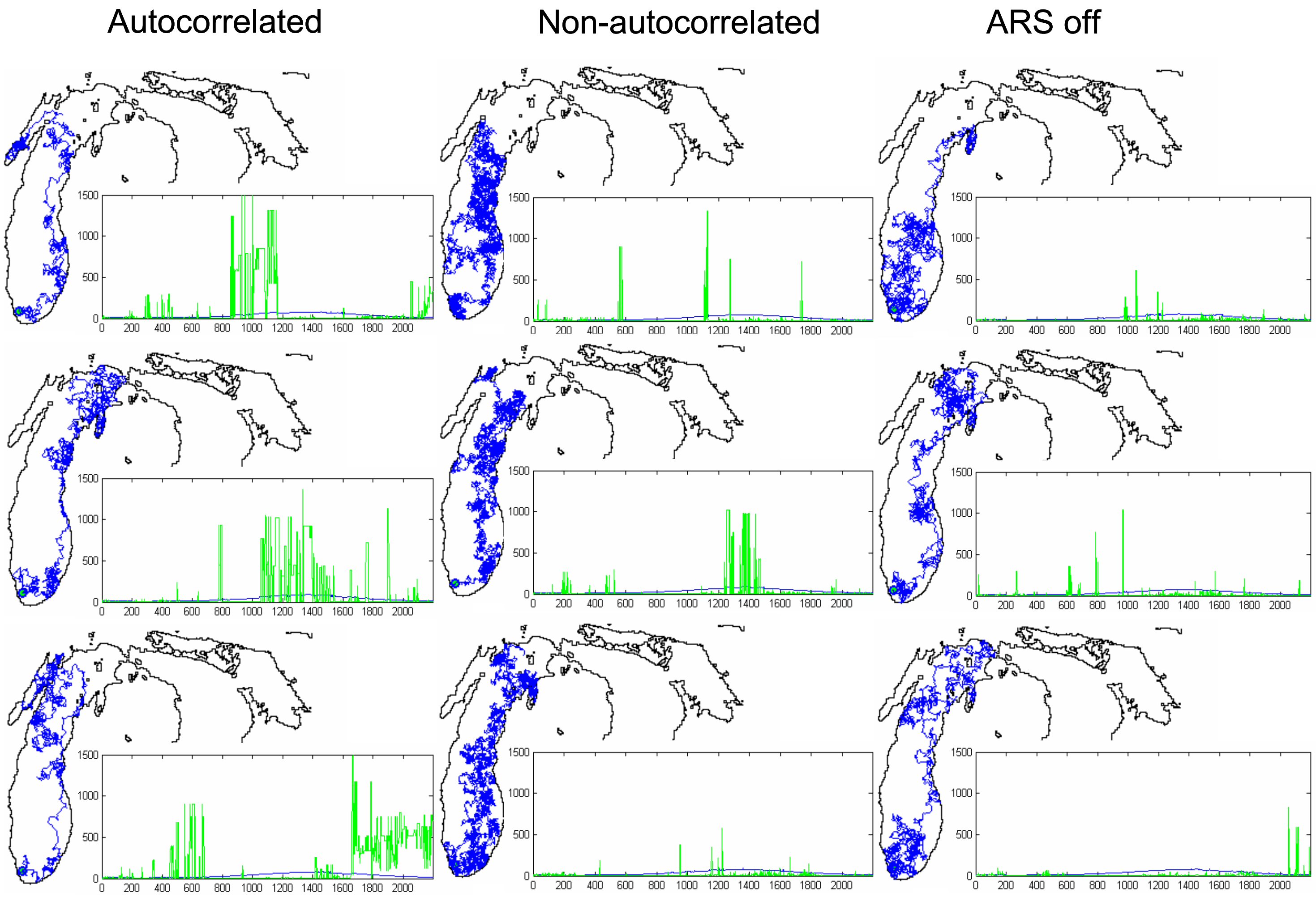

Figure 1-2: Example fish movement paths when release from the CSSC using 4/1 km timestep^{-1} for 2 years using autocorrelation, no autocorrelation and autocorrelation without ARS. Inset timeseries graphs are the carbon transformed values of phytoplankton encountered (green) and the zooplankton (blue). High values of longer duration are found when individuals use autocorrelated ARS.

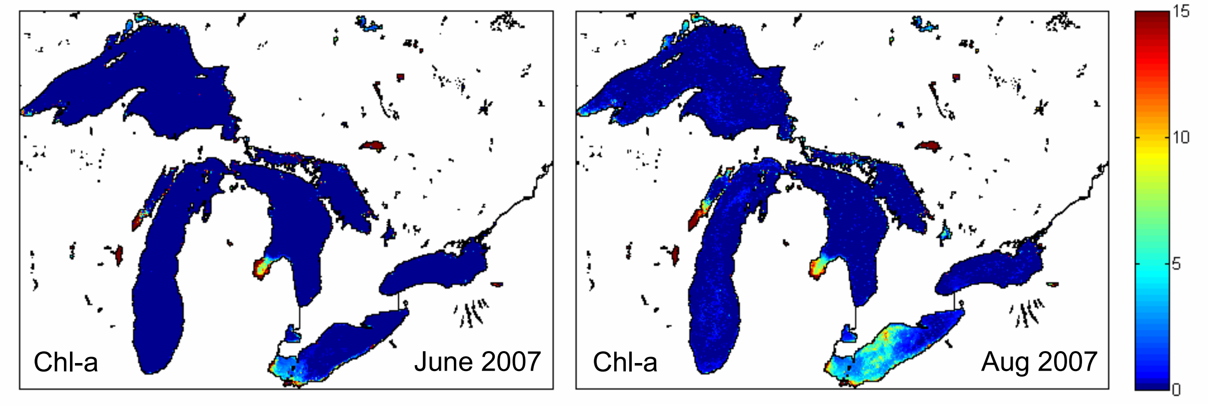

Figure 1-3: Sample chlorophyll-a values for June and August 2007 from MODIS used in the model (courtesy Environment Canada Remote Sensing Lab).

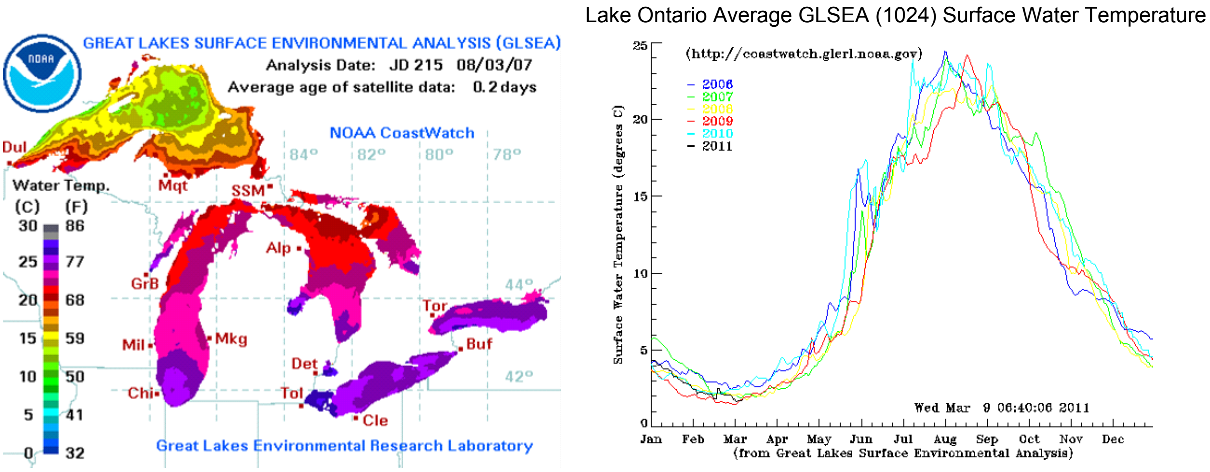

Figure 1-4: Lake surface temperature values for August 2007 and yearly temperatures for Lake Ontario 2006-2011 accessed from the NOAA Great Lakes Surface Environmental Analysis lab (GLSEA).

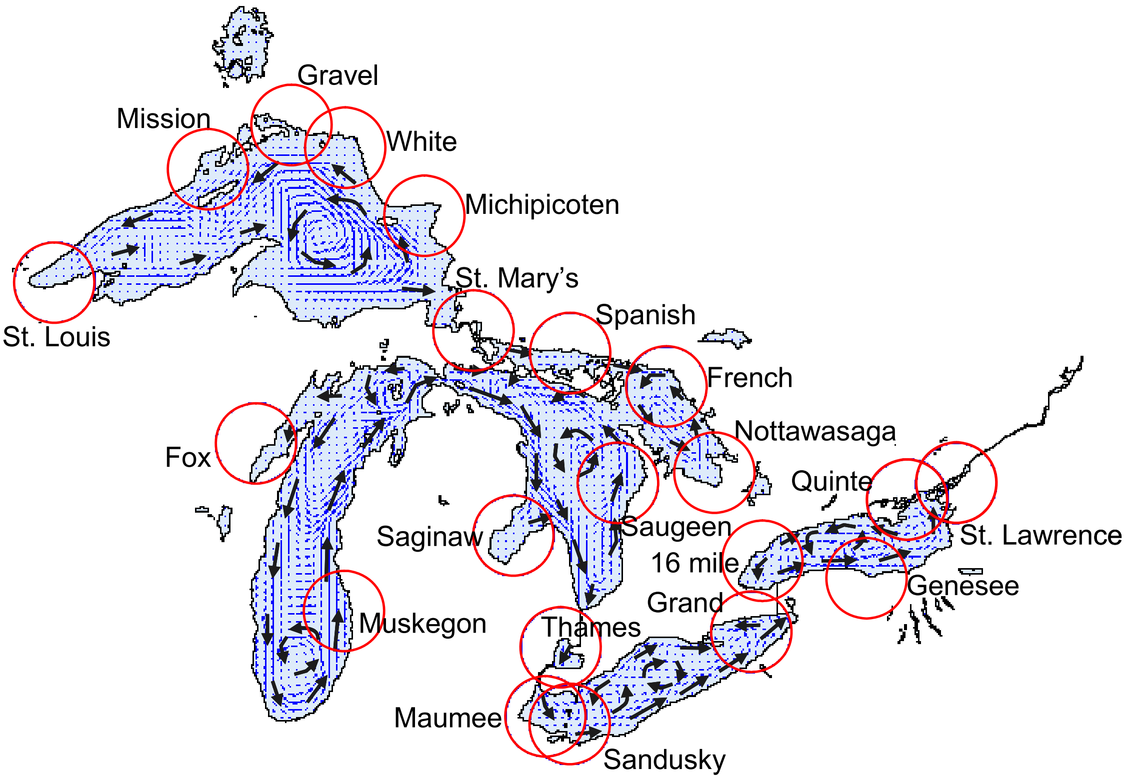

Figure 1-5: Map of average currents and proximity to spawning rivers (circles) used in the model.

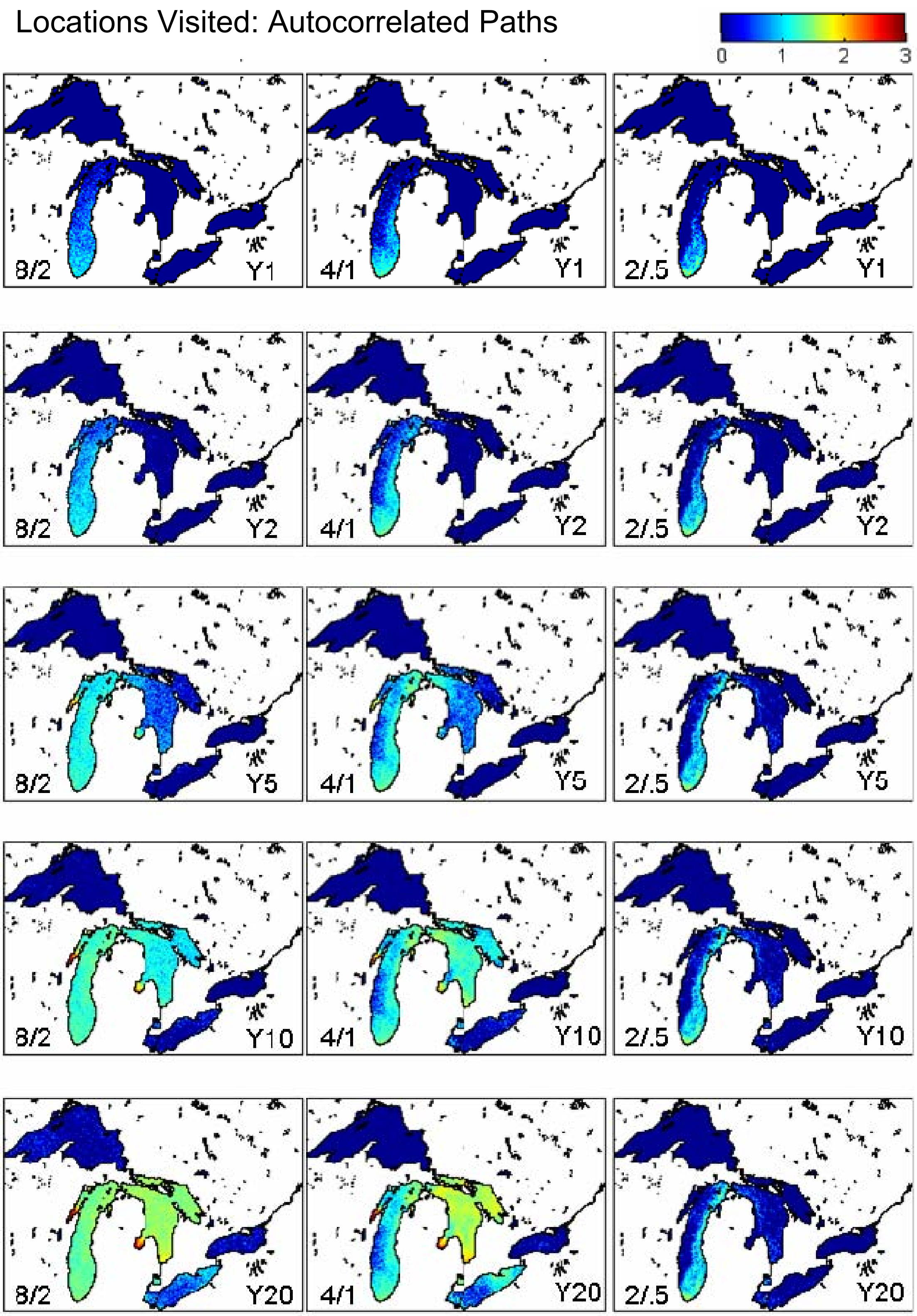

Figure 1-6: Autocorrelated, ARS (default). Spread maps show log # of visits for movement rates of 8/2, 4/1, 2/.5 km timestep^{-1} for 1, 2, 5, 10 and 20 years with start near Chicago.

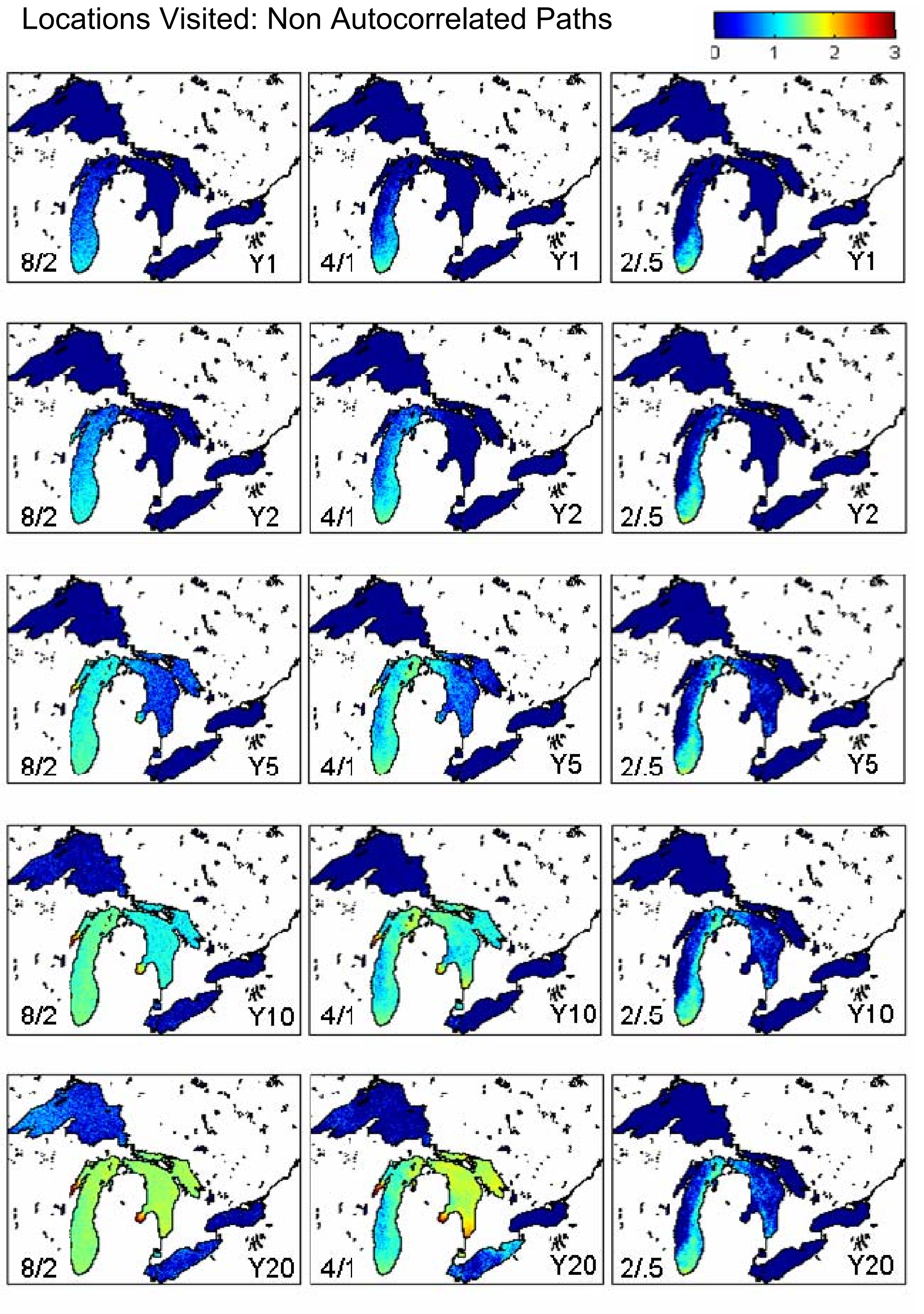

Figure 1-7: Non-autocorrelated, ARS. Spread maps show log # of visits for movement rates of 8/2, 4/1, 2/.5 km timestep^{-1} for 1, 2, 5, 10 and 20 years with start near Chicago.

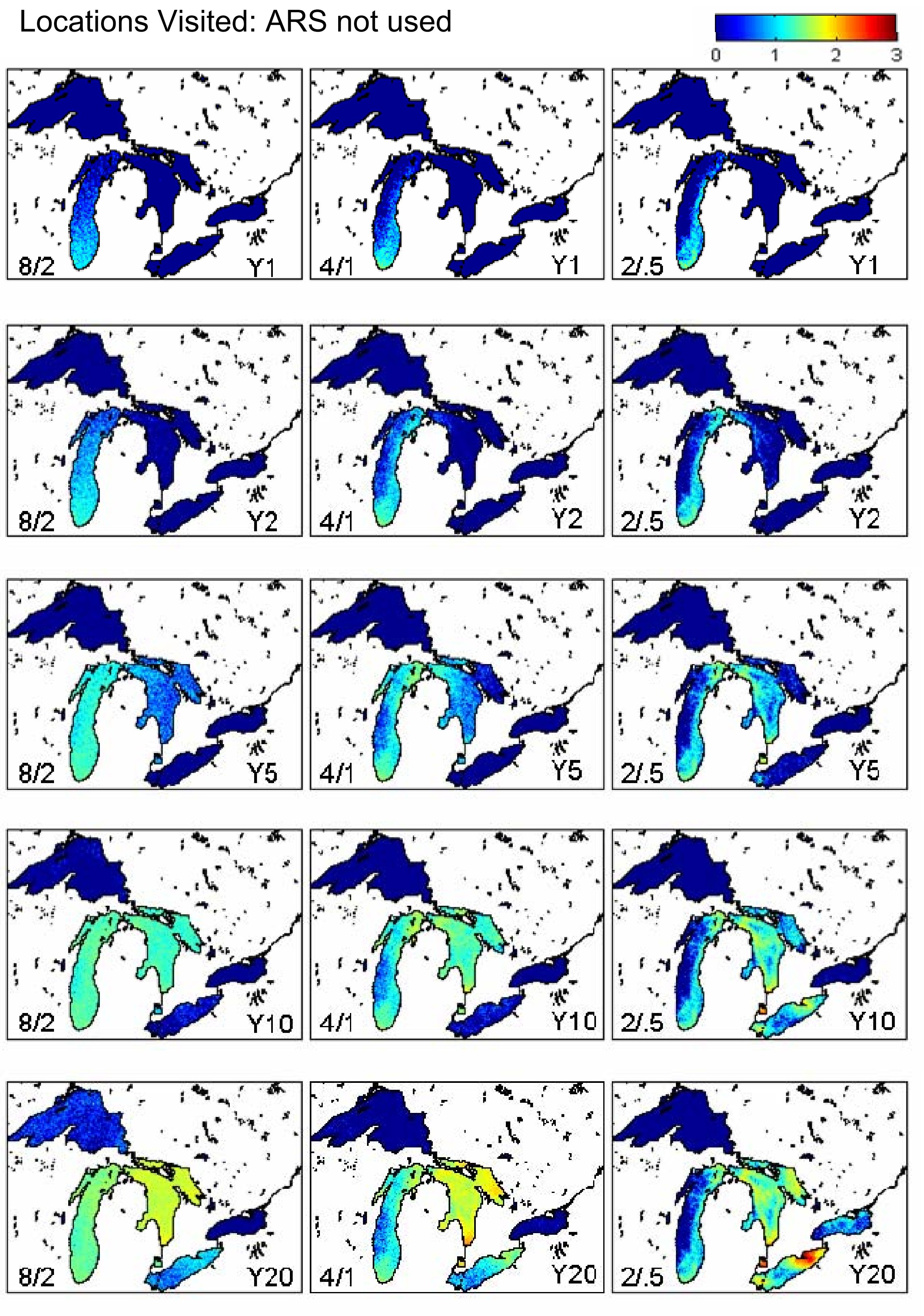

Figure 1-8: Autocorrelated but no ARS. Spread maps show log # of visits for movement rates of 8/2, 4/1, 2/.5 km timestep^{-1} for 1, 2, 5, 10 and 20 years with start near Chicago.

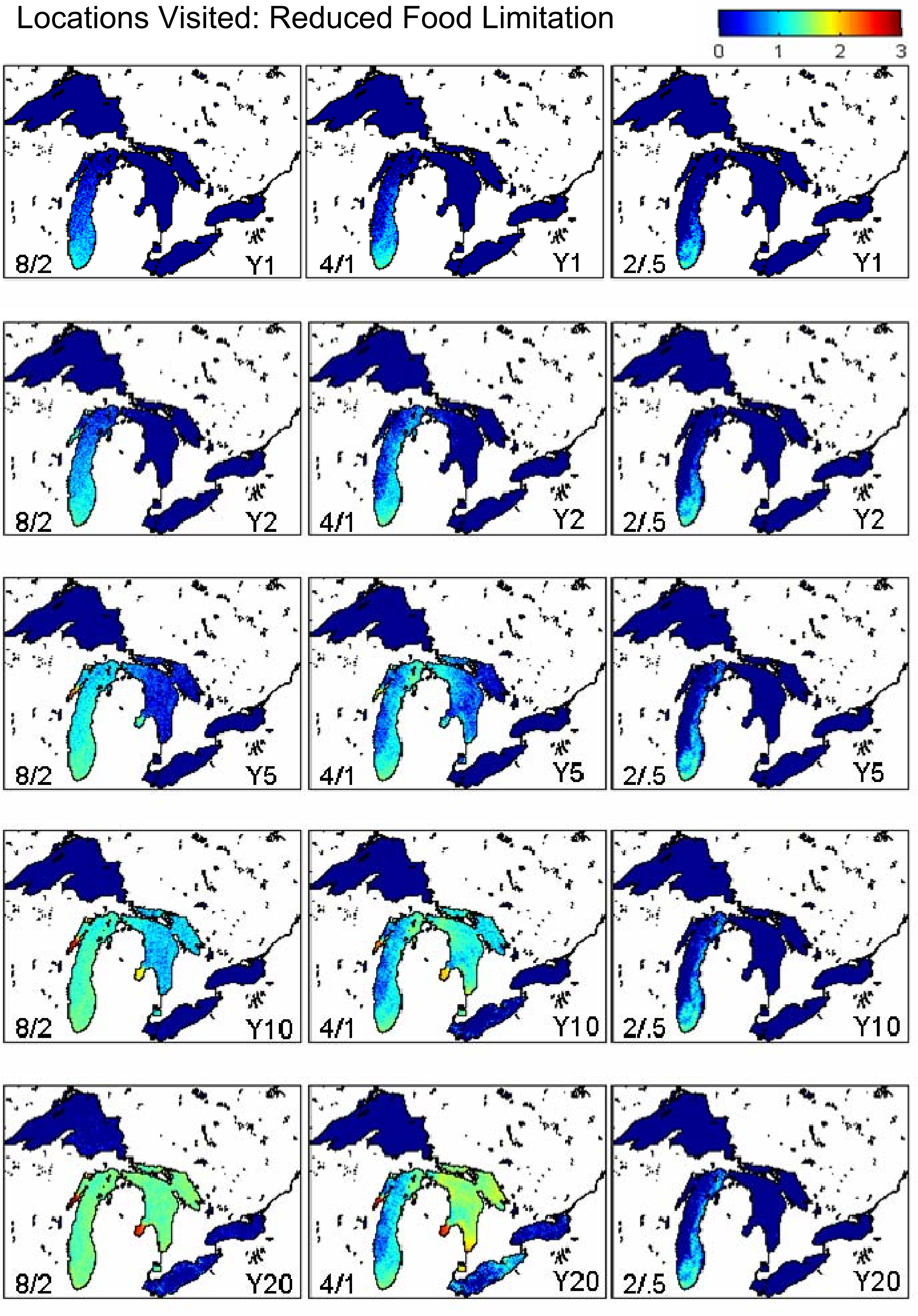

Figure 1-9: Food limit to begin ARS reduced to ½. Spread maps show log # of visits for movement rates of 8/2, 4/1, 2/.5 km timestep^{-1} for 1, 2, 5, 10 and 20 yrs with start near Chicago.

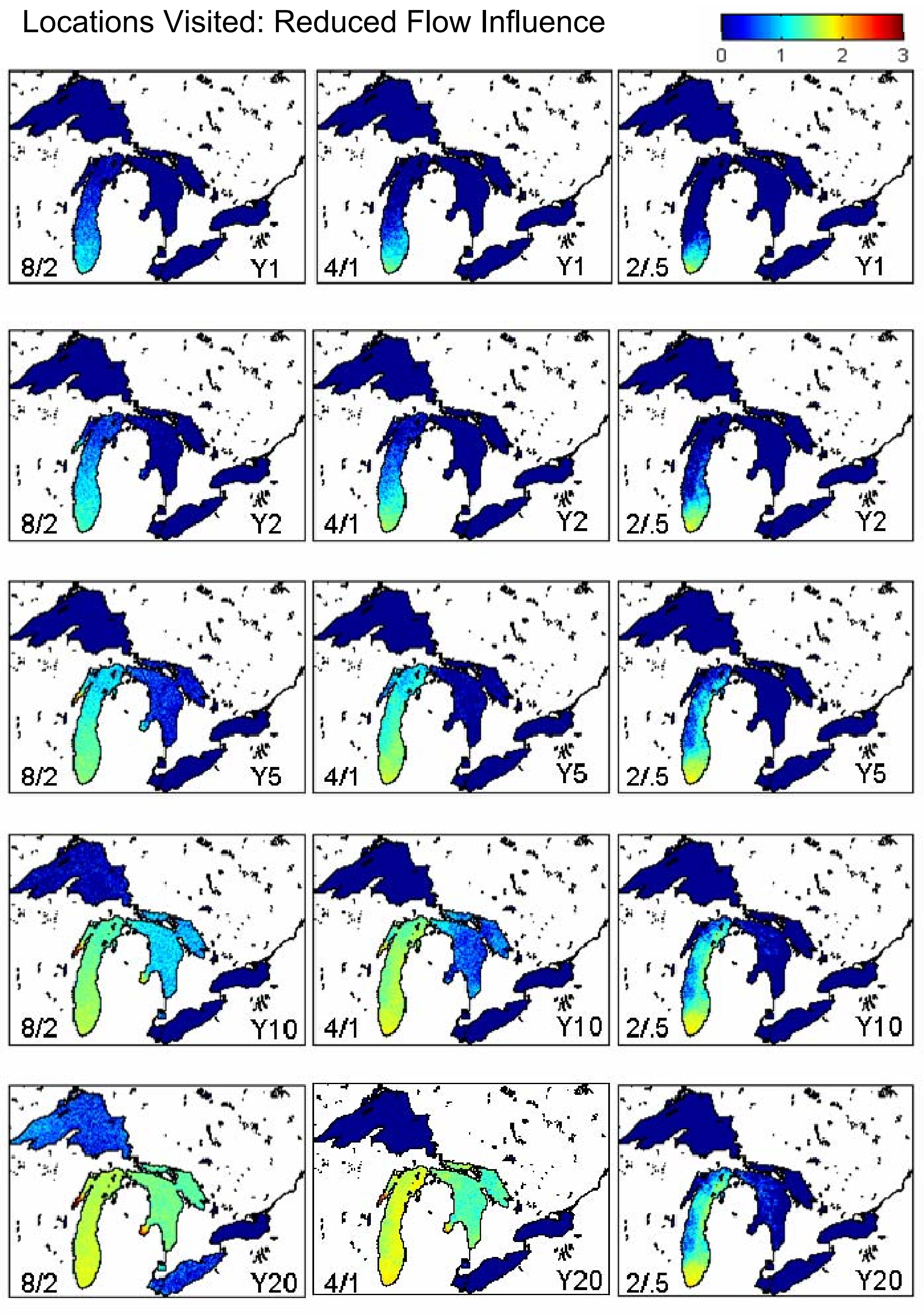

Figure 1-10: Flow influence reduced 0.1x from 0.25x. Spread maps show log # of visits for movement rates of 8/2, 4/1, 2/.5 km timestep^{-1} for 1, 2, 5, 10 and 20 yrs with start near Chicago.

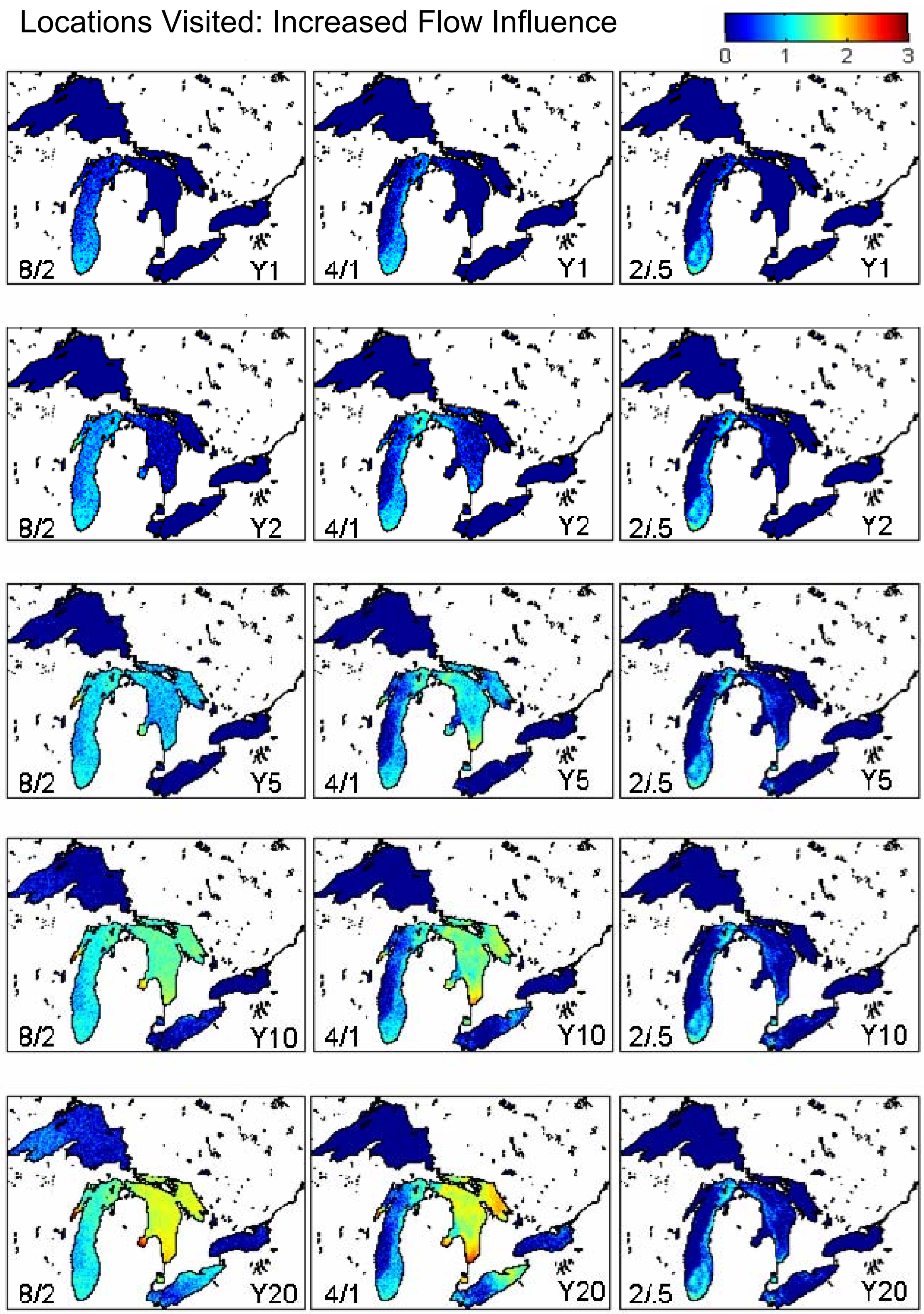

Figure 1-11: Flow influence increased 0.5x from 0.25x. Spread maps show log # of visits for movement rates of 8/2, 4/1, 2/.5 km timestep^{-1} for 1, 2, 5, 10 and 20 yrs with start near Chicago.

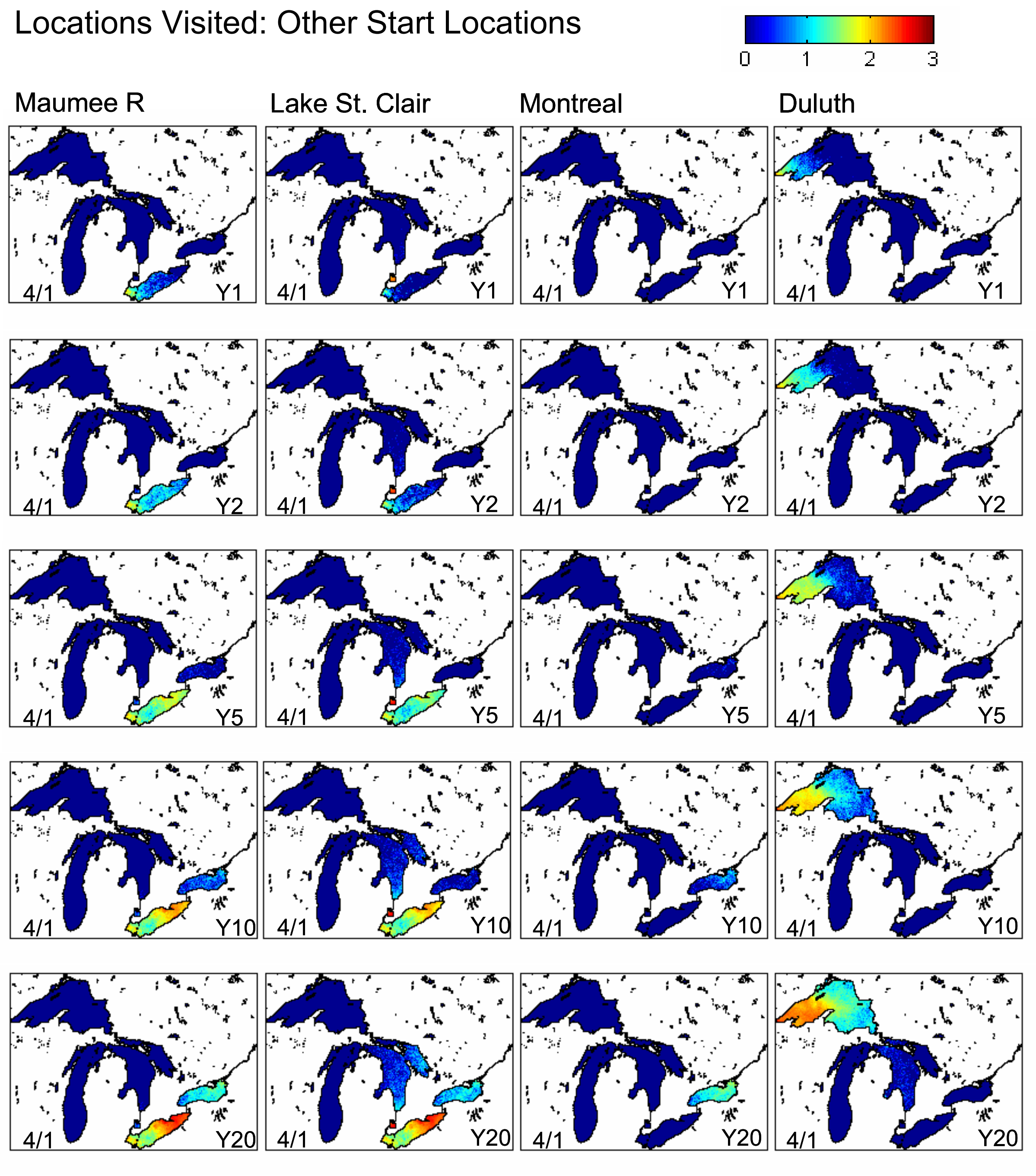

Figure 1-12: Autocorrelated, ARS using different start locations: Maumee River in Lake Erie, Thames River in Lake St. Clair, Montreal on the St. Lawrence River, and the St. Louis Estuary near Duluth, MN on Lake Superior. Spread maps show log # of visits for movement rates of 8/2, 4/1, 2/.5 km timestep^{-1} for 1, 2, 5, 10 and 20 yrs with start near Chicago.

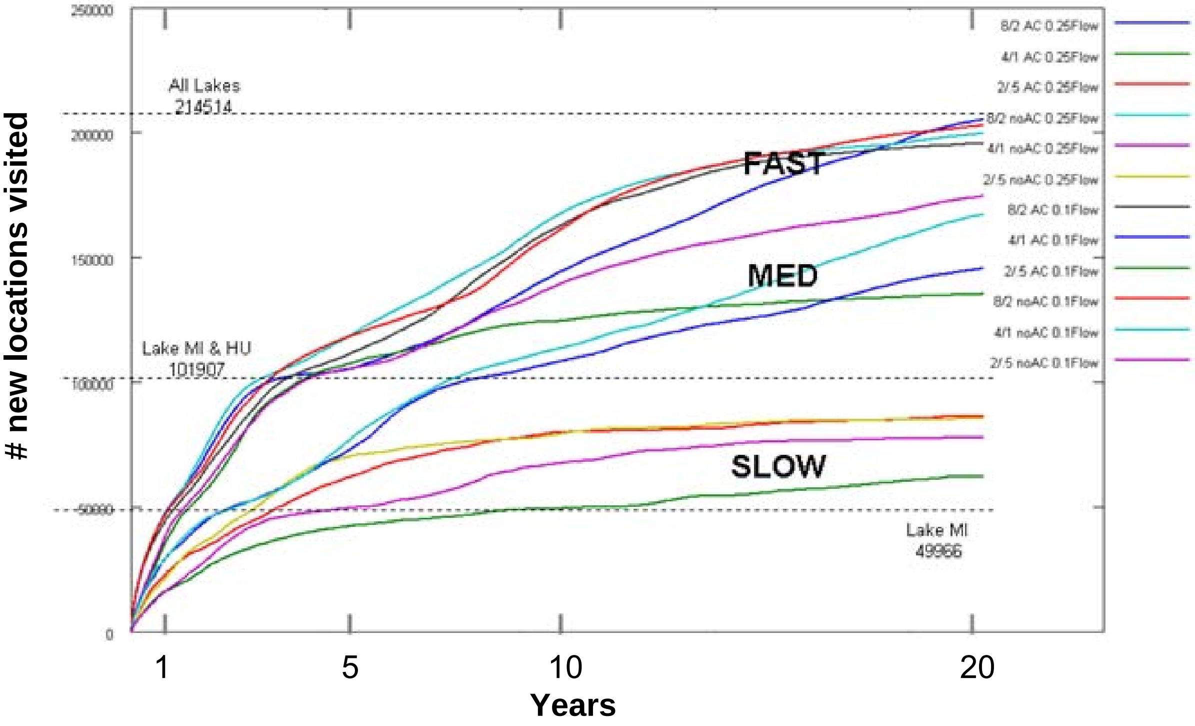

Figure 1-13: Cumulative new sites visited over 20 years for different searching behaviours with starting site near Chicago. Steplengths ranged from 8/2 (fast), 4/1 (med), 2/.5 (slow) km timestep^{-1} using autocorrelation or no autocorrelation and flow influence of 0.25x and 0.1x. The cumulative sizes (km^2) of Lake Michigan and Lake Huron and the entire Great Lakes model arena are noted.

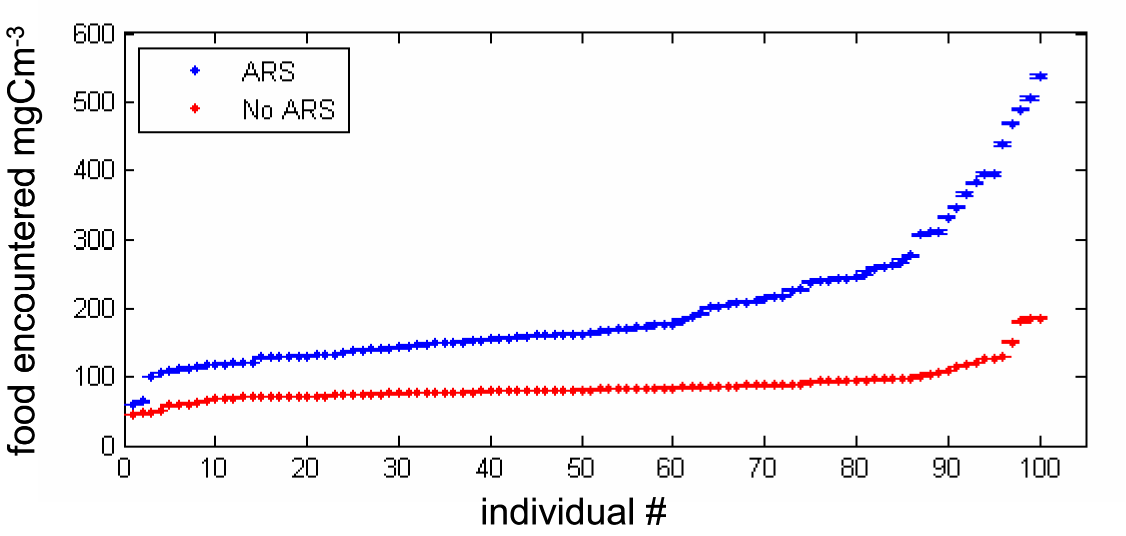

Figure 1-14: Ranked mean+/-SE phytoplankton and zooplankton encountered (mgCm^{-3}) for each individual using ARS and without ARS. Individuals were released from the CSSC and used 4/1 km timestep^{-1}, autocorrelated movement for 2 years.

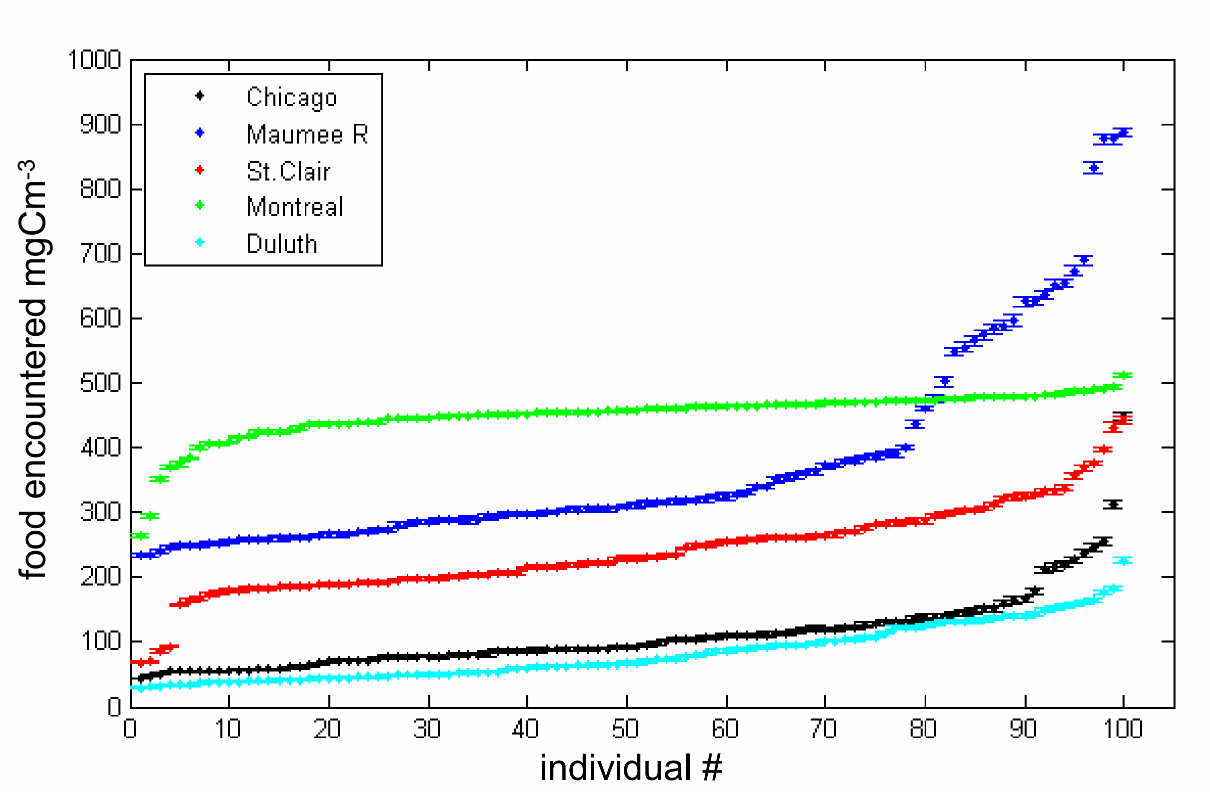

Figure 1-15: Ranked mean+/-SE total phytoplankton and zooplankton encountered (mgCm-3) for each individual over 2 years from release sites in Lake Michigan (Chicago), Lake Erie (Maumee), Lake St. Clair (Thames R.), St. Lawrence River (Montreal) and Lake Superior (St. Louis Estuary, Duluth, MN).

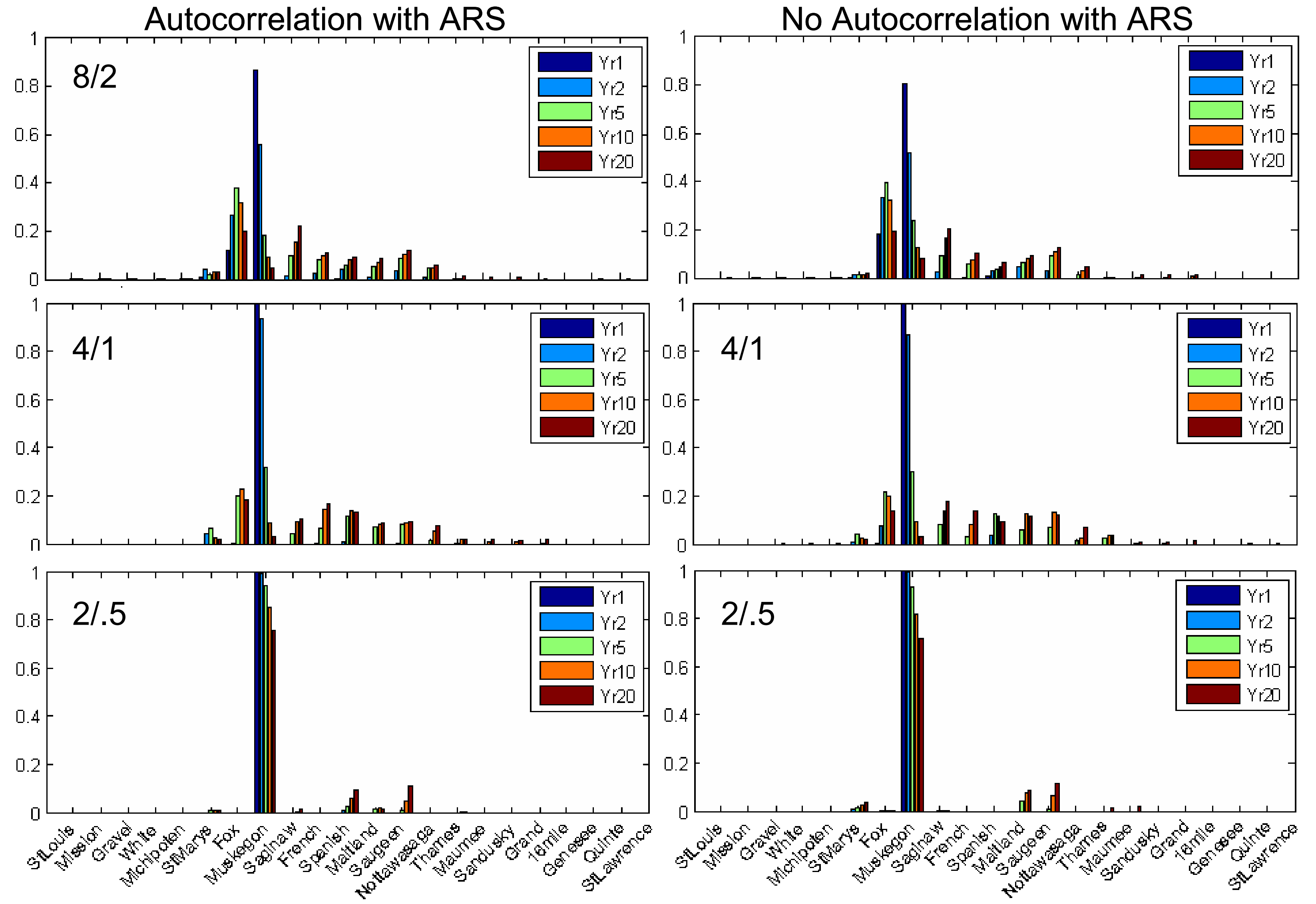

Figure 1-16a: Autocorrelated vs non-autocorrelated movement. Probability of proximate rivers being encountered when water temperatures > 18C at 1, 2, 5, 10 and 20 years with starting point near Chicago. Rivers are considered possible spawning locations when they are within 25 km of fish location.

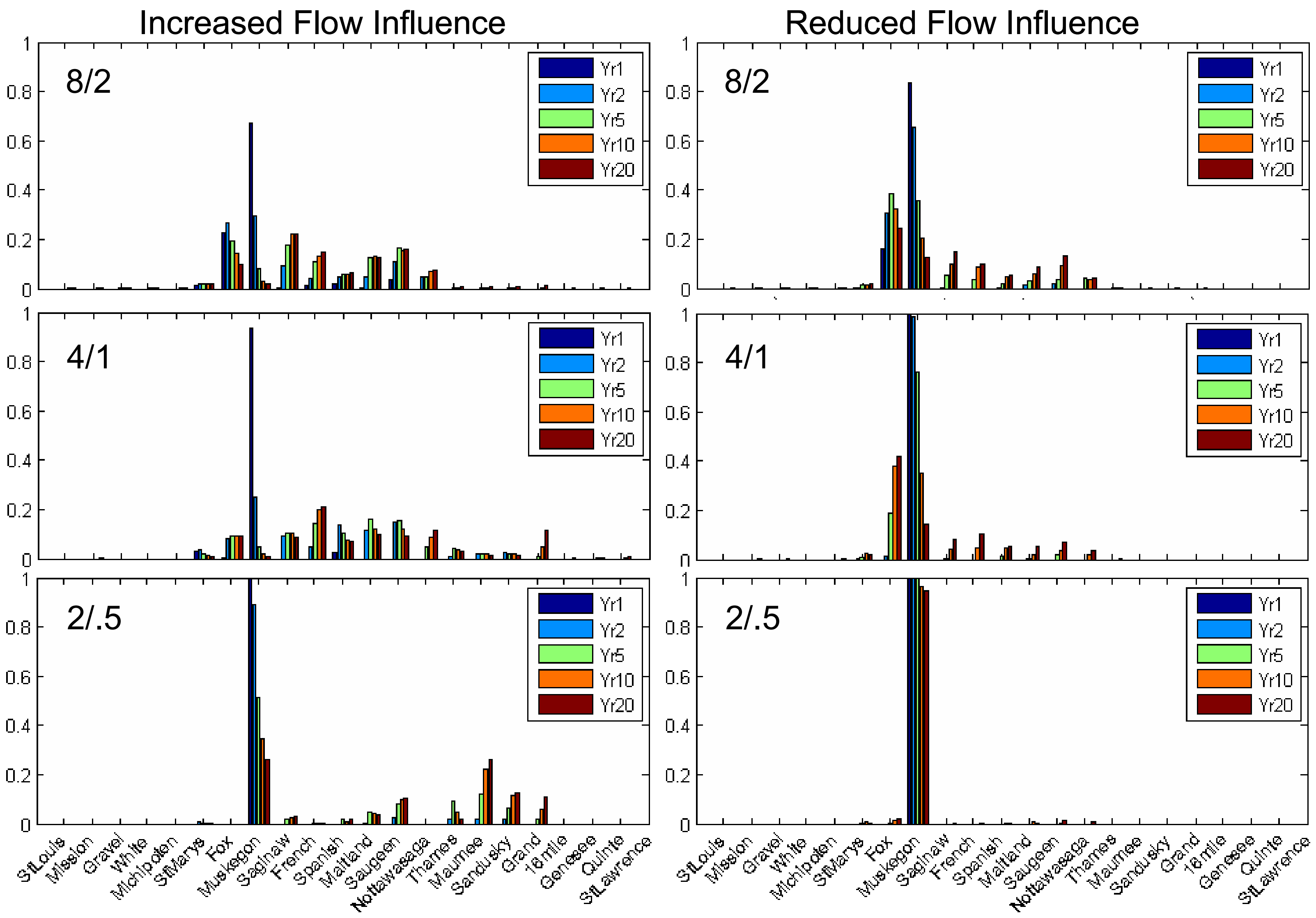

Figure 1-16b: Increased vs. reduced flow influence. Probability of proximate rivers being encountered when water temperatures > 18C at 1, 2, 5, 10 and 20 years with starting point near Chicago. Rivers are considered possible spawning locations when they are within 25 km of fish location.

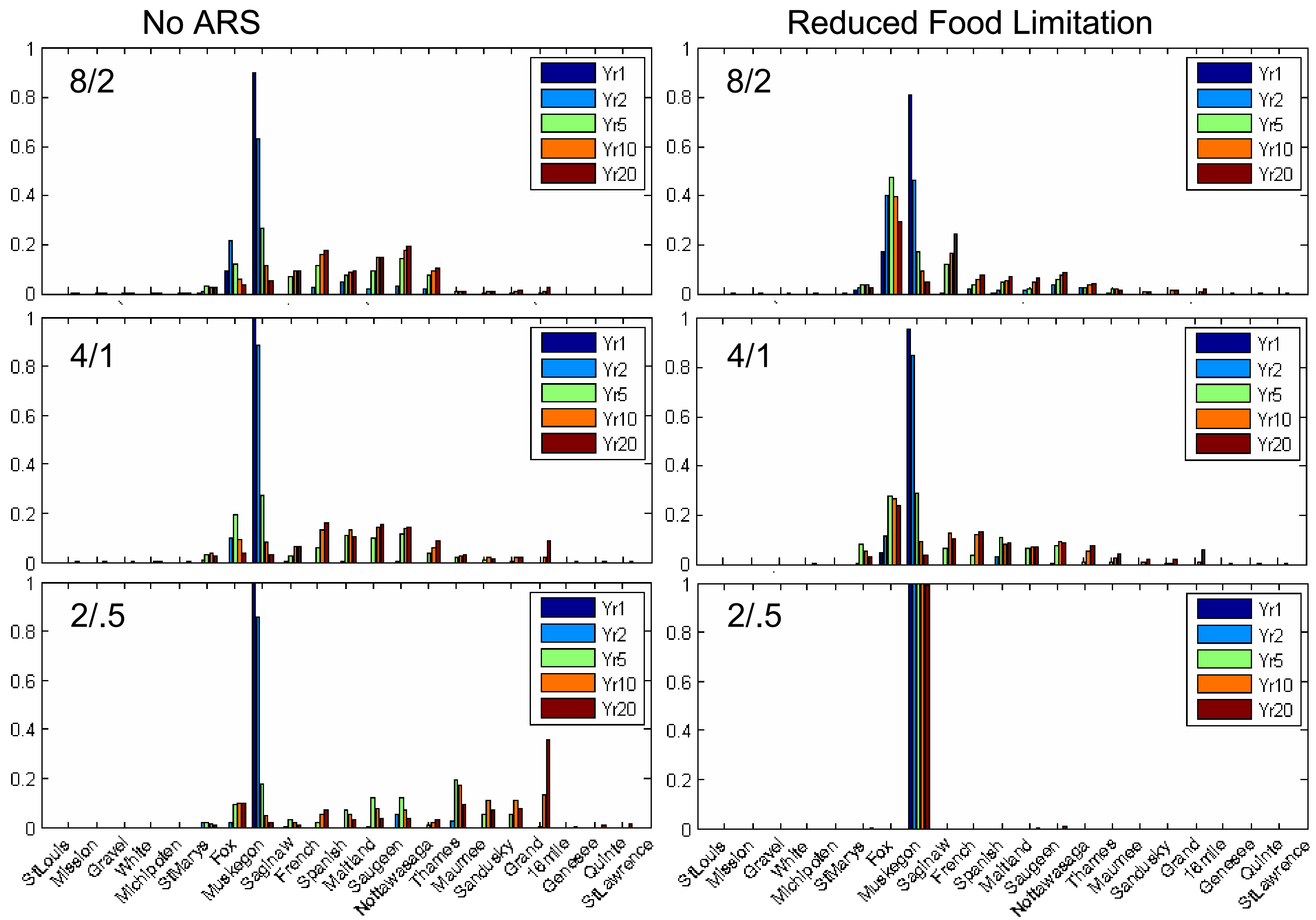

Figure 1-16c: No ARS vs reduced food level to produce ARS behaviour. Probability of proximate rivers being encountered when water temperatures > 18C at 1, 2, 5, 10 and 20 years with starting point near Chicago. Rivers are considered possible spawning locations when they are within 25 km of fish location.

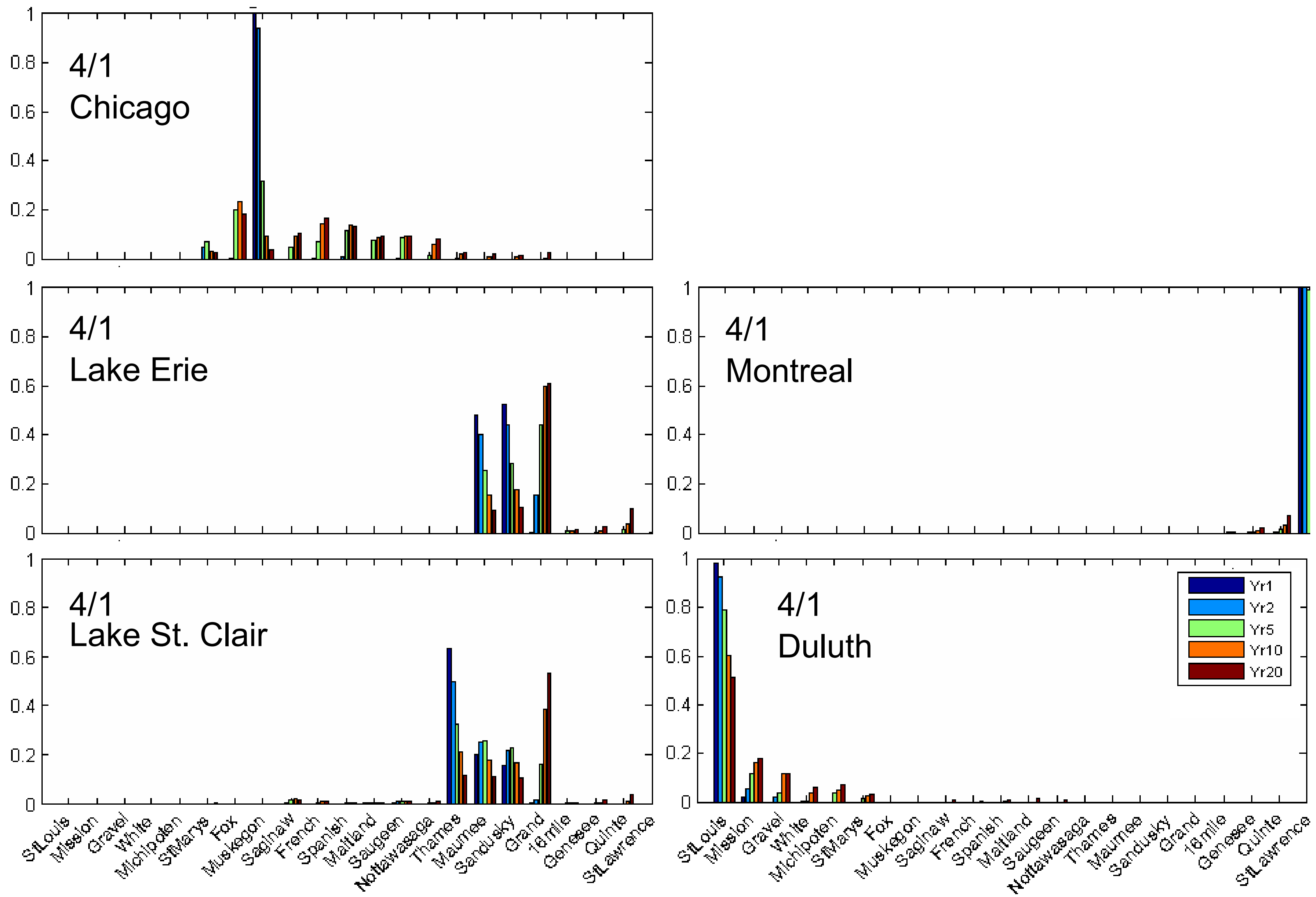

Figure 1-16d: Other starting locations: Lake Erie (Maumee), Lake St. Clair (Thames R.), St. Lawrence River (Montreal) and Lake Superior (St. Louis Estuary, Duluth, MN). Probability of proximate rivers being encountered when water temperatures > 18C at 1, 2, 5, 10 and 20 years. Rivers are considered possible spawning locations when they are within 25 km of fish location.

RISK OF ASIAN CARP ESTABLISHMENT IN THE GREAT LAKES. PART 1: SPAWNING PROBABILITIES

Kim M.D. Cuddington, Warren J.S. Currie and Marten A. Koops

INTRODUCTION

In the event of Asian carp arriving in the Great Lakes system, we need to establish estimates of the risk that such a release will result in an established carp population. This risk can be thought of as composed of two parts: the probability that carp will successfully spawn, and the probability that such spawning will result in positive population growth. In this report, we focus on the former probability: that carp manage to spawn at all at low fish density. We determine the number of fish that must breach protective measures in order for spawning to take place with significant probability.

Asian carp require a suitable river for spawning. Therefore, the arrival of male and female fish in a lake is not sufficient for a spawning event. The lake must have rivers suitable for spawning. Carp require rivers of sufficient size and flow for successful spawning (Jennings 1988; Costa-Pierce 1992; Kolar et al. 2005). However, suitable rivers are not rare in the Great Lakes. For example, at least five rivers connected to Lake Michigan have been identified as potential spawning habitat (i.e., Pere Marquette, Grand, Saint Joseph, Big Cedar, Ford). Therefore, the only questions that remain are whether it is probable that carp will locate these rivers, and if they do so, is it likely that a male and female will be present in the same river at the same time. This requirement that both a male and female fish arrive in a suitable river has led some to suggest that it is unlikely that spawning could take place at low fish density. Here, we explore this probability under several different scenarios of carp behaviour, and numbers of suitable spawning rivers.

The encounter of a male and female fish in a suitable river can viewed as a variant of the birthday paradox: the calculation of the probability that at least two people in a group of randomly selected individuals will share the same birthday. It is called a paradox because the mathematical calculation contradicts naive intuition. Contrary to the intuition of many, the probability that two people share a birthday is greater than 50 percent for a relatively small group of people (n=23). This difficulty with intuition most likely relates to the fact that the birthday problem asks whether any of the people in a given group has a birthday matching any of the others, not one in particular. As a result, in this small group of people there are over two hundred combinations to consider.

This probability is of import when calculating quantities in widely various applications such as the probability that airplanes will collide, or that there are matches between random length clone fragments in DNA mapping (Soderlund et al. 2000). The theory behind the calculation of this probability was also used by Schnabel (1938) in mark-recapture statistics. Similarly, we are concerned with the probability that any fish spawn in any river feeding into a given lake.

However, the birthday problem is related to, but not exactly the same problem as calculating the probability that a male and female fish will meet in a river when fish density is low. Wendl (2003) expanded the calculation for the birthday problem to derive the probability that two different kinds of objects would collide in the same bin, and we will use this formula to derive the probability that a male and female fish arrive in the same river to spawn.

METHODS

Modelling the probability of successful spawning in a given lake

If we assume that carp can use environmental cues to identify rivers suitable for spawning, that once in a river, pheromone cues make encounter between male and female unproblematic, and furthermore, that fish are ready for spawning at about the same time, we can show that the probability of at least one spawning event is quite likely at very low fish density.

Using Wendl's (2003) formulation regarding the collision of two different kinds of objects in a given number of bins, we can calculate the probability that there are no simultaneous occurrences of male and female fish in the same river as:

$$P_0(m, f, r) = \frac{1}{r^{m+f}} \sum_{i=1}^{m} \sum_{j=1}^{f} S_2(m, i) S_2(f, j) \prod_{k=0}^{i+j+1} r - k$$

where m is the number of male fish in the lake, *f* is the number of female fish, *r* is the number of rivers, and S_2 refers to Stirling numbers of the second kind. So, for example, $S_2(n, k)$ represents the number of ways we can partition *n* fish among *k* rivers. The probability that there is at least one meeting of a male and female fish in the same river is given by $1 - P_0$.

For relatively small number of suitable rivers, we find that the probability of one successful spawning is rather high (> 50%) and increases rapidly as the number of fish increases, even for a larger number of suitable rivers (Figure 2-1a).

The expected number of rivers with successful spawning can be obtained using Nakata's (2008) expansion of Wendl's work, where the expected number of meetings between male and female fish in the same river is calculated as:

$$E(m, f, r) = r(1 - (1 - \frac{1}{r})^{f})(1 - (1 - \frac{1}{r})^{m})$$

For a low number of rivers, and a small number of fish, we find the expectation is that all rivers will have a successful spawning event (Figure 2-2). For larger numbers of suitable rivers, we expect about 4 rivers with successful spawning with only 20 fish (10 males and females).

If we instead assume that not all fish present in the lake arrive at suitable spawning rivers, then these probabilities will be reduced. For example, fish may have some difficulty in locating rivers, or may incorrectly identify rivers as suitable. We can simulate these difficulties by assuming a low percentage of fish (20%) arrive at suitable rivers, and calculate the probability of spawning based on this portion of the population (Figure 2-1b). In this case, for a large number of rivers, 15 or more female fish are required for a 50% probability of spawning.

These probabilities are not unique. That is, a different number of male and female fish can also yield similar probabilities. It is only when the sex ratio is significantly skewed (5:1 or greater) that we would see substantial reductions in these probabilities (Figure 2-3). However, this calculation is complicated by the ability of males to spawn with multiple females.

Finally, even if we assume that there is variability about spawning time of individuals, the probability at least one successful mating is still rather high for low fish numbers. In this case, we modify the meaning of *r*, and use it to refer to time/space bins of a particular river at a particular time. Since both warm waters and high flow may be required for spawning (Verigin et al. 1978, Pflieger 1997), we assume that spawning is driven by lake-wide seasonal signals, and is of finite duration (3 months: June, July, August). Then, if we assume that carp eager to spawn will linger in a suitable river for 2 weeks, for each river we have 6 distinct time periods. If we treat each two-week period as a discrete interval, we can then calculate the probability of a male and female carp meeting in a given river in at least one of these distinct time periods in a given river (Figure 2-4a).

With the requirement that male and female fish meet within a specific time window, we find a reduction in the probability of a successful mating, but the effect is not very large. For a large number of suitable rivers, we have still have a 50% probability of one successful spawning with 10 female fish (20 total fish). Moreover, multiple partial spawning events per individual are possible (Pflieger 1997, Jennings 1988, 2002). Therefore, it may be that the probability of one successful spawning should be treated as the summation over all 6 time intervals. In which case, we would have a much higher probability for a smaller number of fish (Figure 2-4b).

CONCLUSION

It is well known that intuitions about probability and risk are not always reliable (e.g., Kahneman et al. 1982). This seems to be particularly true when our probability calculation involves combinatorics: a counting up of the number of ways in which an event can occur. Managers may believe that a small number of Asian carp that have escaped into a Great Lake, such as Erie, are quite unlikely to find spawning grounds and mates. Our calculation, using a variant of the birthday problem, demonstrates that this intuition is probably false.

In general, if a small number of fish are evenly distributed over a number of rivers, the probability of a successful mating is reduced as the number of suitable rivers increases. However, even 10 female fish (20 total) represent a greater than 50% probability of successful mating for a relatively large number of rivers. This calculation assumes that fish are ready to spawn at the same time, and can identify suitable rivers.

If we require that fish will only wait to encounter the opposite sex in a given river for a small time interval, the probability of spawning is reduced. However, even for the scenario of many suitable rivers, the probability of successful spawning is still 50% for 20 female fish. Of course, if a smaller time interval was required, and there were an even larger number of rivers, a larger carp population would be required.

If fish have difficulty in locating or identifying suitable rivers (e.g., they are triggered to spawn by water temperature and flow rate, but cannot determine if a river is of sufficient length for successful reproduction), then the number of fish required for a significant probability of spawning is increased. The increase in fish number will be determined the percentage of the small population that are successful in locating a suitable river. However, for our calculation with a 20% success rate, about 20 female fish (40 total) were required for a 50% probability of spawning.

If we combine these factors such that carp are unable to accurately distinguish between suitable and unsuitable rivers, and must be present in a river over a very short time interval our expected probability of spawning would be quite small. Further, when related to the probability of positive population growth, unsuitable rivers would act as spawning sinks. However, we caution against optimism given that multiple spawning attempts are possible, which will inflate spawning probabilities in opposition to these limiting factors.

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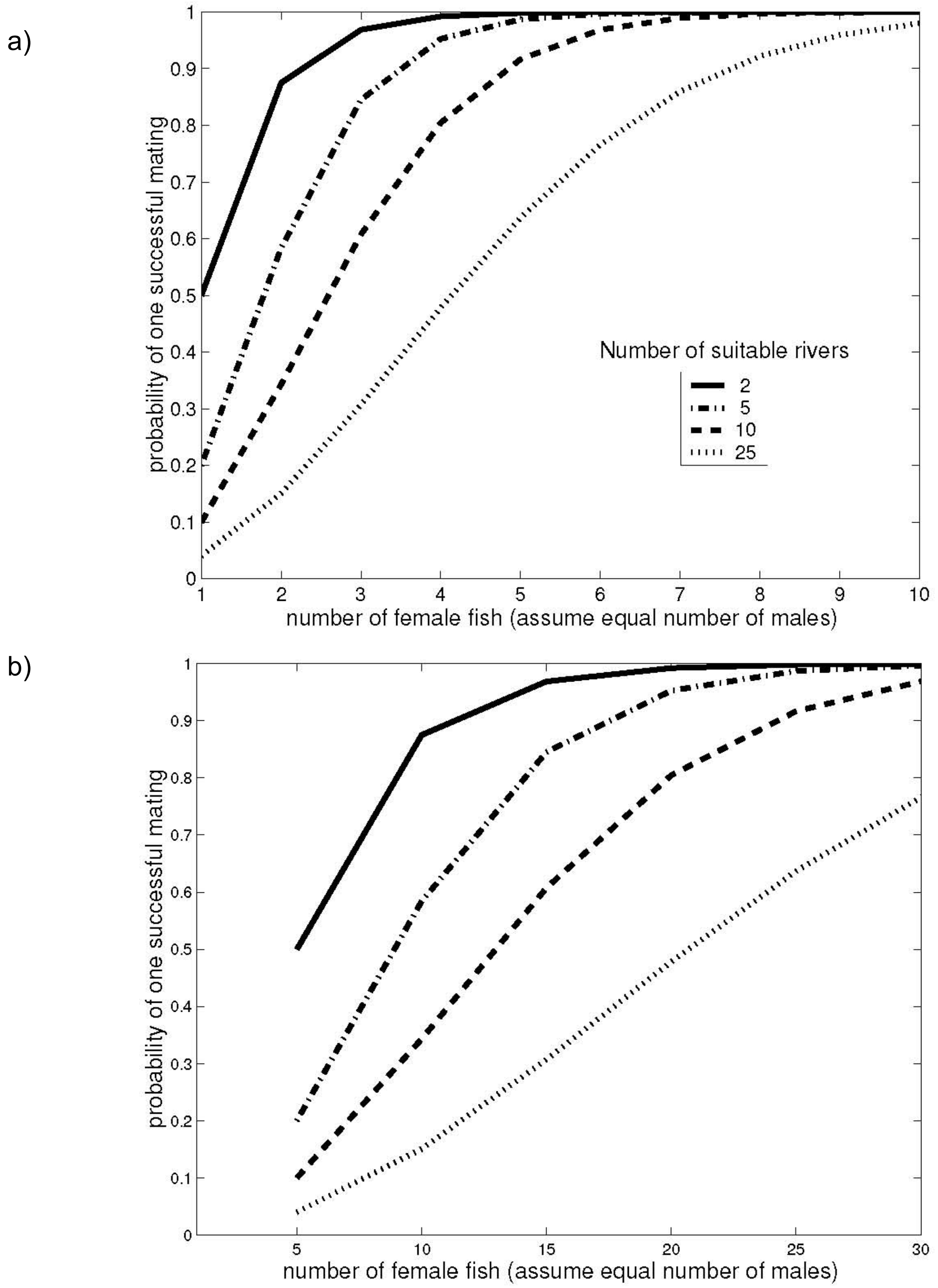

Figure 2-1: The probability of a male and female fish occupying the same river as a function of the number of female fish and the number of suitable spawning rivers. We assume that there are equal numbers of male and female fish. Fish are either a) always able to locate suitable rivers, or b) are only able to locate suitable rivers with a 20% probability.

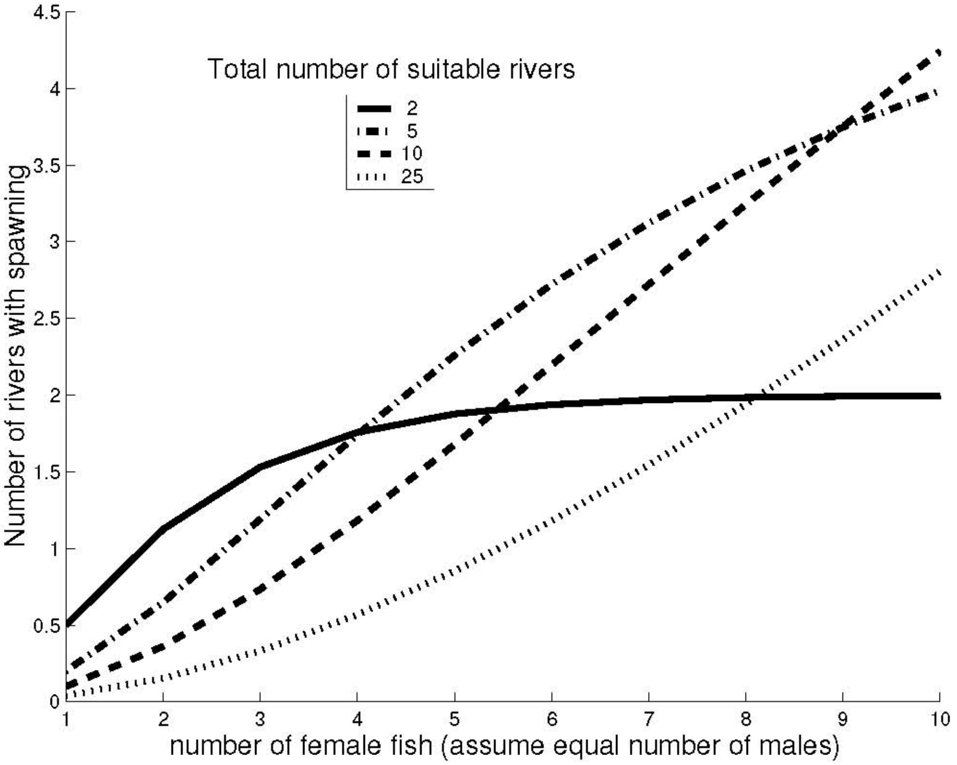

Figure 2-2: The expected number of rivers with spawning pairs as a function of the number of female fish and the number of suitable spawning rivers. We assume that there are equal numbers of male and female fish, and that fish are always able to locate suitable rivers.

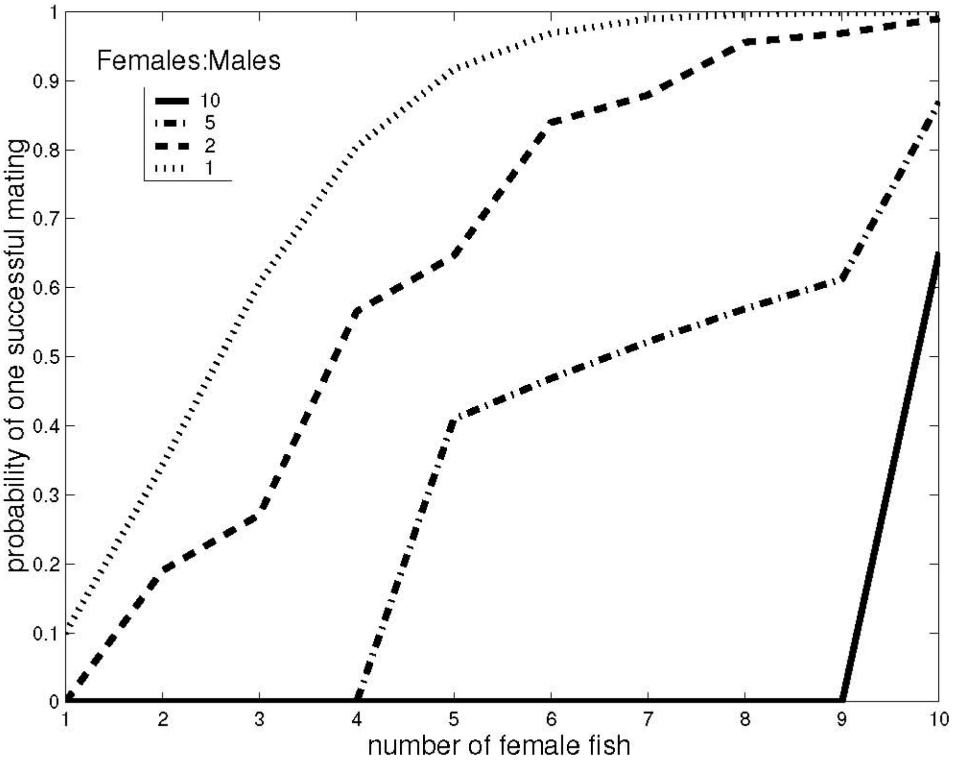

Figure 2-3: The probability of a male and female fish occupying the same river as a function of the number of female fish, and the ratio of female to male fish. There are 10 suitable rivers.

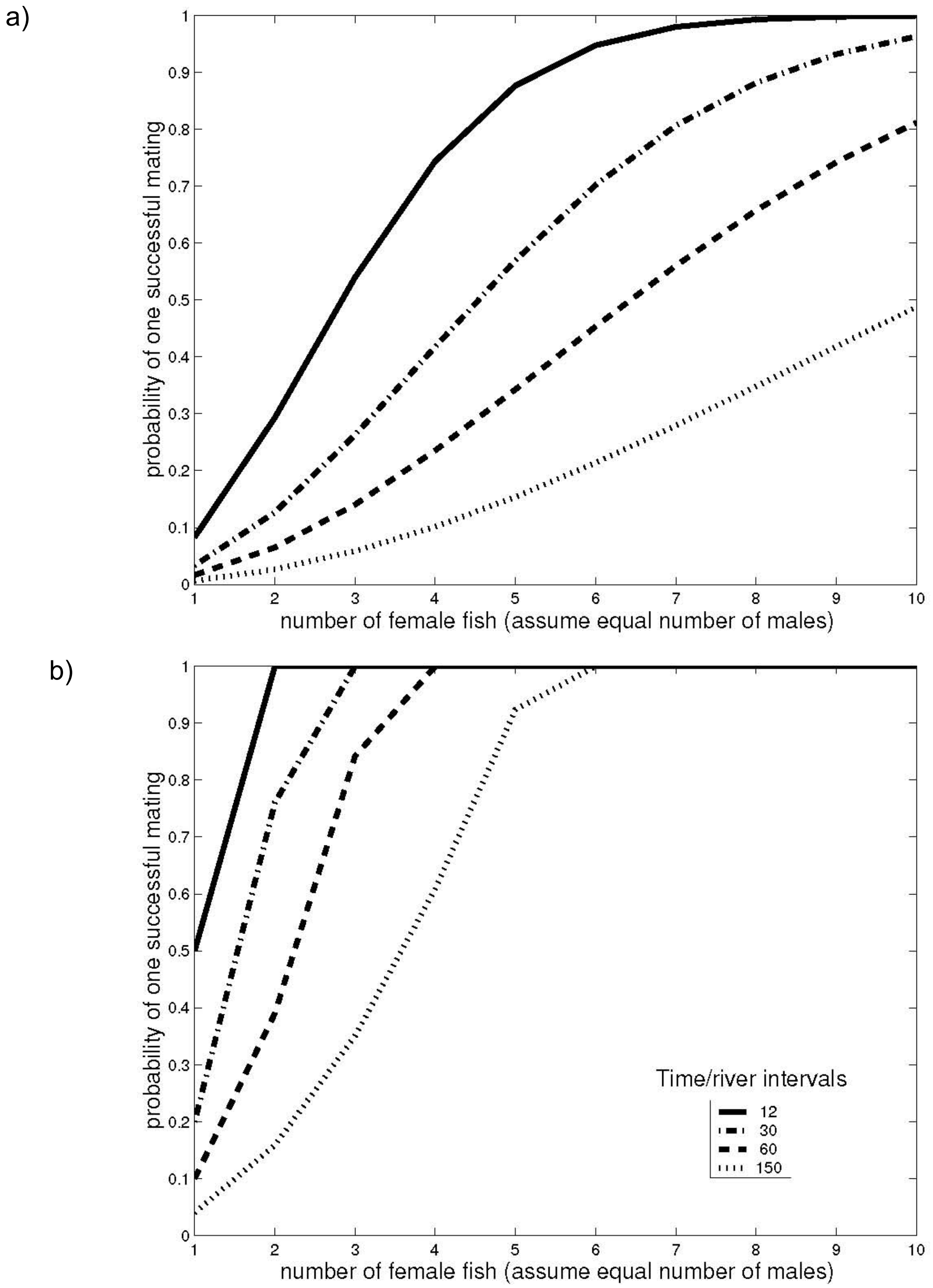

Figure 2-4: The probability of a male and female fish occupying the same river as a function of the number of female fish and the number of 2-week time/river intervals. We assume that there are equal numbers of male and female fish. Fish are can spawn either a) once only or b) in each of the 6 time intervals.

RISK OF ASIAN CARP ESTABLISHMENT IN THE GREAT LAKES. PART 2: PROBABILITY OF ESTABLISHMENT

Kim M.D. Cuddington, Warren J.S. Currie and Marten A. Koops

INTRODUCTION

In the event of Bighead (*Hypophthalmichthys nobilis*) or Silver (*Hypophthalmichthys molitrix*) carps arriving in the Great Lakes system, we need to establish estimates of the risk that such a release will result in an established carp population. This risk can be thought of as composed of two parts: the probability that carp will successfully spawn, and the probability that such spawning will result in positive population growth. In this report, we focus on the latter probability, that spawning carp establish a population in the Great Lakes.

We expect that any accidental releases would involve small numbers of fish. As a result, given the difficulty in finding mates, and environmental stochasticity, one may conclude that such releases are quite unlikely to result in positive population growth. We have previously demonstrated that the restriction of spawning to specific river systems may imply that Allee effects do not have a very large impact on population growth. In this contribution, we specifically test the effect of small initial population size on population growth of these species.

We note that some previous work has concluded that Asian carp species will be food-limited in the Great Lakes (Cooke and Hill 2010). However, these authors also demonstrated that carp will have positive growth in most high productivity sites in the system, and may have overestimated energetic costs. Consequently, we start from the position that food limitation will not be a serious obstacle for either species.

We describe a stage-structured model of the population growth of Asian carps, parameterize this model with literature data, and then use it to analyze the probability of population establishment under various scenarios. We find that establishment is quite likely for a wide range of scenarios, but may be quite sensitive to the age of first reproduction.

METHODS

Modelling the probability of population establishment in a given lake

We model population growth of carp species using a stage-structured population model with an annual timestep and pre-breeding census (Fig 3-1). In each year, adult fish in the lake distribute themselves among the various rivers and spawn, with a given probability related to environmental conditions and mate finding. We parameterized the model using literature data where available. There is considerable range in data, which produces overlapping parameter estimates for Bighead and Silver carp, and moreover, almost all studies are for large river systems (e.g., Missouri and Mississippi). As a result, at this time, we did not develop separate models for Bighead and Silver carp.

Deterministic factors

Life history

In the structured population model, the stage categories correspond to life history stages. We grouped eggs, larvae and juvenile fish into one class (*J*) that represents the portion of life history spent in the spawning river and associated wetlands. Fish in this class either die over the winter or survive and become part of the first subadult class at the beginning of the next growing season. At the beginning of the first subadult stage (*SA1*), fish move from the protected wetlands to the larger lake during the spring. Survival over the year is related to mean body size in each class. Fish that survive to subadult stage 2 enter the reproductively mature adult class at age 3. We used a division of two classes for subadults (*SA1* and *SA2*), and a single division for adults (*A*) because growth at smaller sizes affects survival more profoundly than at larger sizes.

We assume that fish reach sexual maturity at age 3, but note that Kolar et al. (2007) found that sexual maturity in Bighead Carp is dependent on climate and may be reached between ages 2 and 7, with males often maturing one year earlier than females. In North American rivers (e.g., Schrank and Guy 2002) an average age of sexual maturity for Bighead Carp may be age 3, although Nuevo et al (2004) do report mature males of age 2 in the middle Mississippi. Williamson and Garvey (2005) also found that Silver Carp in the middle Mississippi matured earlier (age 2) than in the species native range.

Therefore, if we do not include environmental stochasticity or the subdivision of the spawning adults and juveniles among separate rivers, we can describe the dynamics of a low density population of female fish in the spring immediately before spawning as the simple stage-structured model:

$$\begin{bmatrix} J_{t+1} \\ SA1_{t+1} \\ SA2_{t+1} \\ A_{t+!} \end{bmatrix} = \begin{bmatrix} 0 & 0 & 0 & \frac{F}{2}P_J \\ P_{SA1} & 0 & 0 & 0 \\ 0 & P_{SA2} & 0 & 0 \\ 0 & 0 & P_A & P_A \end{bmatrix} \begin{bmatrix} J_t \\ SA1_t \\ SA2_t \\ A_t \end{bmatrix}$$

where *F* is the mean number of eggs produced per female fish (divided by 2 since we assume a 1:1 sex ratio), P_J is the probability of an egg resulting in a live juvenile fish the next spring, P_{SA1} is the probability of a fish surviving its first year as a subadult in the open lake, P_{SA2} is the probability of a subadult surviving its next year to reach age 3 (sexual maturity), while P_A is the probability of an adult fish surviving from one year to the next. Mean values for these population parameters were taken from the literature.

Growth and survivorship

Carp have fast growth rates (Jennings 1988, Johal et al. 2001, Schrank and Guy 2002). Three-year-old Bighead Carp collected from the lower Missouri River in 1998-1999 averaged 550 mm in length, while 5-year-olds averaged 700 mm (Schrank and Guy 2002). Nuevo et al. (2004) found that three-year-old Bighead Carp in the Mississippi River ranged from 757 to 852 mm, and 5-year-old fish ranged from 807 to 909 mm. In the same study, back calculated lengths averaged 273 mm at age 1, 500 mm at age 2, 672 mm at age 3, 830 mm at age 4, 813 mm at age 5 and 921 mm at age 6 . Also in the middle Mississippi river, back-calculated lengths for Silver Carp at age 1 averaged 317.7mm, age 2: 530.9 mm, age 3: 649.8 mm, age 4: 704.1 mm and age 5: 723.3 mm (Williamson and Garvey 2005). For Bighead Carp at least, these sizes and growth rates are comparable to the native range, but higher than reported in other temperate areas (see references in Nuevo et al 2004).

We assume that sizes in the Great Lakes will be on the lower end of these ranges, and the use of low values will give us a conservative estimate of annual survivorship. We use an average length for the first subadult stage at 250 mm (age 1), the second stage at 500 mm (age 2), and adults (which groups all sexually mature fish 3 years and older) at 700 mm. We use a value of 20 mm to represent the average length of the juvenile stage (age 0). The average weight values were calculated using published length-weight relationships.

Values for the slope and intercept of the relationship of $\log_{10}$(weight)= slope$\log_{10}$(length)− intercept vary with location, species and sex. Schrank and Guy (2002) reported the relationship between weight and length was highly similar between male and female Bighead Carp in the lower Missouri River (Table 3-2). For Bighead Carp in the middle Mississippi, Nuevo et al. (2004) used two different relationships for 1999 and 1998. Wanner and Klumb (2009) report that length-weight relationships for both Bighead and Silver carp varied between the upper and lower Missouri. Williamson and Garvey (2005) give length-weight relationships for Silver Carp that varied slightly between males (Table 3-2).

We used a length-weight relationship near the median of the literature values of: $\log_{10}$(weight)= 3.12·$\log_{10}$(length) − 5.32, to produce the length/weight classes of juveniles: 20 mm/0.05 g, subadults of age 1: 250 mm/145 g, subadults age 2: 500 mm/1260 g, adults 700 mm/3600 g. Annual survivorship, P_X , of the different stages was assumed to be related to body size and was estimated using Lorenzen's (1996) relationships between body weight and natural mortality for juvenile $\mathrm{P_J} = 1 - (1 - \mathrm{e})^{2.7\mathrm{W}^{-.315}}$ and $\mathrm{P_X} = 1 - (1 - \mathrm{e})^{3.3\mathrm{W}^{-.261}}$ for adult and subadult fish, using the average weight values for each class.

Fecundity

The number of larval fish produced per mature female per year will be a function of the probability of spawning, and the number of eggs produced per female. We assume that sperm is not limiting for a mated pair. For example, Lohmeyer and Garvey (2009) found that reaches that produced relatively high densities of larvae contained juveniles from the same cohort, and suggest that year-class strength may depend more on adult production of larvae rather than survival to the juvenile stage.

Observations of the egg masses of both Silver and Bighead carp indicate that these species have very large potential reproductive output. Schrank and Guy (2002) report 226,213 to 769,964 eggs for Bighead Carp in the Missouri river. Garvey et al (2007) give means for Bighead Carp (118,485 eggs) with a wide range 4,792-1,938,333 eggs. In this same study, the authors report mean eggs for Silver Carp at 269,388 eggs in the successful year (2004) with a range of 26,650 to 3,683,150. In the middle Mississippi river, Silver Carp averaged 156,312 eggs per fish with a range of 57,283 to 328,538 eggs (Williamson and Garvey 2005). We take the lower end of this range and use 200,000 eggs as a conservative estimate of mean fecundity.

Positive population growth rates, sensitivities and elasticities

In the absence of environmental variation and division of the juveniles among different rivers, the model predicts a large positive population growth of λ =2.18 per year, once a stable stage distribution has been reached. The dependence of this prediction on the particular parameter values was determined by calculating sensitivity, S, of each matrix element, a_{ij} as:

$$S_{if} = \frac{\partial \lambda}{\partial a_{ij}} = \frac{v_i w_j}{\sum_{i=1}^{st} v_i w_i}$$

where *st* is the number of stages in the matrix, w_j is the *jth* element of the dominant right eigenvector, and v_i is the *ith* element of the dominant left eigenvector, and λ is the dominant eigenvalue. We then estimated the sensitivity for each individual parameter, r_k using the chain rule (Caswell 2001). The effects of proportional changes in the parameter values, or the elasticity, *E*, was then determined by the equation:

$$E_{r_K} = S_{r_K} \frac{r_k}{\lambda}$$

Population growth rate was most sensitive to juvenile survivorship, followed by survivorship as 1 year old subadults (Table 3-1). Elasticity analysis suggests that the sensitivity to juvenile survivorship is primarily due to the small magnitude of this parameter value. When proportional changes are examined, adult survivorship has the largest impact on the population growth rate. However, since adult survivorship is already relatively large, it is likely that in natural populations, growth, and consequently probability of successful invasion, is controlled primarily by juvenile survivorship.

In addition, predicted population growth rate will be sensitive to the other components of model structure. We expect that age at first reproduction will have a large impact on projected rates of increase. We formulated a version of the model with two additional subadult stages, so that sexual maturity was reached at age 5 rather than age 3. We assume that delayed age at first reproduction is associated with slower growth rates so that life history stages were parameterized with the following average size classes: *J*= 20 mm, *SA1*= 200 mm, *SA2*= 300 mm, *SA3*=400 mm, *SA4*=500 mm, *A*=700 mm. In this case, the annual population growth rate is slower, but still positive at λ =1.36. This growth rate has similar sensitivities and elasticities as the model with the younger age at first reproduction.

Stochastic factors

Small population size: Number of spawners and multiple spawning rivers

When population size is small, females may have difficulty in finding mates, especially since spawning partners could be divided over multiple rivers. We take the most strict assumption, where males and females form mated pairs. For two fixed groups of approximately equal size, i.e., a given number of male and female fish in a 50:50 sex ratio, and equivalent joint distributions over the number of rivers, one cannot expect to obtain the maximum number of mated pairs (McKinlay 1974). For example, the expected number of matches is less than 50% of the maximum obtainable if the number of matching categories exceeds the smaller sample size.

The exact solution for the number of males and females in each spawning river will depend on the population size for each sex and on the joint probability distribution of the fish across the suitable spawning locations and times. Taking the simplest case of one spawning event per season, we can approximate the expected number of mated male-female pairs in each river. We assume there are *r* rivers, and that male and female fish are found in the vicinity of each river with equal probability, so that the probability of a female fish being found in a given spawning river is p_i, where $p_i = 1/r$ *for* $i=1, 2, \ldots, r$. We also suppose that the number of males and females are equal such that Males = Females = *n*. In this case, the expected number of mated pairs in each river E(M$_i$), is given as: $E(M_i) = n - \sqrt{n(r-1)/\pi}\,/\,r$ (see derivation and more general cases in Walter 1980). So, for 50 male and 50 female fish distributed across 2 spawning rivers, summing over i, we expect 46 mated pairs, whereas for 20 possible spawning rivers, we expect only 33 (also see Fig 3-2).

This calculation assumes that all fish will be matched with a given spawning river. That is we assume that fish have no failure rate in locating a spawning river. If we instead assume that fish do not actively seek out rivers, and perhaps are only triggered to spawn if they happen to be close to a suitable river when optimum conditions occur, or that the spawning cues are imperfect and can lead to the selection of an unsuitable river, then the number of mated pairs will be much lower. One simple way to approach this is multiply our total number fish by a given probability of encountering a spawning river during the correct environmental conditions. If we take a low but not restrictive value of 20% of the population meeting this criteria, then there is a corresponding reduction in the predicted number of spawners (Fig 3-2).

For each timestep in the population model, we calculated the expected number of spawners per river as the integer value of the mean expectation. We also took the number of individuals in each stage as the integer value of the predicted number. Therefore, the total number of juveniles produced in a given year would be the summation over the number produced in each river as:

$$J_{t+1} = \sum_{i=1}^{r} \operatorname{int}\left(M_i P_J \frac{F}{2} \right)$$

If this number was less than one pair per river, the presence of a spawning pair was determined by a drawing a random number from a uniform distribution between 0 and 1 and scoring a presence of a spawning pair if the random number was between zero and the expectation.

Environmental stochasticity: Probability of spawning and survivorship

Spawning of Asian carp occurs in large rivers (Jennings 1988; Costa-Pierce 1992; Kolar et al. 2005). In the early to late spring, as water level rises, fish move upstream to spawn (Verigin et al., 1978; Pflieger, 1997). However, over a season, there may be several times environmental conditions trigger spawning. Conditions of high flow and warm water are most often correlated with spawning events in both species (Verigin et al. 1978, Pflieger 1997), and low flow conditions have been observed to correspond with year class failures (DeGrandchamp et al. 2007 for the Illinois river, and references therein). In the native range, in the Pearl river, from 2006-2008 the abundance of larval fish for both Bighead and Silver carp was significantly and positively related to discharge (Tan et al. 2010). However, in the Illinois river DeGrandchamp et al. (2007) observed larvae over several months in a year where flow velocities only exceeded 0.7 m/s for one week, and these authors speculate that high river stage may augment larval survival, but that higher levels are not required for successful spawning. In agreement with this, both Lohmeyer and Garvey (2009) and Schrank et al. (2001) report that larval production coincided with quite small increases in discharge (about 100 m^3/s) after water temperatures reached a suitable range (18-30ºC Nico et al. 2005, Jennings 1988, Schrank et al. 2001).

We assume that there are minimum conditions required for spawning which may not be met in a given year. However, because multiple partial spawning events per individual are possible (Pflieger 1997, Jennings 1988, 2002), and because the conditions required may actually be quite minimal, we also assume that spawning failure in a given year would be a relatively rare event for any of the Great Lake's rivers. Therefore, we simulated environmental variability for each river using a random series of probabilities drawn from a uniform distribution, and standardized to have a given variance and mean of 0.5. We examined two scenarios: low environmental variance (σ =0.2) and high environmental variance (σ =0.8). Spawning only took place when the probability for that year, e_t was greater than 0.05.

We simultaneously examined the effect of environmental stochasticity on the two most sensitive population parameters, juvenile (*J*) and subadult stage 1 (*SA1*) survivorship. We assume that the same environmental factors that might affect spawning (e.g., low flow conditions) would affect juvenile survivorship, and the subadult survivorship (where we assume that subadults are most vulnerable when making the transition from the river wetland system to the lake). At every timestep, the survival of juvenile fish and subadult fish of age 1 was related to the random probability describing environmental stochasticity in a given river by multiplying the survivorship P_J or P_{SA1} by e_t.

RESULTS

Population establishment probabilities

To determine the probability of Asian carps successfully invading one of the Great Lakes, we examined three scenarios of accidental introduction: a single release of a number of adults, a single release of subadults of age 1, and a leaky barrier where a number of subadults of age 1 enter the lake each year. We defined a successful invasion as equalling or exceeding a population size of 1000 female adults in any given year over a 20 year timeframe.

We considered various scenarios: low environmental variance (σ =0.2) and high environmental variance (σ =0.8) that affected spawning, juvenile (*J*) and subadult (*SA1* only) survivorship as previously described, and either 1, 5 or 10 spawning rivers. We explored the outcome for scenarios over a range of introduced fish population sizes. We examined the probability of successful invasion by calculating the number of successful populations in 100 simulations for each scenario.

We find that for reproduction at age 3 and fish that actively locate rivers with suitable spawning conditions, the establishment of a large breeding population is quite likely even for a relatively small number of introduced fish (Fig 3-3). When environmental variation is low, dividing reproductively active fish among many spawning rivers decreases the probability of establishment in a 20 year time frame with a small initial number of fish. However, when a threshold number of introduced female fish is met (10 fish for 10 spawning rivers), probability increases abruptly to nearly 100%. The number of fish required is higher and the increase in establishment probability is lower for a single introduction of subadult fish than for a single introduction of adult fish or a continual leak of subadult fish.

For large environmental variance, the threshold number of fish required for positive establishment probability remains the same, but the increase in this probability with an increase in the initial or annual number of fish is much slower. In addition, for environmental variance that is not correlated between rivers, establishment probability increases with the number of spawning locations, after the threshold number of fish is exceeded. Presumably the multiple spawning locations buffer the population against the effects of bad years in a single river.

If we instead assume that fish cannot actively locate rivers with suitable spawning conditions, or cues for identifying river suitability are imperfect, then we find that establishment is quite unlikely when potential spawners are distributed among a large number of rivers. Establishment takes somewhat longer, but is very likely at both high and low environmental variance (close to 100%) when there are very few suitable rivers (Fig 3-4a,b).

When we assume that sexual maturity occurs at age 5, instead of age 3, we find that a much longer timeline is required for establishment. Populations with small initial densities fail to establish after 100 hundred years, and those with larger sizes take over 50 years. When this timeline is so long, stochastic events outside the model framework are quite likely to cause extinction before establishment (Fig 3-4 c,d).

CONCLUSION

The models suggest that even a single event where a few individuals are accidentally introduced in one of the Great Lakes has, under some conditions, a significant probability of establishing a population of Asian carps. A stage-structured population model parameterized with literature data suggests that positive population growth is the expectation, and that this growth is most sensitive to juvenile survivorship and age at first reproduction.

Establishment of a Great Lakes population was most likely when either a number of adults were released on one occasion, or when a number of subadults breached a containment barrier annually. We note that, although it was not examined, the most dangerous scenario would be the case for a number of adult fish were introduced annually. The number of adult fish in a single release required for close to 100% establishment probability in 20 years depended on the exact scenario, but was usually less than 10.

One of the key factors determining the probability of establishment is the number of suitable spawning rivers, and the ability of fish to locate and linger near these rivers. If fish have the ability to locate suitable rivers when spawning conditions are good, the probability of establishment is quite large, even for small population sizes and a large number of rivers (Fig 3-3). If however, fish only accidentally encounter rivers during conditions of warm waters and relatively high flow, then, for a large number of suitable rivers and a small number of released fish, it is unlikely establishment will occur. In addition, establishment over a smaller number of rivers will take slightly longer in this case (Fig 3-4a,b).

The most sensitive stage to management or control actions is the juvenile stage. Relatively small decreases in juvenile survival will have relatively large effects on the viability and establishment of an Asian carp population. Finally, the largest impact on establishment probability was age at first reproduction. If carp have a prolonged and slow period of growth as subadults, then it is very unlikely that population establishment will occur, at least within a short timeframe. The slower population growth rate associated with this life history means that the population will spend a large amount of time at low density, and are more likely to suffer stochastic extinction events.

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Table 3-1: Parameters and values used in the stage-structured population model of Asian carps in the Great Lakes.

Parameter	Value	Sensitivity	Elasticity	Description
F	200,000	0.00	0.22	Mean number of eggs per adult female
P_J	0.0012	413.48	0.22	Survivorship of juvenile fish (mean body size 20 mm)
P_{SA1}	0.3242	1.51	0.22	Survivorship of 1-year-old subadults (250 mm)
P_{SA2}	0.5993	0.82	0.22	Survivorship of 2-year-old subadults (500 mm)
P_A	0.6776	1.05	0.33	Survivorship of adults (700 mm)

Table 3-2: Slopes and intercepts of reported length-weight relationships for Bighead and Silver carp

($\log_{10}$(weight)= slope $*$ $\log_{10}$(length) − intercept)

Species	Slope	Intercept	Description	Reference
Bighead	3.15	-5.42	Males, lower Missouri	Schrank and Guy (2002)
	3.13	-5.40	Females, lower Missouri	Schrank and Guy (2002)
	3.33	-5.96	1998, middle Mississippi	Nuevo et al. (2004)
	2.97	-4.82	1999, middle Mississippi	Nuevo et al. (2004)
	2.96	-4.86	Gavins point, Missouri	Wanner and Klumb (2009)
	2.75	-4.30	Interior Highlands, Missouri	Wanner and Klumb (2009)
Silver	3.11	-5.29	males	Williamson and Garvey (2005)
	3.10	-5.25	females	Williamson and Garvey (2005)
	3.70	-6.92	Gavins point, Missouri	Wanner and Klumb (2009)
	3.13	-5.35	Interior Highlands, Missouri	Wanner and Klumb (2009)

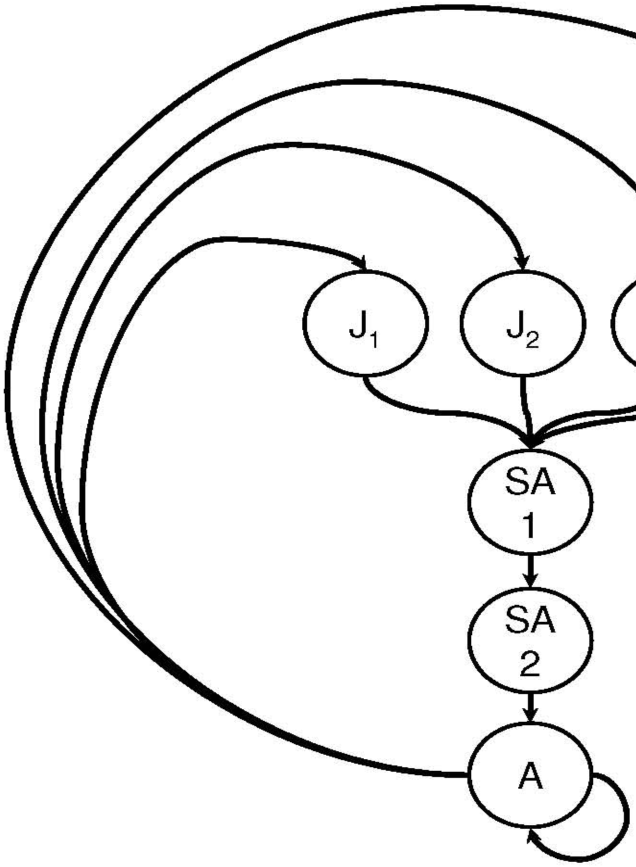
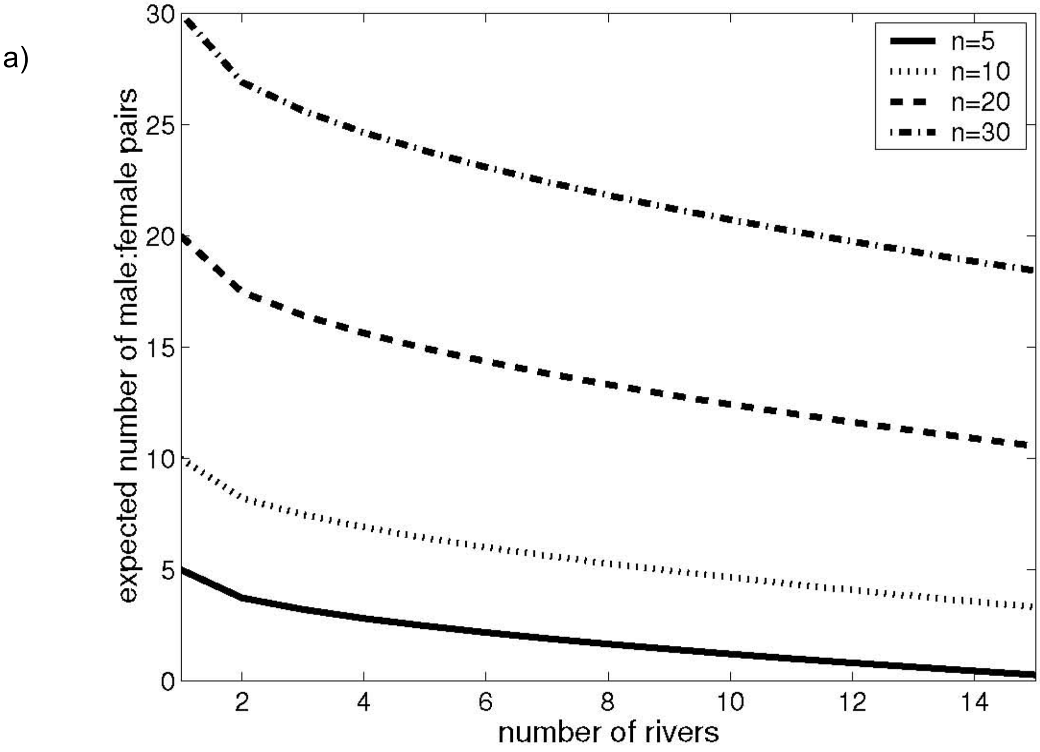


Figure 3-1: Schematic of the stage-structured population growth model of Asian carps. Adult fish (A), spawn over a number of suitable rivers, producing juvenile fish (J) in each of these watersheds. Juveniles produce subadults in the lake basin with some survivorship probability, and similarly subadults in class 1 given rise to subadults in class 2, and subsequently, reproducing adults.

a)



b)

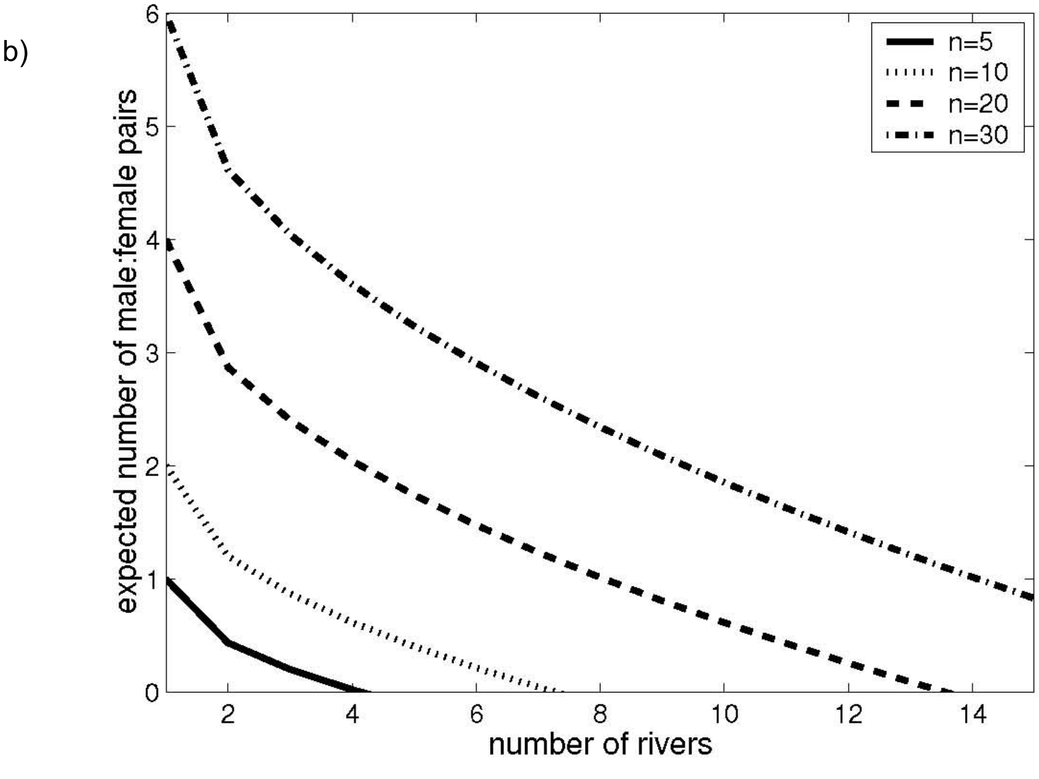


Figure 3-2: The predicted number of mated pairs as a function of population size, n, where there are an equal number of male and female fish, and the number of suitable spawning rivers. Fish are either a) always able to locate a suitable spawning location or b) quite unlikely (20% probability) to locate a spawning location.

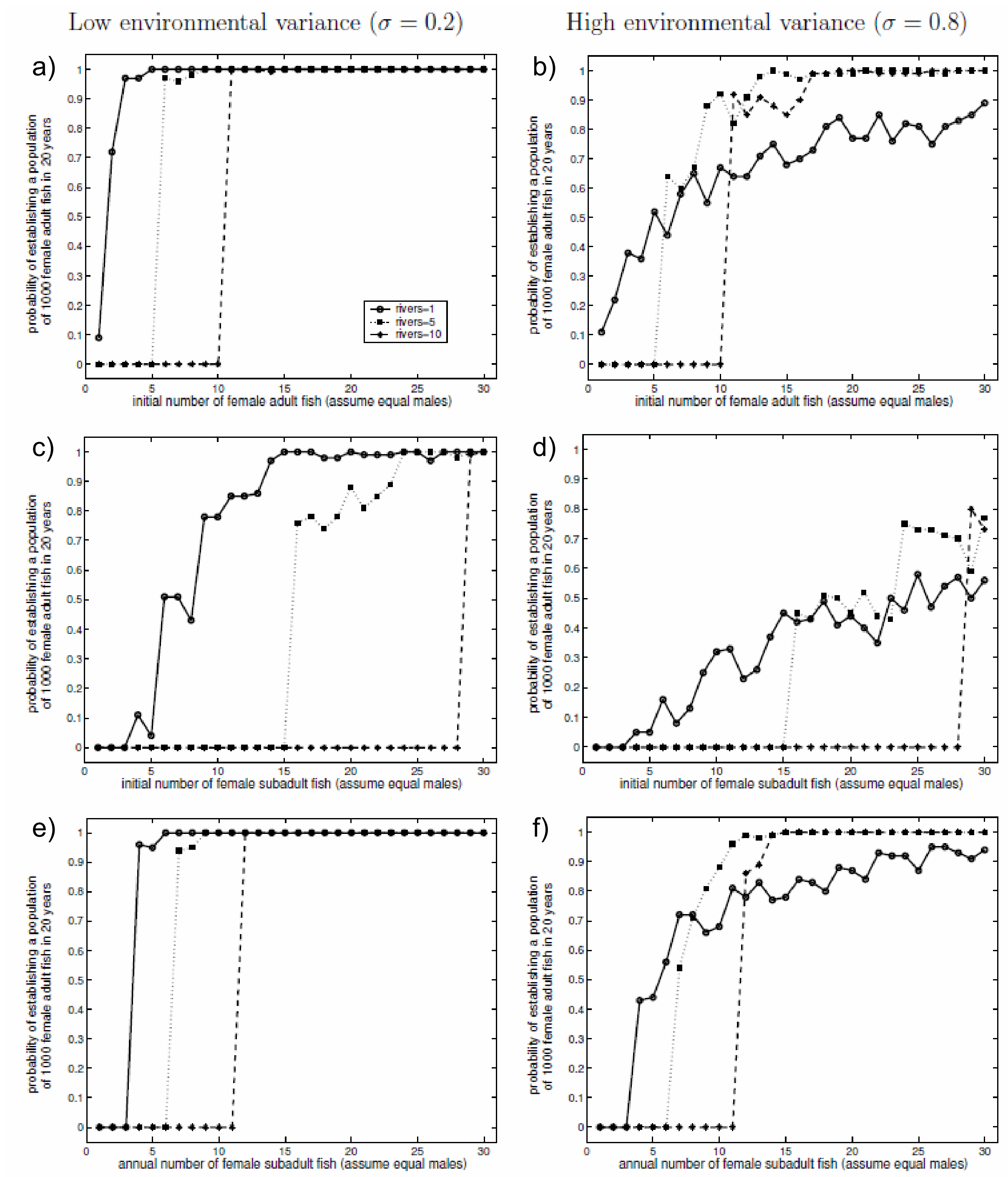


Figure 3-3: Probability of establishing a population as a function of initial or annual introduction size and stage, the number of spawning rivers, and the magnitude of environmental variance for the stage-structured population model with sexual maturity at age 3 and fish always able to locate spawning rivers. The three introduction scenarios are a & b) an initial number of adult (A) fish, c & d) an initial number of subadult fish of class 1 (SA1), or e & f) an annual number of subadult fish of class 1

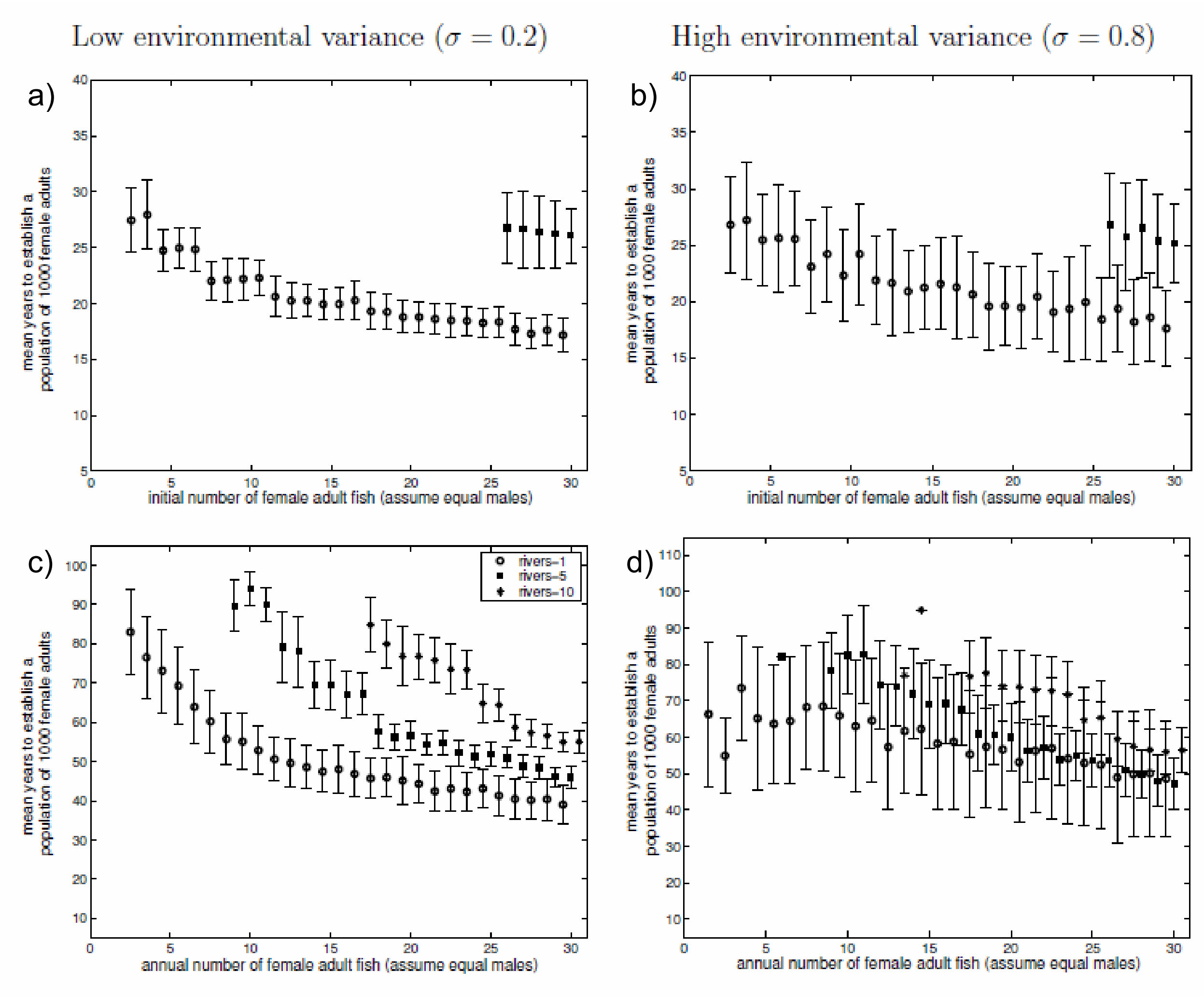


Figure 3-4: Mean time to establish a population as a function of initial number of adult fish, the number of spawning rivers, and the magnitude of environmental variance. For the cases where a & b) sexual maturity occurs at age 3 and fish have a small probability (20%) of locating a spawning river, and c & d) sexual maturity occurs at age 5, and fish can always locate a spawning river.

PRELIMINARY ASSESSMENT OF THE TROPHIC CONSEQUENCES OF ASIAN CARP ESTABLISHMENT IN OFFSHORE LAKE ONTARIO

Thomas J. Stewart, Hongyan Zhang and Warren J.S. Currie

INTRODUCTION

Silver Carp (*Hypophthalmichthys molitrix*) and Bighead Carp (*Hypophthalmichthys nobilis*), hereafter referred to as Asian carp, are encroaching on the Great Lakes basin, and it appears increasingly probable that they will be introduced to Great Lakes waters. Other studies are investigating the risk of arrival, survival, establishment and spread (this volume) while here we focus on the potential ecological impact of an established, self-sustaining post-juvenile population of Asian carp in offshore Lake Ontario.

Alewife (*Alosa pseudoharengus*) are the dominant prey fish in Lake Ontario (Owens et al. 2003, Stewart and Sprules 2010) and their response to ecological change has the potential to change the structure and function of the Lake Ontario food web. Alewife exert high predatory demand on lower trophic level production (Rand et al. 1995, Stewart and Sprules 2010), their planktivory influences the size and species composition of the zooplankton community (O'Gorman et al. 1991; Johannsson et al. 1991; Johannsson 2003), and they are the preferred prey of the salmon and trout predators (Brandt 1986; Rand and Stewart 1998; Lantry 2001). In both, Lakes Michigan and Huron, the collapse of Alewife has been associated with precipitous declines in salmon and trout recreational fishing (Hansen and Holey 2002; Riley et al. 2008). Indirect, food web mediated, trophic impacts of Asian carp on Alewife would be associated with unpredictable consequences to food web dynamics and increased risk of decline in recreational fishing, especially the publically-favoured Chinook Salmon (*Oncorhynchus tshawytscha*).

Simulating the establishment of a new species into an existing trophic model of a food web is difficult even if the ecology of the new species is well known. Even more challenging for this simulation is that the ecology of Asian carp, especially their diets, feeding behaviour, and bioenergetics are only poorly understood. While Silver Carp are considered primarily phytoplanktivorous and Bighead Carp zooplanktivorous, they are each highly flexible in their diet (Kolar et al. 2005). Since both species of Asian carps are important aquaculture fishes worldwide, studies investigating feeding have been undertaken in aquaria (Cooke et al. 2009, Dong and Li 1994, Rahmatullah and Beveridge 1993, Smith 1989), rivers (Nuevo et al. 2004, Pongruktham et al. 2010, Sampson et al. 2009, Schrank et al. 2003, Williamson and Garvey 2005), ponds (Berday et al. 2005, Cremer and Smitherman 1980, Ma et al. 2010, Opuszynski et al. 1991), lakes and reservoirs (An et al. 2010, Domaizon and Devaux 1999, Fukushima et al. 1999, Ke et al. 2007, Lu et al. 2002, Radke and Kahl 2002, Spataru and Gophen 1985, Voros et al. 1997, Xie and Yang 2000, Zhou et al. 2011, Zhou et al. 2009) indicating an extremely wide range of feeding habits. Both species of Asian carps will consume zooplankton, phytoplankton (including cyanobacteria) and detritus, with the sizes of particles taken determined primarily by gill morphology (Kolar et al. 2005). Silver Carp have spongiform gills that allow them to remove particles down to bacterial sizes (Hampl et al. 1983), while Bighead Carp can efficiently consume only larger forms of phytoplankton. Greater volumes of water are filtered if larger particles are selected (Smith 1989) so when available, both carps tend to preferentially select zooplankton (Dong and Li 1994, Lu et al. 2002, Zhou et al. 2009) and phytoplankton cell size tends to decrease when fish are present (An et al. 2010, Fukushima et al. 1999, Lu et al. 2002, Ma et al. 2010, Radke and Kahl 2002, Spataru and Gophen 1985). Extremely few studies have investigated feeding by carps on protozoa but tend to indicate that while they are not highly preferred, the carps can change the composition of the microbial food web (Fukushima et al. 1999, Sun et al. 2004, Zhou et al. 2011). No studies have determined Asian carp feeding rates when protozoans are a dominant food source as occurs in many of the Great Lakes (Munawar and Lynn 2002).

In this paper, establishment of Asian carp in offshore Lake Ontario is simulated by deriving empirically-based replicate mass balanced descriptions of the offshore food web during 2001-2005 (Stewart and Sprules 2010), that include Asian carp. We simulate a range of Asian carp biomasses and vary diets to represent a breadth of potential Asian carp feeding modes. Novel initial simulated food web structures, with fixed levels of lower trophic level productivity, and varied scenarios describing Asian carp biomass and diets are specified. Constrained optimization techniques (Kavanagh et al. 2004) are applied to attempt the rebalance the food webs. The results of replicated mass balanced food webs are used to evaluate 1) is it trophically possible to sustain Asian carp in the offshore food web of Lake Ontario and at what levels of biomass, 2) what are the potential trophic consequences to the biomass of Alewife and Chinook Salmon and 3) what is the relationship between levels of Asian carp sustainable biomass, feeding modes and the level of predation pressure on Alewife?

METHODS

The food webs are described using Ecopath software (Christensen and Walters 2004) using units of carbon (g C·m^{-2}). Mass balance for each species-group can be described as,

$$B_i \cdot (P/B)_i - \sum_{j=1}^{n} B_j \cdot (Q/B)_j \cdot DC_{ji} - B_i \cdot (P/B)_i \cdot (1 - EE_i) = 0$$

where Bi is the biomass of (i), (P/B)i is the production to biomass ratio, $(Q/B)_j$ is the consumption to biomass ratio, DC_{ij} is the fraction of prey (i) in the average diet of predator (j), and EE_i is the ecotrophic efficiency (proportion of a species-group production that is lost to predation). A system of the above linear equations for each species-group is set-up and B and DC values are iteratively varied and the equations solved to estimate the EE value of each biomass-group, with the condition that each EE vale must be less than 1. A second equation balances the flow within each group such that,

$$Q_i = P_i + R_i + GS_i \cdot Q_i$$

where, for the biomass of (i), Qi is consumption, Ri is respiration, and GSi is the proportion of unassimilated food.

Replicated mass balanced solutions describing the offshore Lake Ontario food web during 2001-2005 (Stewart and Sprules 2010) were used as a basis from which to develop new food web structures that simulated Asian carp establishment. Only changes from the original species groups biomasses and diets (Stewart and Sprules 2010), and development of Asian carp biomass, diets, and bioenergetic ratios are described here.

Low Dreissenid Model

The low dreissenid model was based on the average of the 25 replicate mass balanced models determined for 2001-2005 from Stewart and Sprules (2010). This averaged model was not completely balanced, even though all 25 replicates were individually balanced, and balancing required a 10% increase in the biomass of copepods and a 20% increase in the biomass of Mysids. This adjusted model is designated as the low dreissenid model (LDH)

Recalculation of dreissenid mussel biomass

Stewart and Sprules (2010) used relative changes in dreissenid densities from 1990 to 2003 to estimate the biomass of dreissenids in 2003, and applied these densities for the 2001-2005 time period. For this study, lake wide depth strata weighted dreissenid densities were recalculated based on new data (Dr. Jim Watkins, Cornell University, unpublished data). Dreissenid densities were converted to biomass based on a relationship between density and shell-free dry weight (SFDW) from the graphical data reported in Dermott and Geminiuc (2003). The equation was estimated as

$$SFDW\ (g\ m^{-2}) = Density\ (\#\ m^{-2}) \times 0.0107\ (R^2 = 0.52, P=0.002)$$

The updated mean dreissenid biomass was higher than applied in the LDM, and was used to develop a high dreissenid biomass model (HDM).

Following the methods described in Stewart and Sprules (2010), the food web structure, with updated estimates of dreissenid biomass, was balanced using the Ecopath (version 5.0) autobalance routine (Kavanagh et al. 2004). The procedure randomly selects the initial values of biomass (B) and DC (the fraction of each prey in the average diet of predator) for each-species group from a pre-defined range of values specified by confidence interval widths (CIW). The B and DC values were assumed to have a uniform distribution. After the initial values are selected, a second perturbation step randomly varies species-group estimates of B and prey DC values until a solution with an EE < 1 for all species groups is obtained. The cost function decision logic provided with the software that simultaneously minimizes the maximum EE values and the sum of all EE values > 1 was chosen for the second perturbation step (Kavanagh et al. 2004, Link et al. 2006) to optimize the search. The CIW of species-group B and DC estimates and balancing procedures were the same as described in Stewart and Sprules (2010) and applied to derive 25 replicate mass balance solutions. These 25 replicates were averaged to describe the HDM, and this average-based model required no further adjustments to achieve mass balance.

Asian carp bioenergetic ratios and diets

For each species of Asian carp the consumption to biomass ratio (Q/B) was calculated using three different methods (Chen et al. 1989, Palomares & Pauly 1998, Cooke and Hill 2010) and then averaged. Chen et al. (1989) developed relationships between daily ration (% of body weight) of Asian carp and water temperature. These equations were applied to average monthly Lake Ontario surface water temperature (see Stewart and Bowlby 2008) and daily values summed to determine an annual ration or Q/B ratio. Palolares and Pauly (1998) developed a model of Q/B as a function of fish asymptotic weight, mean annual water temperature, the aspect ratio of the caudal fin, and food type. Using this formula, a Q/B for diets of plankton only and plankton and detritus were calculated. The model of Cooke and Hill (2010) was applied, assuming p value is 1 and average individual carp biomass is 2400g, to calculated daily food consumption and then summed up to annual food consumption. Q/B was calculated by dividing the annual food consumption by 2400g.

Production to biomass ratio (P/B) was assumed equal to total natural mortality and was calculated based on Pauly's (1980) empirical relationship, which links natural mortality (M), two parameters of the von Bertalanffy Growth Function (VBGF) and mean environmental temperature:

$$M = K^{0.65} \bullet L_{\infty}^{0.279} \bullet T^{0.463}$$

Parameters of VBGF for Asian carp were from Yuan and Shi (1993). Yuan and Shi conducted their study in a reservoir (centered at 41°53’N, 124°12’E) with similar latitude of Lake Erie and Lake Ontario. An average Lake Ontario temperature of 8.85 ºC was applied.

Chen (1982) reported the seasonal (spring, summer, fall) diet components of Asian carp caught from Donghu Lake, Hubei, China. We took a simple average of the seasonal values to derive annual diet proportions for detritus, bacteria, phytoplankton, and zooplankton. For this simulation, we assumed Asian carp in offshore Lake Ontario would only consume particulate organic carbon (POC). Zooplankton species-group proportions were based on the relative production among the zooplankton species-groups in the base mass balanced models for Lake Ontario.

We also developed four other general Asian carp diets assuming a dominant diet (50% of the total diet) was either phytoplankton, zooplankton, or detritus and a diet that was evenly distributed among components (25 % of each of phytoplankton, zooplankton, microbes, and detritus). Partitioning among species-groups (microbes and zooplankton) was based on the relative production among the microbial and zooplankton species-groups in the base mass balanced models for Lake Ontario.

Simulating Asian Carp Establishment

For each diet description a new food web was described with initial Asian carp biomass of 0.1, 0.5, 1.0, and 1.5 g $C \cdot m^{-2}$. The lowest biomass is comparable in magnitude to the biomass of Chinook Salmon and all trout and salmon combined in offshore Lake Ontario while the final biomass would be comparable to the biomass of all prey-fish combined, which is mostly Alewife.

The Ecopath (version 5.0) autobalance routine was used to derive mass balance solutions to these initial food web descriptions. In this application, the CIW of the B and DC values for lower trophic level species-groups (lower than prey-fish) were set to zero, thereby fixing primary, microbial, and invertebrate production and diets. For fish other than Asian carp, the CIW was set at 80% for biomass and zero for DC values to allow for some variation in fish biomass to accommodate Asian carp. The CIW of Asian carp B was set at 50% to allow for mass balance solutions of intermediate Asian carp biomass from initial values, and the DC values were set at 10% to allow only slight deviation from the initial specified diets.

For each run of the autobalance routine a new initial B and DC values for all species groups was selected within a range of 50% of the confidence interval (CI). Starting with these initial values, unique to each run, values from within a range of 100% of the CI were randomly selected to attempt to achieve a balance. This was repeated up to 10,000 times or until a mass balance solution was obtained. If a mass balance solution was not obtained after 10,000 attempts the process was repeated. The EE values for all species-groups were also required to be less than or equal to 0.98.

For each initial biomass and diet scenario we attempted to derive 5 replicate mass balance solutions. It was assumed that a mass balanced solution did not exist within the variation specified if a solution could not be found after more than twenty attempts using the autobalance routine. To determine the potential trophic consequences of Asian carp establishment % changes from the base required to balance the model were calculated for the biomass and EE value (as a measure of predation) for Alewife and biomass of Chinook Salmon.

RESULTS

The LDM and HDM models differed primarily in their level of dreissenid mussel biomass primary production required to achieve mass balance (Table 4-1). The EE values were also higher for phytoplankton, bacteria, and rotifers for the HDM reflecting the higher consumptive demand on these groups by dreissenid mussels.

Calculation of Asian carp Q/B ratios ranged from a low of 6.21 to a high of 22.81 (Table 4-2). For this analysis we used the average value of 11.39. The P/B ratios were estimated to be 0.304 for Silver Carp and 0.352 for Bighead Carp so we applied and average value of 0.328.

The simulated diets for Asian carp represented a broad range of assumed feeding modes for Asian carp (Table 4-3). Species-group composition varied between the LDM and HDM, for the same category of diet, because of the application of relative difference in initial production (Table 4-1) to partition the microbial and zooplankton proportions among species-groups. Asian carp trophic levels were lowest (2.41-2.45) for the observed adjusted seasonal average diet of Silver Carp, and diets constructed based on either a phytoplankton dominated diet or a detritus dominated diet. The next highest trophic levels (2.61-2.63) were for the equally proportion diet, followed by diets dominated by the microbial loop (2.76-2.77). Highest trophic levels (2.77-2.88) were associated with the zooplankton dominated diet and the observed adjusted seasonal average diet of Bighead Carp.

It was not possible to achieve mass balance using the LDM for Asian carp initial biomasses of 1.0 or 1.5 (g C·m^{-2}) for any diet composition. Mass balance was achievable for lower Asian carp biomass of 0.1 (g C·m^{-2}) with no changes required to balance for most diets (Table 4-4). For the zooplankton dominated diet, balance required a drop in mean Alewife biomass of 19.6% and an increase in Alewife EE of 33.6 % (Table 4-4). For an initial carp biomass of 0.5 (g C·m^{-2}) using the LDM, changes were required to all biomasses to achieve mass balance for all diet compositions. Mass balance required a drop in mean Alewife biomass of 23.2 to 32.4 % depending on diet, with a tendency for a higher percent drop associated with higher trophic level diets (Table 4-4). Alewife EE values increased from 34.9 to 71.0 % with higher values associated with higher trophic level diets. Chinook Salmon biomass varied with mean changes from -1.5 % to 20.3 %.

For most of the simulated Asian carp biomasses and diets, using the HDM, it was possible to achieve mass balance without changing the biomass of any fish species (Table 4-5). In other words, there was enough surplus lower trophic level production to accommodate the addition of Asian carp. It was not possible to achieve mass balance with a simulated Bighead Carp diet and an Asian carp biomass of 1.5 (g C·m^{-2}). Mass balance required biomass changes for the zooplankton diet and higher levels of simulated Asian carp biomass (1.0 to 1.5 g C· m^{-2}). Mean Alewife biomass declined from 14.6 to 25.1 %, Alewife EE increased from 27.7 to 30.9 and Chinook Salmon biomass varied with an increase in the mean of 4.4 to 14.6%.

DISCUSSION

The results of these simulations must be interpreted with extreme caution. While the assumption required for building and balancing the initial food web models are scientifically sound, the simulation of Asian carp establishment require some simplifying assumptions that substantially deviate from the reality of an actual Asian carp establishment in Lake Ontario. The simulations are not dynamic and only explore consequences of simple variations in the supply and demand as a consequence of variation in the biomass of fish species and Asian carp diets. This ignores a vastly unpredictable and complicated set of interactions within and among species populations within a spatially complex medium and is thus far removed from a representation of a real Great Lakes food web. Trophic level biomass and production below fish was fixed as was the diets of everything other than Asian carp. Only post-juveniles Asian carp were simulated assuming no losses due to predation.

The differing derived food web states represented by the LDM and HDM reflect current uncertainty associated with effect of dreissenid mussel on the dynamics of Lake Ontario lower trophic level production, and a full exploration of this uncertainty is beyond the scope of this analysis. In the context of these simulations, the models represent a range of productivity states and degree of dreissenid mediation of lower trophic level dynamics. The LDM, is more typical of a low productivity state with only minor trophic flows through the dreissenid populations. Low productivity results from upstream (Lake Erie), nearshore mussel-mediated dynamics (Hecky et al. 2004), or some other unknown watershed effect (Stewart and Sprules 2010). The HDM model represents a higher productivity state with very high flows of lower trophic production through dreissenid mussels. The higher production required to sustain the high level of dreissenid biomass is inconsistent with the accepted trend to lower productivity state in offshore Lake Ontario (Holeck et al. 2008; Stewart and Sprules 2010). However, it could be associated with an unaccounted source of productivity, such as an increase in hypolimenetic production associated with increased water clarity. More investigation will be required to resolve whether the LDM or HDM best represent offshore Lake Ontario, but for this analysis, the two representations provide a useful contrast.

The food web representations are based on observations from Lake Ontario during 2001-2005. Up to that time, the epilimnetic crustacean zooplankton community had shown only modest changes, with declines in productivity but no change in species diversity despite invasion and expansion of predatory cladocerans (*Bythotrephes longimanus and Cercopagis pengoi*; Stewart et al. 2009). More recently, the Lake Ontario ecosystem experienced a significant shift in the zooplankton community structure with precipitous declines in cyclopoid copepods coincident with increasing abundance of the predatory cladocerans, and likely increases in hypolimnetic production associated with calanoid copepods (Lars Rudstam, Cornell University, personal communication). A more complete understanding of the potential risks of Asian carp invasion will require that more recent lower trophic level changes be assessed and encorporated into updated models of food web structure.

Despite these simplifying assumptions and qualifying remarks, some general insights regarding the trophic consequences of Asian carp establishment in Lake Ontario are possible. For many food webs, and most certainly for offshore Lake Ontario, not all the lower trophic level production is consumed. It is unclear how much unused production is available to Asian carp in Lake Ontario. The LDM suggest there is very little, while the HDM suggests that there is more. However, regardless of what representation is applied, the simulations suggest that Asian carp, over a broad range of assumed diet compositions, could exploit unused production and sustain biomasses comparable to existing Lake Ontario prey-fish populations. It is possible that this could occur without reducing the food supply to other trophic levels. This means that Asian carp could increase the total fish production in Lake Ontario and still maintain current fish community structure.

Lower sustainable biomasses of Asian carp are associated with the LDM. Also, as the biomass of Asian carp increases mass balance requires that Alewife biomass and production declines. The biomass of Chinook Salmon appears to be unaffected by the changes in Alewife biomass as the models suggest that there are sufficient remaining Alewife to meet the consumptive demand of Chinook Salmon. However, the EE value for Alewife increases, with higher ranges suggesting an almost doubling (> 90%; Table 4-4).

An increase in Alewife EE means an increase in predation pressure on Alewife. Predation pressure on Alewife has been, and remains, a fisheries management concern in Lake Ontario as it could result in a collapse of Alewife, especially if there is a weather related decline in Alewife recruitment (Jones et al. 1993; Rand and Stewart 1998; Stewart et al. 1999; Stewart and Sprules 2010). A collapse of Alewife would result in a collapse of the Chinook Salmon population and a severe decline in the associated recreational fishery. Also, after an Alewife collapse the food supply of Asian carp would likely increases as zooplankton are released from the predatory pressure from Alewife. If Asian carp were able to exploit these new resources, they may be able replace Alewife as the primary zooplanktivore, and permanently truncate the supply of lower trophic production to other top predators.

The results from the HDM model suggest that even higher biomasses of Asian carp could be sustained without adverse effects on other species-groups. However, an Asian carp diet dominated by zooplankton would adversely effect Alewife at higher levels of biomass. The higher Asian carp biomasses associated with the HDM model were achieved by exploiting the higher levels of lower trophic production required to support dreissenid mussels. This implies that Asian carp and dreissenid mussel may compete for the same lower trophic level food supply. Dreissenid mussel biomass was fixed in these simulations, but if it was allow to vary, even higher levels of Asian carp biomass might be sustainable if dreissenid biomass declined.

Simulations from both models suggest that moderate to high Asian carp biomass could be sustained without impact to the food resources of other trophic levels. This seems very unlikely and may be a consequence of the simplifying assumption of the analysis. Asian carp feed at the lowest trophic levels but it is not clear whether they will feed on mostly zooplankton, phytoplankton, or the currently high level of microbial production. They can potentially compete directly for food with protozoans, all zooplankton, dreissenid mussels and all prey-fish species. Lower trophic levels turnover rapidly and thus they are highly variable in space and time, interact in complex ways, and can easily be disrupted. Changes to lower trophic levels will impact higher trophic levels. The potential of even a moderately large biomass of Asian carp to disrupt the trophic flows among all trophic levels is high and the food web consequences are impossible to predict with any degree of confidence.

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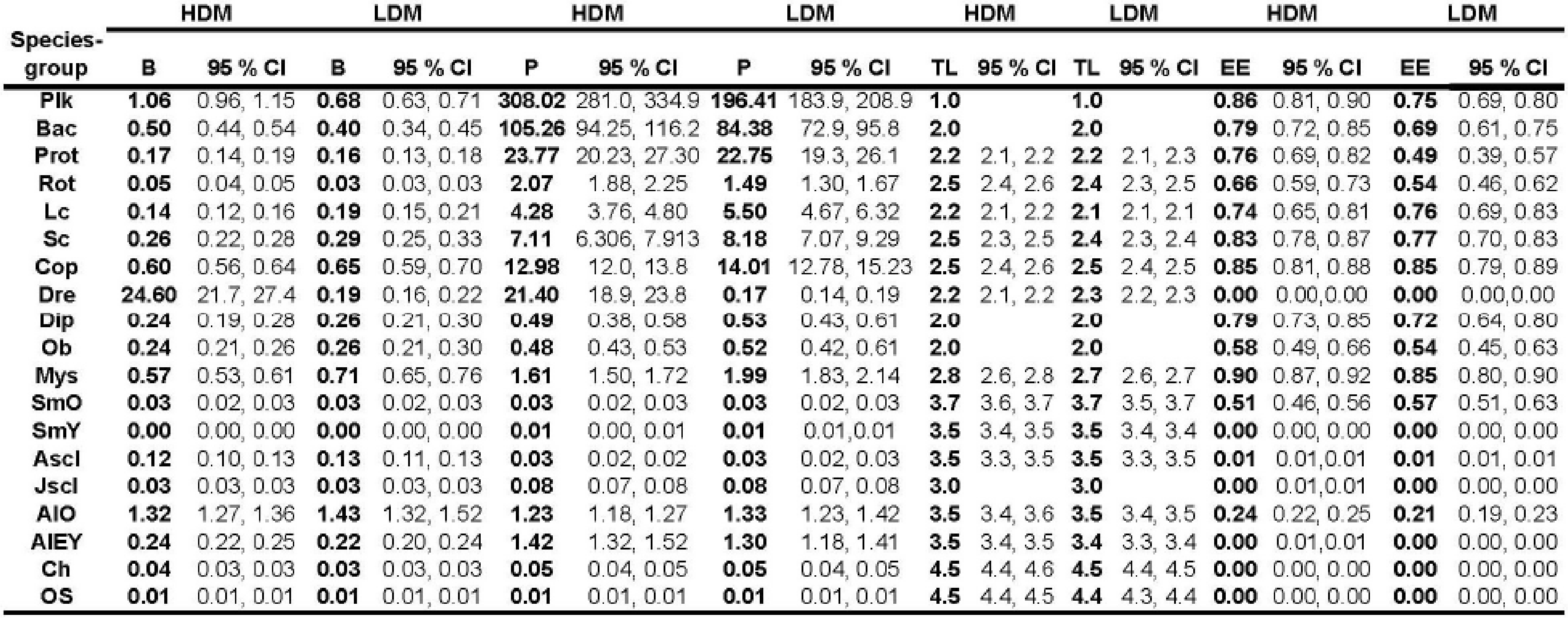
Table 4-1: Means and confidence intervals of biomass (B), production (P), trophic level (TL) and ecotrophic efficiency (EE) by species-group for the low dreissenid model (LDM) and high dreissenid model (HDM) determined from the 25 replicated mass-balance solutions without Asian carp representing offshore Lake Ontario during 2001-2005. (Plk=Phytoplankton, Bac=heterotrophic bacteria, Prot = Nanoflagellates and ciliates , Rot=Rotifers and veligers, Lc=Large cladocerans, Sc=Small cladocerans, Cop=Copepods, Dre=Dreissenid mussels, Dip=Diporeia, Ob=Other benthos, Mys=Mysis, SmO=smelt age 1 and older, SmY=Smelt YOY, Ascul=Adult sculpin, Jscul=juvenile sculpin, AlO=Late YOY and older Alewife, AlEY= Early YOY Alewife, Ch=Chinook salmon, OS=Other salmonines)

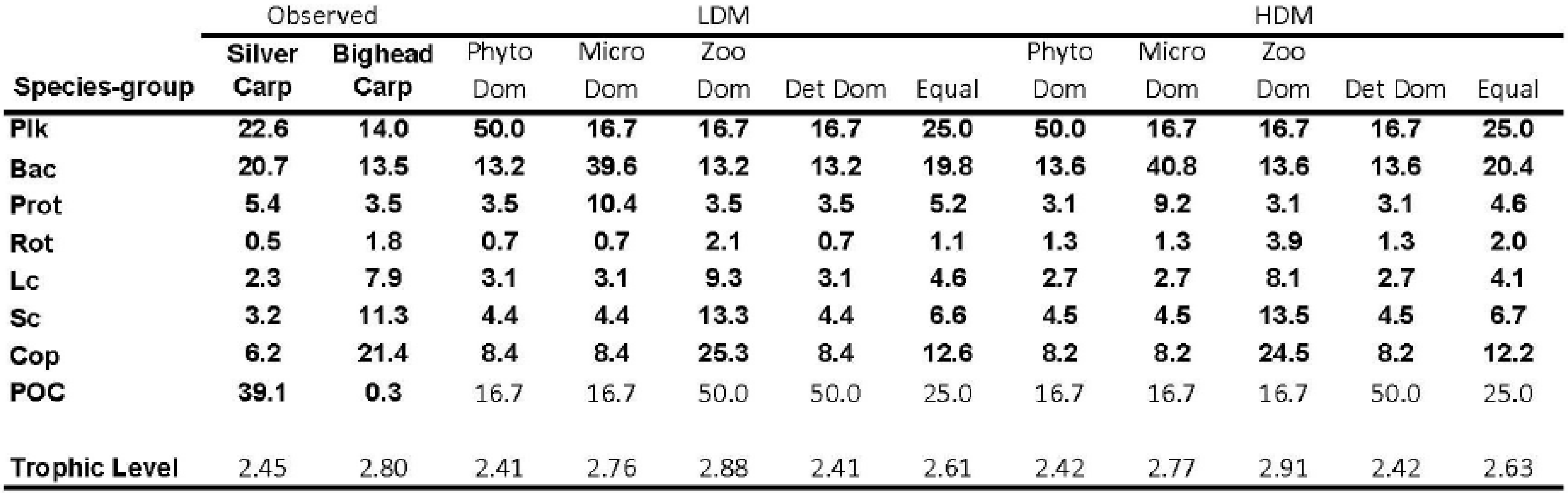


	HDM		LDM		HDM		LDM		HDM		LDM		HDM		LDM	
Species-group	B	95 % CI	B	95 % CI	P	95 % CI	P	95 % CI	TL	95 % CI	TL	95 % CI	EE	95 % CI	EE	95 % CI
Plk	1.06	0.96, 1.15	0.68	0.63, 0.71	308.02	281.0, 334.9	196.41	183.9, 208.9	1.0		1.0		0.86	0.81, 0.90	0.75	0.69, 0.80
Bac	0.50	0.44, 0.54	0.40	0.34, 0.45	105.26	94.25, 116.2	84.38	72.9, 95.8	2.0		2.0		0.79	0.72, 0.85	0.69	0.61, 0.75
Prot	0.17	0.14, 0.19	0.16	0.13, 0.18	23.77	20.23, 27.30	22.75	19.3, 26.1	2.2	2.1, 2.2	2.2	2.1, 2.3	0.76	0.69, 0.82	0.49	0.39, 0.57
Rot	0.05	0.04, 0.05	0.03	0.03, 0.03	2.07	1.88, 2.25	1.49	1.30, 1.67	2.5	2.4, 2.6	2.4	2.3, 2.5	0.66	0.59, 0.73	0.54	0.46, 0.62
Lc	0.14	0.12, 0.16	0.19	0.15, 0.21	4.28	3.76, 4.80	5.50	4.67, 6.32	2.2	2.1, 2.2	2.1	2.1, 2.1	0.74	0.65, 0.81	0.76	0.69, 0.83
Sc	0.26	0.22, 0.28	0.29	0.25, 0.33	7.11	6.306, 7.913	8.18	7.07, 9.29	2.5	2.3, 2.5	2.4	2.3, 2.4	0.83	0.78, 0.87	0.77	0.70, 0.83
Cop	0.60	0.56, 0.64	0.65	0.59, 0.70	12.98	12.0, 13.8	14.01	12.78, 15.23	2.5	2.4, 2.6	2.5	2.4, 2.5	0.85	0.81, 0.88	0.85	0.79, 0.89
Dre	24.60	21.7, 27.4	0.19	0.16, 0.22	21.40	18.9, 23.8	0.17	0.14, 0.19	2.2	2.1, 2.2	2.3	2.2, 2.3	0.00	0.00,0.00	0.00	0.00,0.00
Dip	0.24	0.19, 0.28	0.26	0.21, 0.30	0.49	0.38, 0.58	0.53	0.43, 0.61	2.0		2.0		0.79	0.73, 0.85	0.72	0.64, 0.80
Ob	0.24	0.21, 0.26	0.26	0.21, 0.30	0.48	0.43, 0.53	0.52	0.42, 0.61	2.0		2.0		0.58	0.49, 0.66	0.54	0.45, 0.63
Mys	0.57	0.53, 0.61	0.71	0.65, 0.76	1.61	1.50, 1.72	1.99	1.83, 2.14	2.8	2.6, 2.8	2.7	2.6, 2.7	0.90	0.87, 0.92	0.85	0.80, 0.90
SmO	0.03	0.02, 0.03	0.03	0.02, 0.03	0.03	0.02, 0.03	0.03	0.02, 0.03	3.7	3.6, 3.7	3.7	3.5, 3.7	0.51	0.46, 0.56	0.57	0.51, 0.63
SmY	0.00	0.00, 0.00	0.00	0.00, 0.00	0.01	0.00, 0.01	0.01	0.01,0.01	3.5	3.4, 3.5	3.5	3.4, 3.4	0.00	0.00, 0.00	0.00	0.00, 0.00
Ascl	0.12	0.10, 0.13	0.13	0.11, 0.13	0.03	0.02, 0.02	0.03	0.02, 0.03	3.5	3.3, 3.5	3.5	3.3, 3.5	0.01	0.01,0.01	0.01	0.01, 0.01
Jscl	0.03	0.03, 0.03	0.03	0.03, 0.03	0.08	0.07, 0.08	0.08	0.07, 0.08	3.0		3.0		0.00	0.01,0.01	0.00	0.00, 0.00
AlO	1.32	1.27, 1.36	1.43	1.32, 1.52	1.23	1.18, 1.27	1.33	1.23, 1.42	3.5	3.4, 3.6	3.5	3.4, 3.5	0.24	0.22, 0.25	0.21	0.19, 0.23
AlEY	0.24	0.22, 0.25	0.22	0.20, 0.24	1.42	1.32, 1.52	1.30	1.18, 1.41	3.5	3.4, 3.5	3.4	3.3, 3.4	0.00	0.01,0.01	0.00	0.00, 0.00
Ch	0.04	0.03, 0.03	0.03	0.03, 0.03	0.05	0.04, 0.05	0.05	0.04, 0.05	4.5	4.4, 4.6	4.5	4.4, 4.5	0.00	0.00, 0.00	0.00	0.00, 0.00
OS	0.01	0.01, 0.01	0.01	0.01, 0.01	0.01	0.01, 0.01	0.01	0.01, 0.01	4.5	4.4, 4.5	4.4	4.3, 4.4	0.00	0.00, 0.00	0.00	0.00, 0.00

Table 4-2: Source, formulas and calculated values for Silver Carp and Bighead Carp Q/B ratios.

Source	Formulas	Q/B		Notes
		Silver Carp	Bighead Carp	
Chen et al. (1989)	$D_{silver}=0.2683\cdot e^{(0.1503\cdot T)}$ $D_{bighead}=0.0075\cdot T^{2.2715}$	6.21	7.13	Feed on plankton and detritus
Palomares and Pauly (1998)	$\log(Q/B)=7.964-0.204\cdot \log(W_{\infty})-1.965\cdot T'+0.083\cdot A+0.532\cdot h+0.398\cdot d$	22.14 8.85	18.17 7.27	Feed on plankton only
Cooke and Hill (2010)	$C=CA\cdot W^{CB}\cdot p\cdot V^{x}\cdot e^{(X\cdot(1-V))}$	12.54	8.8	

Table 4-3: Initial diets composition (%) of Asian carp applied in simulations. Species-groups abbreviations are described in Table 4-1. (Phyto Dom = Phytoplankton dominated diet, Micro Dom= Microbial Loop dominated diet, Det Dom= Detritus dominated diet, Equal= Equal proportioned diet).



	Observed		LDM					HDM				
Species-group	**Silver Carp**	**Bighead Carp**	Phyto Dom	Micro Dom	Zoo Dom	Det Dom	Equal	Phyto Dom	Micro Dom	Zoo Dom	Det Dom	Equal
Plk	**22.6**	**14.0**	**50.0**	**16.7**	**16.7**	**16.7**	**25.0**	**50.0**	**16.7**	**16.7**	**16.7**	**25.0**
Bac	**20.7**	**13.5**	**13.2**	**39.6**	**13.2**	**13.2**	**19.8**	**13.6**	**40.8**	**13.6**	**13.6**	**20.4**
Prot	**5.4**	**3.5**	**3.5**	**10.4**	**3.5**	**3.5**	**5.2**	**3.1**	**9.2**	**3.1**	**3.1**	**4.6**
Rot	**0.5**	**1.8**	**0.7**	**0.7**	**2.1**	**0.7**	**1.1**	**1.3**	**1.3**	**3.9**	**1.3**	**2.0**
Lc	**2.3**	**7.9**	**3.1**	**3.1**	**9.3**	**3.1**	**4.6**	**2.7**	**2.7**	**8.1**	**2.7**	**4.1**
Sc	**3.2**	**11.3**	**4.4**	**4.4**	**13.3**	**4.4**	**6.6**	**4.5**	**4.5**	**13.5**	**4.5**	**6.7**
Cop	**6.2**	**21.4**	**8.4**	**8.4**	**25.3**	**8.4**	**12.6**	**8.2**	**8.2**	**24.5**	**8.2**	**12.2**
POC	**39.1**	**0.3**	16.7	16.7	50.0	50.0	25.0	16.7	16.7	16.7	50.0	25.0
Trophic Level	2.45	2.80	2.41	2.76	2.88	2.41	2.61	2.42	2.77	2.91	2.42	2.63

Table 4-4: Means and range of changes in Asian carp biomass, and percent change in Alewife biomass, Chinook Salmon biomass, and Alewife EE from 5 replicate mass-balance solutions to the LDM model. No change in final Asian carp biomass means it was possible to achieve mass balance without adjusting the biomass or diets of any species-group.

Diet	Model	Asian Carp Trophic Level	Initial Asian Carp Biomass ($g C m^{-2}$)	Final Asian Carp Biomass ($g C m^{-2}$)		Change (%) in Alewife Biomass		Change (%) in Chinook Biomass		Change (%) in Alewife EE	
				Mean	Range	Mean	Range	Mean	Range	Mean	Range
Phyto Dom	LDM	2.41	0.1	no change		0.00	0, 0	0.00	0, 0	0.00	0, 0
Detr Dom	LDM	2.41	0.1	no change		0.00	0, 0	0.00	0, 0	0.00	0, 0
Silver Carp	LDM	2.45	0.1	no change		0.00	0, 0	0.00	0, 0	0.00	0, 0
Equal	LDM	2.61	0.1	no change		0.00	0, 0	0.00	0, 0	0.00	0, 0
Micro Dom	LDM	2.76	0.1	no change		0.00	0, 0	0.00	0, 0	0.00	0, 0
Bighead Carp	LDM	2.80	0.1	no change		0.00	0, 0	0.00	0, 0	0.00	0, 0
Zoo Dom	LDM	2.88	0.1	0.08	0.01, 0.12	-19.61	-35., -8.7	2.87	-39., 35.3	33.64	-20., 94.7
Phyto Dom	LDM	2.41	0.5	0.55	0.48, 0.61	-23.17	-38., -4.6	4.33	-31., 29	40.69	-5.2, 93.6
Detr Dom	LDM	2.41	0.5	0.44	0.37, 0.48	-28.21	-38., -15.	20.33	-8.9, 36.3	61.04	32.9, 95.3
Silver Carp	LDM	2.45	0.5	0.44	0.40, 0.48	-27.97	-37., -20.	-1.47	-23, 19.3	34.91	13.8, 71.0
Equal	LDM	2.61	0.5	0.50	0.41, 0.59	-26.15	-35., -17.	9.33	-30., 39	46.71	6.93, 91.3
Micro Dom	LDM	2.76	0.5	0.48	0.44, 0.61	-26.32	-34., -2.9	15.40	8.66, 24	54.68	26.5, 71.0
Bighead Carp	LDM	2.80	0.5	0.53	0.47, 0.58	-32.43	-37., -24.	17.87	8.66, 33	70.98	58.9, 84.3
Zoo Dom	LDM	2.88	0.5	0.46	0.40, 0.57	-29.54	-38., -18.	13.40	-4.9, 33.6	53.18	45.0, 61.8

Table 4-5: Means and range of changes in Asian carp biomass, and percent change in Alewife biomass, Chinook Salmon biomass, and Alewife EE from 5 replicate mass-balance solutions to the HDM model. No change in final Asian carp biomass means it was possible to achieve mass balance without adjusting the biomass or diets of any species-group.

Diet	Model	Asian Carp Trophic Level	Initial Asian Carp Biomass (g C m-2)	Final Asian Carp Biomass (g C m^{-2})		Change (%) in Alewife Biomass		Change (%) in Chinook Biomass		Change (%) in Alewife EE	
				Mean	Range	Mean	Range	Mean	Range	Mean	Range
Phyto Dom	HDM	2.41	All	no change		0.00	0, 0	0.00	0, 0	0.00	0, 0
Detr Dom	HDM	2.41	All	no change		0.00	0, 0	0.00	0, 0	0.00	0, 0
Silver Carp	HDM	2.45	All	no change		0.00	0, 0	0.00	0, 0	0.00	0, 0
Equal	HDM	2.61	All	no change		0.00	0, 0	0.00	0, 0	0.00	0, 0
Micro Dom	HDM	2.76	All	no change		0.00	0, 0	0.00	0, 0	0.00	0, 0
Bighead Carp	HDM	2.80	0.1, 0.5, 1.0	no change		0.00	0, 0	0.00	0, 0	0.00	0, 0
Zoo Dom	HDM	2.88	0.1	no change		0.00	0, 0	0.00	0, 0	0.00	0, 0
Zoo Dom	HDM	2.88	0.5	no change		0.00	0, 0	0.00	0, 0	0.00	0, 0
Zoo Dom	HDM	2.88	1	1.10	0.79, 1.32	-14.56	-26., -6.4	14.58	-18., 35.4	27.74	13.1, 34.4
Zoo Dom	HDM	2.88	1.5	1.28	1.12, 1.42	-25.09	-31., -20.	4.41	-17., 32.9	30.89	5.53, 74.8

GENERAL CONCLUSIONS

The modelling presented here predicts that Bighead Carp (*Hypophthalmichthys nobilis*) and Silver Carp (*Hypophthalmichthys molitrix*) have the potential to spread rapidly through the Great Lakes, establish populations even with small initial abundances, and disrupt Great Lakes food webs. More specific conclusions are:

Spread

- These carps could reach any part of the lake they initially invade within the first year.
- By the second year, a small percentage of individuals could invade a second lake; by the tenth year, a majority could invade a third lake.
- Spread could be faster if carps move greater distances with the predominant flows in the Great Lakes.
- Spread could be slower if carps initially invade a high productivity area (e.g., Lake Erie) or if food requirements are lower.
- If the Chicago Sanitary and Ship Canal is the invasion point, then Green Bay, Traverse Bay and Muskegon River are the most likely sites to attract individuals (in descending order).
- The temporal order of arrival (from a Chicago invasion point) is Muskegon River, Traverse Bay and Green Bay. Including these sites in a monitoring plan will improve the chances of early detection.

Establishment

- High probabilities (> 0.5) of a successful mating are achieved with very few (< 10) adults, even if there are a large number of suitable rivers (e.g., 25).
- The probability of a successful mating decreases if these carps imperfectly identify river suitability, if there are more rivers, if the sex ratio is skewed, or if spawning is not synchronized among individuals.
- However, high probabilities of a successful mating are still achieved with relatively few adults (< 20).
- Even a single release event of a few individuals can have a significant probability of establishing a population.
- A release of adults has a higher probability of establishing a population than an equivalent release of sub-adults.
- Regular release of individuals (e.g., due to a leaky barrier) increases the probability of establishing a population.
- The probability of establishment declines with fewer fish released, more potential spawning rivers, reduced ability to locate suitable rivers, and later age at maturity.
- The most sensitive stage to management/control actions in the juvenile stage.
- The largest impact on establishment probability is age at first maturity.

Impact

- Moderate to high carp biomasses could be sustained in a system like the offshore of Lake Ontario.
- High carp biomass will likely result in reduced Alewife biomass.
- High carp biomass increased the predation pressure on Alewife, increasing the risk of an Alewife population collapse, which would lead to the collapse of the Chinook Salmon population and fishery.
- Low carp biomass might have minimal consequences.
- Bighead and Silver Carps may be able to sustain high levels of biomass and disrupt lower trophic pathways of carbon flow with unpredictable food web consequences.