Evidence of host switching: sea lampreys disproportionately attack Chinook salmon when lake trout abundance is low in Lake Ontario

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Abstract

Lake trout (*Salvelinus namaycush*) is the presumed preferred host of the invasive sea lamprey (*Petromyzon marinus*) in the Great Lakes, but little is understood about this preference outside of laboratory experiments. By preference we mean sea lamprey attacks on hosts are disproportionate to host relative abundance. The purpose of this study was to quantify host preference of sea lampreys in the field for the first time. We focused our analysis on Lake Ontario, where the two dominant host species for sea lampreys are lake trout and Chinook salmon (*Oncorhynchus tshawytscha*). Sea lampreys exhibited a strong preference for lake trout when host abundance was ≥ 32% lake trout, but sea lamprey preference switched to Chinook salmon when host abundance was ≤ 13% lake trout. Model results were equivocal with respect to determining whether the primary predictor of sea lamprey preference was relative or absolute abundance of lake trout. Other evidence, particularly the different spatial distributions of the two hosts, suggests that sea lamprey preference for lake trout is based on a higher encounter probability, driven by absolute abundance of lake trout. This study confirms a widely held suspicion that observed sea lamprey-induced marking rates on lake trout, used to assess the status of sea lamprey control in the Great Lakes, can be influenced by the abundance of alternative hosts. As an alternative host for sea lamprey parasitism, Chinook salmon may contribute to the persistence of lake trout in Lake Ontario.

Keywords

predation; parasitism; prey preference; prey switching; Great Lakes

Introduction

Lake trout (*Salvelinus namaycush*) are presumed to be the preferred hosts for invasive sea lampreys (*Petromyzon marinus*) in the Great Lakes (Harvey et al., 2008; Pycha and King, 1975; Swink, 2003). But, juvenile sea lampreys attack many other Great Lakes species, especially large-bodied ones (Farmer and Beamish, 1973; Swink, 2003), and population level impacts have been observed or hypothesized for several species: Chinook salmon (*Oncorhynchus tshawytscha*, McLeod et al., 2011), lake whitefish (*Coregonus clupeaformis*, Spangler et al., 1980; Ebener et al., 2010), burbot (*Lota lota*, Stapanian et al., 2006), and coregonines and suckers (*Coregonus* spp. and *Catostomus* spp., Harvey et al., 2008).

In spite of their pelagic habitat and fast swimming speeds, Chinook salmon are commonly attacked by sea lampreys. Most (62%) of the age-2 precocious Chinook salmon had sea lamprey-induced marks in Lake Huron in 1970 (Smith and Tibbles, 1980). Sea lamprey marking rates on Lake Huron Chinook salmon ranged from 0.14 to 0.33 marks per fish in 1988-1992 (Johnson et al., 1995). The abundance of juvenile sea lampreys was significantly positively correlated with Chinook salmon abundance in Lake Huron, suggesting that Chinook salmon could be an important component of the sea lamprey diet (Young et al., 1996).

Little is understood about how sea lamprey parasitism varies with host abundance (Bence et al., 2003; Koonce, 1987). Knowledge in this area would allow us to improve our estimates of host damage. Current estimates based on observed sea lamprey marking rates are subject to survivor bias (marks are only observed on hosts that survived attacks, Adams et al., *This issue*) and from sampling bias (few host species other than lake trout are regularly surveyed on a lake-wide spatial scale). Although the focus of this study is predator-prey dynamics, we refer to sea lampreys as parasites (rather than predators) and lake trout and Chinook salmon as hosts (rather than prey).

The purpose of this study was to take the first step toward quantifying host preference of sea lampreys in the field. In this paper, the term preference is used to indicate sea lamprey attacks on hosts disproportionate to host relative abundance. In order to see a switch in preference in the field, feeding observations must be made over a wide range of relative abundances of hosts. That's why so many switching studies are carried out in the laboratory where the experimenter can control prey densities (Bayliss, 1982). We chose Lake Ontario as our case study, focusing on two host species: lake trout and Chinook salmon. Lake Ontario has a history of a relatively stable sea lamprey population, with variable lake trout abundance and increasing Chinook salmon abundance (Lantry et al., 2015). These conditions present a prime opportunity to observe host switching in sea lampreys, wherein sea lampreys switch their preference from lake trout to Chinook salmon below some threshold of the relative abundance of lake trout.

Our objectives were to characterize the preference of sea lampreys for lake trout in Lake Ontario and determine if and when their preference switches to Chinook salmon based on field observations. Greater understanding of host preference may aid in efforts to control sea lampreys and manage their hosts in the Great Lakes (Stewart et al., 2003) as well as to inform conservation of sea lampreys in their native range (Maitland et al., 2015).

Methods

Evidence of host preference and host switching was explored using logistic regression models of sea lamprey parasitism on lake trout and Chinook salmon in Lake Ontario. Recall that we defined preference as sea lamprey attacks disproportionate to host relative abundance. The two key quantities are the proportion of hosts that are lake trout and the proportion of sea lamprey-induced marks that are on lake trout, assuming that lake trout and Chinook salmon are the only available hosts. The proportion of marks on lake trout was assumed to be a function of the proportion of hosts that were lake trout,

$$(1) \qquad ln\left(\frac{M_1}{1-M_1}\right) = \gamma_0 + \gamma_1\ ln\left(\frac{P_1}{1-P_1}\right),$$

where M_1 is the proportion of sea lamprey-induced marks on lake trout,

$$M_1 = \frac{S_1 O_1/E_1}{S_1 O_1/E_1 + S_2 O_2/E_2},$$

S_i is the estimated lake-wide abundance of species i ($i = 1$ for lake trout; $i = 2$ for Chinook salmon), O_i is the observed number of marks on E_i examined individuals of species i, $P_1 = S_1/\sum S_i$ is the proportion of host abundance that were lake trout, and γ_0 and γ_1 are parameters to be estimated. When fitting the logistic regression, the response was scaled to the total number of observed marks, $\sum O_i$, as the sample size. Because the scaled responses were not integers, the quasibinomial family was used in the general linear model rather than the usual binomial family. This is a natural log transformation of the simple ratio predation model (Murdoch, 1969) with the addition of a switching parameter, γ_1. If $\gamma_1 \neq 1$, there is evidence of a switch in host preference that depends on the proportion of hosts that were lake trout. If $\gamma_1 = 1$, there is no host switching, and preference over all host proportions is simply estimated by e^{γ_0} (equivalent to the constant c in the simple ratio predation model, Murdoch, 1969). If $\gamma_1 = 1$ and $\gamma_0 > 0$, then $M_1 > P_1$ and sea lampreys exhibit a preference for lake trout; if $\gamma_1 = 1$ and $\gamma_0 < 0$, then $M_1 < P_1$ and they exhibit a preference for Chinook salmon. Scatter plots of residuals from the full model were visually examined for qualitative evidence of patterns related to year, lake trout abundance, Chinook salmon abundance, adult sea lamprey relative abundance, and adult sea lamprey size.

Lake-wide abundance of hosts was estimated by two separate Lake Ontario statistical catch-at-age models (Table 1), one for lake trout (Brenden et al., 2011, Travis Brenden, Michigan State University, personal communication), and one for Chinook salmon (Kimberly Fitzpatrick, Cornell University, personal communication; estimates are preliminary and have not been endorsed by the Lake Ontario Committee or the Lake Ontario Technical Committee; data can be found in Connerton, 2019; Bishop et al., 2019; Connerton and Eckert, 2019; Lake, 2017; Prindle and Bishop, 2019; Sanderson et al., 2019; Yuille and Holden, 2017). Abundance of lake trout was calculated as the sum of age 3 and older fish (Brenden et al., 2011). Abundance of Chinook salmon was calculated as the sum of age 1 and older fish, corresponding to the spawning adults which were surveyed. For both species, the fish included in the abundance estimates are susceptible to sea lamprey predation.

Host parasitism rates were derived from observed sea lamprey marks on hosts. Host parasitism was estimated as the number of A1 marks per host > 431 mm, following current practice for Lake Ontario (Lantry et al., 2015; Larson et al., 2003). This rate is calculated as the total number of marks (including multiple marks on a single host) divided by the total number of fish examined for marks. The A1 classification indicates that the marks pierced the skin and are "fresh" or little healed (Ebener et al., 2003; King Jr., 1980). For lake trout, observations of marks (Table 1) and measures of total length (Figure 1) came from two fishery independent gill net surveys: the Lake Ontario and Bay of Quinte fish community index gill netting survey conducted during June-September in Canada waters (Hoyle, 2018) and the lake trout assessment survey conducted during September-October in US waters (Lantry et al., 2018). For Chinook salmon, observations of marks and measures of total length came from the fall spawning migration up a fish ladder on Beaverdam Brook (a tributary of the Salmon River) into the New York State Department of Environmental Conservation Salmon River Fish Hatchery, Albion NY, (Prindle and Bishop, 2018).

The relative abundance of adult sea lampreys in Lake Ontario was assessed annually by mark-recapture studies in five index streams (Humber River, Duffins Creek, and Bowmanville River in Canada and Black and Sterling Rivers in the US) during their spawning migration (Mullett et al., 2003). The spawning migration occurs after sea lampreys spend 6-18 months in the lake feeding on fish as juveniles. The stream pooled Petersen estimates (Seber, 1970) were then summed for a lake-wide adult index (Barber et al., *This issue*). Individual sea lampreys captured during these studies were weighed, and the median annual weight was used as an index of sea lamprey size in the exploration of model residuals.

Additional models were fit to the parasite-host data that accounted for the sizes of the two host species, because Great Lakes sea lampreys have a demonstrated preference for large fish (Bence et al., 2003; Farmer and Beamish, 1973; Rutter and Bence, 2003). Without accounting for host size, we expect that sea lamprey preference for lake trout will be underestimated, because Chinook salmon tend to be larger than lake trout in Lake Ontario (Figure 1).

Expected marking rates were modeled as a logistic function of host size (Rutter and Bence, 2003) for both host species combined (allowing marking rates to vary with host size regardless of species) and for each host species separately (allowing for species-specific size relations),

$$W = \frac{\theta}{1 + exp[-\alpha(L - \beta)]} ,$$

where W is the expected number of marks following a negative binomial distribution (Prichard and Bence, 2013), L is host length (in mm), θ is the asymptotic marking rate, β is the length of the host at the inflection point, and $\alpha\theta/4$ is the slope at the inflection point. Models were fit using maximum likelihood with the nlminb function of R (R Core Team, 2018). All three parameters were estimated in the natural log-transformed space to constrain them to be positive.

The expected proportion of sea lamprey-induced marks on lake trout based on the abundance and size distribution of the host species was calculated as

$$\tilde{P}_{1,\, size} = \frac{S_1 \widetilde{W}_{13}}{S_1 \widetilde{W}_{13} + S_2 \widetilde{W}_{23}} ,$$

$$\tilde{P}_{1,\ size+species} = \frac{S_1\widetilde{W}_{11}}{S_1\widetilde{W}_{11} + S_2\widetilde{W}_{22}} ,$$

where $\widetilde{W}_{ig}$ is the annual mean predicted marking rate for species i calculated for group g of the data ($g = 1$ for lake trout alone, $g = 2$ for Chinook salmon alone, and $g = 3$ for both species combined). We then fit two additional parasitism models by replacing the P_1 in Model 1 with the expected proportions from asymptotic marking rates depending on host size alone (Model 2, $\tilde{P}_{1,\ size}$) and on host size and species (Model 3, $\tilde{P}_{1,\ size+species}$).

Finally, we fit two additional logistic regression models, where the independent variable of the relative abundance of lake trout, $ln[P_1/(1-P_1)]$, was replaced by the absolute abundance of lake trout ($ln(S_1)$, Model 4) and by the absolute abundance of Chinook salmon ($ln(S_2)$, Model 5).

Results

Without taking host size into account (Model 1), the estimate for γ_1 was significantly different from 1 (5.54 with standard error 1.37), indicating a switch in host preference. Sea lampreys exhibited a preference for Chinook salmon when the combined abundance was $\leq$ 13% lake trout, switching to a preference for lake trout when combined abundance was $\geq$ 32% lake trout (γ_0 = 4.95 with standard error 1.30, Figure 2). The steepest increase in the proportion of marks on lake trout occurred when the combined abundance was 32.6% lake trout. No linear or nonlinear relations were evident in plots of the residuals from the full model versus year, lake trout abundance, Chinook salmon abundance, sea lamprey abundance, or sea lamprey size.

Sea lamprey preference for lake trout was also evident when modeling marking rates as a function of host size (Figure 3). Marking rates on lake trout most steeply increased at a host length 132 mm shorter than that on Chinook salmon (Table 2). The asymptotic marking rate of lake trout was 1.4 times that of Chinook salmon. However, taking host size into account, either for both species together (Model 2, residual deviance 48.8) or each species separately (Model 3, 50.1) did not improve the fit achieved with Model 1 (residual deviance 47.4, t = 3.82, P = 0.0021, Figure 4), even with the inclusion of additional estimated parameters.

The proportion of marks on lake trout was also well explained by the absolute abundance of lake trout, with slightly less residual deviance (Model 4, residual deviance 47.3, t = 3.86, P = 0.0020, Figure 5) than by the proportional abundance of lake trout (Model 1). The estimate for γ_1 was 1.78 with standard error 0.43. Here, the γ_1 parameter loses its interpretation as a switching indicator, because this model depends on the abundance of only one host species. The estimate for γ_0 was 4.73 with standard error 1.22. The steepest increase in the proportion of marks on lake trout occurred when the absolute abundance of lake trout was 0.69 million fish.

In contrast, the absolute abundance of Chinook salmon was not a strong predictor of the proportion of marks on lake trout (Model 5, residual deviance 85.7, t = -1.76, P = 0.10).

Discussion

This study provides an example of a parasite with a strong host preference that switches when the relative and absolute abundance of the preferred prey is low. This is in contrast to the prediction by Murdoch (1969) that prey switching will not occur when the predator has strong prey preferences (Murdoch et al., 1975; Rubega and Inouye, 1994). In spite of their strong host preference in the Great Lakes, we consider the sea lamprey to be a generalist predator, attacking a wide range of fish species (Schoener, 1971). This varied diet is supported by studies of stable isotopes in Lake Superior (Harvey et al., 2008) and fatty acids in Lake Michigan (Happel et al., 2017). In the Atlantic, sea lamprey attacks have been documented on 54 host species (Silva et al., 2014). When prey abundance is high, most generalist predators feed on a single primary prey (Andersson and Erlinge, 1977). If that primary prey population declines, predators turn to less abundant alternatives (Angelstam et al., 1984). Switching behavior has been documented for several so-called generalist predators (Cornell, 1976; Murdoch, 1969; Patterson et al., 1998). Anecdotal evidence of host switching was observed in South Bay of Lake Huron when sea lamprey-induced marks on white suckers (*Catostomus commersonii*) coincided with the crash of the lake trout population in the 1950s (Coble, 1967).

Evidence for host-switching is based on the fit of the observed data to a switching model. For Lake Ontario during 2000-2014, Model 1 predicted that sea lampreys preferred lake trout in 11 of 15 years and exhibited no preference between lake trout and Chinook salmon the other four years (2006-2008 and 2014). None of the 15 years had a low enough proportion of hosts that were lake trout for Model 1 to predict sea lamprey preference for Chinook salmon. Thus, inferring that sea lampreys prefer attacking Chinook salmon if lake trout are relatively scarce is based on extrapolation beyond the range of data used to build the model. However, we did observe more marks on Chinook salmon than expected from their relative abundance in three years (2007-2009, the three points below the dotted line in Figure 2). These years likely correspond to more relatively small fish in the lake trout population, contributing to the rise in lake trout abundance after 2009 (Brian Lantry, US Geological Survey, personal communication.)

Switching to an alternative prey species makes sense for a number of reasons, most of which lead to an increase in feeding efficiency (Bayliss, 1982). According to optimal foraging theory, a predator chooses the prey that will give the maximum net benefit to the individual (Begg et al., 2003). The net benefit depends on handling time, nutritional value, and the abundance of alternative prey (Van Baalen et al., 2001).

Handling time incorporates the pursuit, capture, and digestion of prey (Fujii et al., 1986). Chinook salmon are much more active than lake trout, searching open water habitat for active pelagic prey (Stewart and Ibarra, 1991), which may make them more difficult for sea lampreys to pursue and attack. Although we found no laboratory studies of sea lampreys feeding on Chinook salmon, relatively low detachment rates (< 18%) have been observed for several species except for burbot (36%) and walleye (*Sander vitreus*, 75%) (Farmer and Beamish, 1973).

Switching to the most common prey species may be a consequence of the predator's searching behavior, e.g., the use of a search image of the locally most abundant prey species (May, 1977). A decrease in prey biomass results in an increase in the foraging costs of the preferred prey through increased search time (Krebs and Davies, 1987). Predators may forage in different patches, form prey search images, decrease prey handling time with experience, or increase searching efficiency within patches (Joern, 1988). Predators are more likely to detect prey if the prey are aggregated (Taylor, 1977). When prey are clumped, nearly double the number of predators have been observed switching to the alternative prey (Bayliss, 1982). If sea lampreys learn, their attack success rate might increase with successive attempts on a given species, as has been observed in the water boatman (*Notonecta glauca*, Hughes, 1979). A predator may also be more efficient at locating prey, if it concentrates on only one species (Bayliss, 1982).

Switching may also be the consequence of differences in energetic content of the prey. If the value of two prey types are quite different, we would expect the predator to specialize on the most valuable prey type and generalize when the latter is scarce (Hughes, 1979; Murdoch et al., 1975). The lipid content of lake trout was greater than that of Chinook salmon in Lake Ontario in 2013 (Mumby et al., 2018) and in Canadian waters of Lake Ontario during 1978-2008 (Neff et al., 2012). This higher energy content comes at the price of lower metabolic and digestion rates (Fall and Fiksen, 2020) for sea lampreys feeding at the lower water temperatures lake trout inhabit (to be discussed later). If lake trout were more profitable prey than Chinook salmon, then we might expect to see an effect on the size of the adult sea lampreys. In this case, the median weight of adult sea lampreys collected in Lake Ontario was not significantly correlated with the proportion of marks on lake trout (*r*=0.34, df=13, *P*=0.21). This supports the contention that prey preference is not necessarily reflected in comparative growth rates (Bayliss, 1982).

Building a switching model that depends on the relative abundance of the prey implies that the predator perceives the relative abundance of prey. The ability to do this depends on the extent to which the predator and prey species overlap spatially. The diversity of hosts attacked will reflect both their relative abundance and spatial distribution (Schoener, 1971). Sea lampreys captured in the open waters of Lake Superior fed primarily on lake trout, but those in Black Bay relied heavily on coregonines and suckers (Harvey et al., 2008). Laboratory preference studies focus on the active choice of predators when faced with more than one vulnerable prey species (e.g., Farmer and Beamish, 1973). Vulnerability of different species to sea lamprey attack in the field is largely unknown. If host populations were partitioned into vulnerable and invulnerable components, foraging arena theory asserts that the attack rates then depend on the exchange rates between the components (Ahrens et al., 2012). If recently metamorphosed sea lampreys (transformers) attack the first host fish they encounter upon exiting their natal stream, then host preference is less an active choice, and more the result of passive encounter probabilities and habitat overlap. For example, transformers are commonly observed attached to bloater (*Coregonus hoyi*) captured in bottom trawling in the Detour Channel of northern Lake Huron (Fleischer, 1993). Farmer and Beamish (1973) contended that sea lamprey preference in the Great Lakes depended largely on the ecological distribution of host species. Weitkamp et al. (2015) asserted that marking rates by western river (*Lampetra* *ayresii*) and Pacific (*Entosphenus tridentatus*) lampreys in the Columbia River estuary were influenced by the habitat selection of potential host species.

Lake trout and Chinook salmon occupy different habitats in Lake Ontario. Lake trout occupy the hypolimnion, near the bottom of the thermocline, and Chinook salmon occupy the metalimnion to maximize their growth rate potential in Lake Ontario (Mason et al., 1995). Chinook salmon feed almost exclusively on alewife in offshore pelagic areas; lake trout consume a broader mix of alewife (*Alosa pseudoharengus*) and other species, feeding on both pelagic and benthic prey in the hypolimnion (Mumby et al., 2018; Rand and Stewart, 1998). The fatty acid profiles of the two host species reflect this, indicating lake trout feed more on rainbow smelt (*Osmerus mordax*) and round gobies (*Neogobius melanostomus*) than Chinook salmon, which feed more on alewives (Happel et al., 2016). The energy content of the host species likely changed during 2000-2104 due to changes in the composition of their prey: alewife condition increased, rainbow smelt abundance declined, and round goby biomass increased in Lake Ontario during 2000-2014 (Weidel et al., 2018). Sea lampreys are poorer swimmers than most teleosts and do not possess swim bladders, so they must expend energy just to maintain position in the water column (Beamish, 1974). Thus, it's energetically advantageous for free swimming juvenile sea lampreys to search for hosts near the lake bottom, where they are less likely to encounter Chinook salmon. However, sea lampreys that feed exclusively on hosts in the hypolimnion have lower growth rates than those feeding on hosts in the thermocline as a result of thermal bioenergetics (Kitchell and Breck, 1980).

This lends theoretical support to the model based on lake trout abundance alone, regardless of Chinook salmon abundance (Model 4). Similar outcomes have been observed in other species. For example, the mollusk (*Lepsiella vinosa*) fed heavily on its preferred species, irrespective of the relative abundance of the alternative species (Bayliss, 1982), and coyotes (*Canis latrans*) only switched to an alternate prey when the absolute abundance of its preferred prey was low (Patterson et al., 1998). Merilaita and Ruxton (2009) suggested frequency-dependent predation should be common where predators face large temporal or spatial fluctuations of prey types. Further evidence from the field would require years of exceptionally high or low host abundance, where high absolute lake trout abundance could coincide with low relative lake trout abundance or vice versa. Otherwise choosing between these two models (Models 1 and 4) based on field observations alone is difficult, because the relative and absolute lake trout abundances were so highly correlated during 2000-2014 (r = 0.78, P = 0.0006, df = 13). If sea lampreys shift their distribution when lake trout become scarce, we should be able to observe this with acoustic telemetry (e.g., Holbrook et al., 2016) or archival tags (e.g., Bergstedt et al., 2012).

Sea lampreys spawning in Portuguese tributaries to the Atlantic Ocean use one of two different feeding strategies (Lança et al., 2013). Sea lampreys either tended to attack pelagic plankton feeders or benthic opportunist fish species. Lança et al. (2013) hypothesized that the feeding strategies were associated with different dispersion tactics. Sea lampreys that parasitize pelagic rather than demersal hosts enhance their dispersion but increase the risk of not returning to fresh water. The risk of not returning to a stream to spawn is presumably less in the more confined Great Lakes than in the Atlantic Ocean.

The presence of Chinook salmon as an alternative host for sea lampreys may serve as a buffer, benefiting both sea lampreys and lake trout when lake trout abundance is low. By concentrating attacks on the most common host, sea lampreys enable the rarer hosts to enjoy higher fitness via frequency-dependent natural selection (May, 1977). Thus, the presence of Chinook salmon in Lake Ontario may contribute to the persistence of lake trout in the system. A predator's switch to alternative prey relieves predation pressure when the prey densities are low, regardless of whether the alternative prey overlaps with the primary prey (Van Baalen et al., 2001). This persistence only arises if the predator switches between prey. However the rapid increase in sea lamprey attacks on lake trout at abundance levels just above the switching point is an impediment to lake trout reproduction. Lake trout may then be caught in a "predator pit" (Walters, 1986) and maintained at low levels by sea lamprey parasitism in spite of lake trout restoration efforts. Even low abundances of actively switching sea lampreys could maintain the lake trout at depressed levels.

Lake trout and Chinook salmon are not the only species attacked by sea lampreys in Lake Ontario. Boating anglers in US waters of Lake Ontario have also observed sea lampreys attached to brown trout (*Salmo trutta*), rainbow trout (*Oncorhynchus mykiss*), coho salmon (*Oncorhynchus kisutch*), and Atlantic salmon (*Salmo salar*) (in order of prevalence, Lantry et al., 2015; Lantry and Eckert, 2018). Sea lamprey marks have also been infrequently identified on other species collected in fishery-independent gill net surveys: northern pike (*Esox lucius*), walleye, burbot (*Lota lota*), and lake whitefish (Hoyle, 2018; Lantry et al., 2018). Thus the proportions of hosts and marks that we calculate from lake trout and

Chinook salmon alone were biased low and introduced noise to our model, because the abundances of these other hosts and the prevalence of sea lamprey-induced marks on them has changed over time (Lantry et al., 2015). The host-switching that we detected had to have been strong enough to overcome this background noise. The preference of Great Lakes sea lampreys for lake trout surely contributed to our ability to detect the host-switching, because prey switching is less pronounced when no single species dominates the predator's diet (Hall-Scharf and Stallings, 2014; Van Leeuwen et al., 2013).

Different strains of lake trout in Lake Ontario were not distinguished in our analyses. The Seneca strain of lake trout (from Seneca Lake, NY) has dominated lake trout stocking in Lake Ontario since 1997 (Brenden et al., 2011), and has been recommended to be the majority of stocked lake trout in the future (Lantry et al., 2014). Most (55%) of the lake trout observed for sea lamprey marks in this study were not identified to strain. The most commonly recorded strain was Seneca (20% of the total, 44% of those identified to strain), with Superior strain a distant second (7% of the total, 15% of those identified to strain). Seneca strain lake trout tend to be caught in deeper colder water than other strains and have a lower chance of being attacked by sea lampreys and a higher chance of surviving if attacked (Lantry et al., 2015; Schneider et al., 1996). However, Senecas may be less adapted to conditions in Lake Ontario than previously thought (Brenden et al., 2011).

Using the observed sea lamprey marking rate as a measure of the true sea lamprey attack rate has a number of shortcomings, but the A1 marks (indicating recent piercing attacks) are believed to be the least affected by them. The classification of sea lamprey marks is subject to error, but the A1 marks are correctly classified most of the time (Ebener et al., 2003, their Table 1 with four A1 marks identified correctly by 67% of 30 people on average). However, the classification error associated with A1 marks exceeds that of A1-A3 marks combined, where the A2 and A3 marks are those that are partially healed (Adams and Jones, *In preparation*; Firkus et al., *This issue*; Nowicki, 2008; Ebener et al., 2003). The observed marking rate is only a good index of the true attack rate if the annual lethality rate from sea lamprey attacks is relatively constant over time (Adams et al., *This issue*). Fresh piercing marks (A1) should be less susceptible to survivor bias, because they may be observed on fatally wounded lake trout before the lake trout die. Survivor bias may be greater for Chinook salmon than lake trout, leading to underestimated marking rates, because host mortality increases with water temperature (Farmer et al., 1977). The A1 marking rate has also been shown to be correlated with recovery rates of dead lake trout in Lake Ontario (Bergstedt and Schneider, 1988). Finally, the use of A1 marks should also help reduce the age-based bias in the healing rates, caused by the contrast between the fast growing, young Chinook salmon and the slow growing, old lake trout in Lake Ontario. An additional complication when analyzing sea lamprey-induced marks on more than one host species is that the duration of the juvenile (parasitic) life stage of the sea lamprey may vary with host selection (Cline et al., 2014; Moody et al., 2011).

Alternative hosts are often blamed for confounding the reported sea lamprey marking rates on Great Lakes lake trout. This study confirms that suspicion in Lake Ontario, where the relative abundance of Chinook salmon affects the marking rate on lake trout. When we varied the proportion of hosts that were lake trout over the range observed (0.252 to

0.516) while holding the total abundance of hosts and the total number of marks on them constant, the resulting marking rate on lake trout ranged as much as 0.034 (Figure 6). Here, the lake trout marking rates are near their maximum when lake trout comprise at least 37% of the host abundance, but are reduced when the proportion of hosts that were lake trout declines below the Model 1 inflection point of 32.6% (in 2006-2008 and 2014).

We hope that the evidence from switching demonstrated in this study and the methods described will motivate further investigations into the host preference of sea lampreys. The effect of alternative hosts on lake trout marking rates is also suspected in other Great Lakes: siscowet lake trout in Lake Superior (Sitar et al., 2008), Chinook salmon in Lake Michigan, and Chinook salmon and lake whitefish in Lake Huron (Hansen et al., 2016). One impediment to such investigations is the lack of lake-wide absolute abundance estimates for the alternative hosts, which are necessary to calculate the proportional abundance relative to other hosts. Understanding the underlying causes of host switching could also be investigated via more complex models that incorporate spatial overlap and quantify host profitability to sea lampreys.

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Tables

Table 1. Lake trout relative abundance (expressed as the proportion of lake trout and Chinook salmon hosts) and lake trout and Chinook salmon parasitism rates (N=number of hosts observed, A1=number of A1 or “fresh” sea lamprey-induced marks per host).

Year	Lake trout relative abundance	Lake trout N	Lake trout A1	Chinook salmon N	Chinook salmon A1
2000	0.516	993	0.023	646	0.000
2001	0.466	991	0.023	657	0.000
2002	0.391	909	0.008	624	0.002
2003	0.387	943	0.020	923	0.015
2004	0.398	891	0.018	744	0.009
2005	0.354	468	0.032	753	0.012
2006	0.316	609	0.025	630	0.006
2007	0.271	399	0.030	481	0.035
2008	0.252	554	0.016	669	0.016
2009	0.370	613	0.010	897	0.012
2010	0.414	785	0.015	719	0.000
2011	0.407	926	0.004	625	0.003
2012	0.402	871	0.025	574	0.003
2013	0.328	1122	0.017	584	0.003
2014	0.284	1268	0.010	675	0.006

Table 2. Estimated parameters relating host length to sea lamprey-induced marking rate for both species combined and for lake trout and Chinook salmon separately.

Species	Alpha	Beta	Theta
Both	0.0200	587	0.0150
Lake trout	0.0207	383	0.0161
Chinook salmon	0.0197	718	0.0105

Figure captions

Figure 1. Annual length frequency distributions of lake trout and Chinook salmon captured in Lake Ontario 2000-2014. Each line represents a separate year.

Figure 2. Relation between the proportion of hosts that were lake trout and the proportion of sea lamprey-induced marks that were on lake trout in Lake Ontario, assuming lake trout and Chinook salmon were the only available hosts. Symbols represent annual observations (2000-2014), symbol size represents number of hosts examined for marks, and lines represent predictions from Model 1 with 95% confidence intervals. The diagonal dotted line represents the null model, with no preference and no switching. The two triangles denote the switch points below which sea lampreys prefer Chinook salmon (left) and above which sea lampreys prefer lake trout (right).

Figure 3. Sea lamprey-induced marking rate as a function of host size for just lake trout, just Chinook salmon, and both species combined in Lake Ontario 2000-2014. Symbols represent observed proportions for each 50 mm size group, symbol size represents the sample size, and lines represent predictions from the negative binomial model.

Figure 4. Proportion of sea lamprey-induced marks that were on lake trout (relative to Chinook salmon) over time in Lake Ontario 2000-2014. Points represent observations, lines represent predictions from three models based on (1) the proportion of hosts that were lake trout (solid), (2) the proportion of hosts that were lake trout and the size of the

mixed hosts (dashed), and (3) the proportion of hosts that were lake trout and species-specific host size (dotted).

Figure 5. Relation between lake trout abundance and the proportion of sea lamprey-induced marks that were on lake trout (relative to Chinook salmon) in Lake Ontario. Symbols represent annual observations (2000-2014), symbol size represents number of hosts captured, and lines represent predictions from Model 1 with 95% confidence intervals.

Figure 6. Model 1 predicted range of sea lamprey-induced marking rates on lake trout in Lake Ontario (shading) when the proportion of hosts that were lake trout (relative to Chinook salmon) varies over the range observed (0.252 to 0.516) while holding the total abundance of hosts and the total number of marks on them constant. Points represent observed marking rates, line represents predicted marking rates from Model 1 for observed proportional abundances.

Figure 1

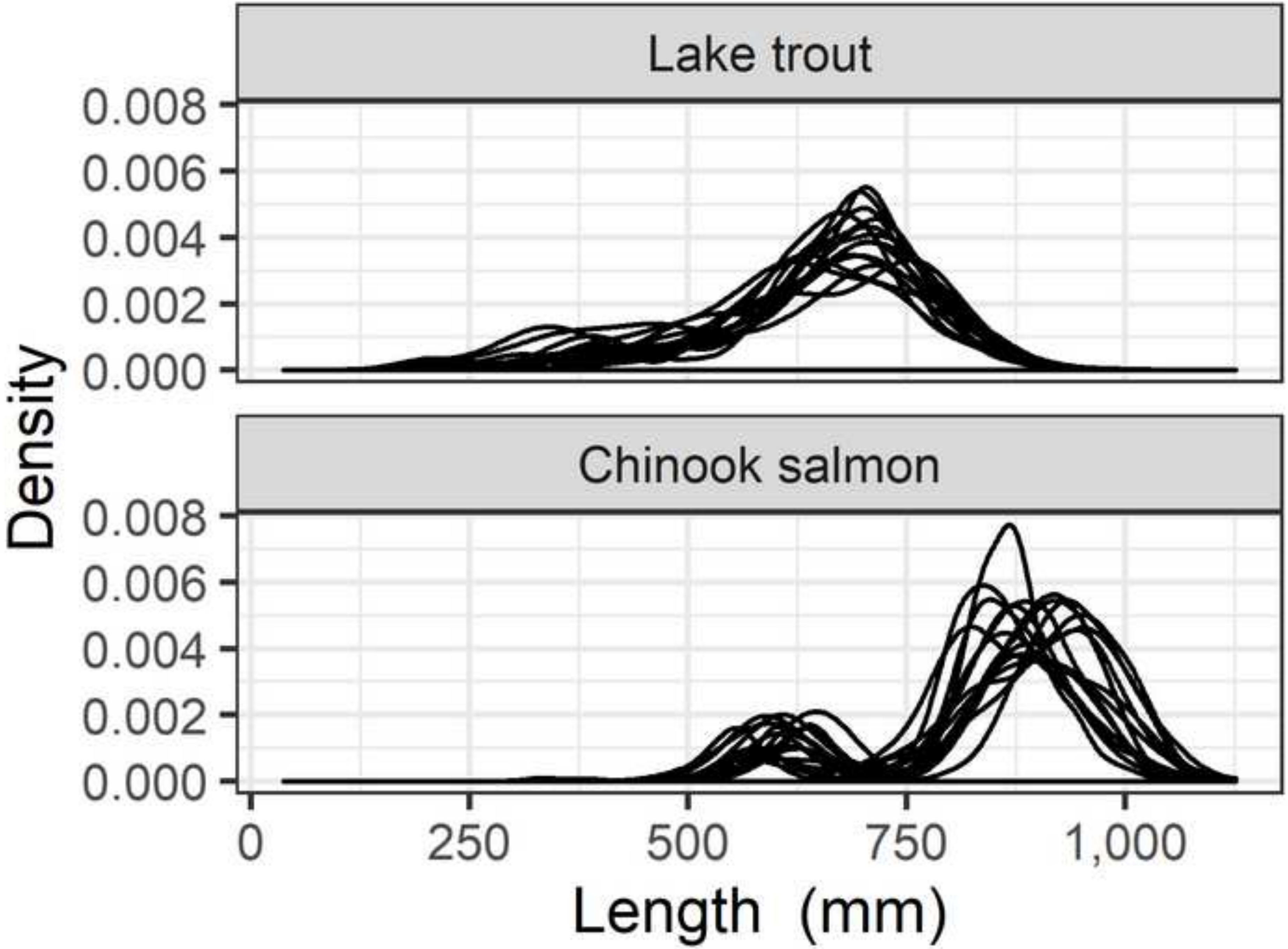

Lake trout
Chinook salmon
Density
0.008
0.006
0.004
0.002
0.000
0
250
500
750
1,000
Length (mm)

Figure 2

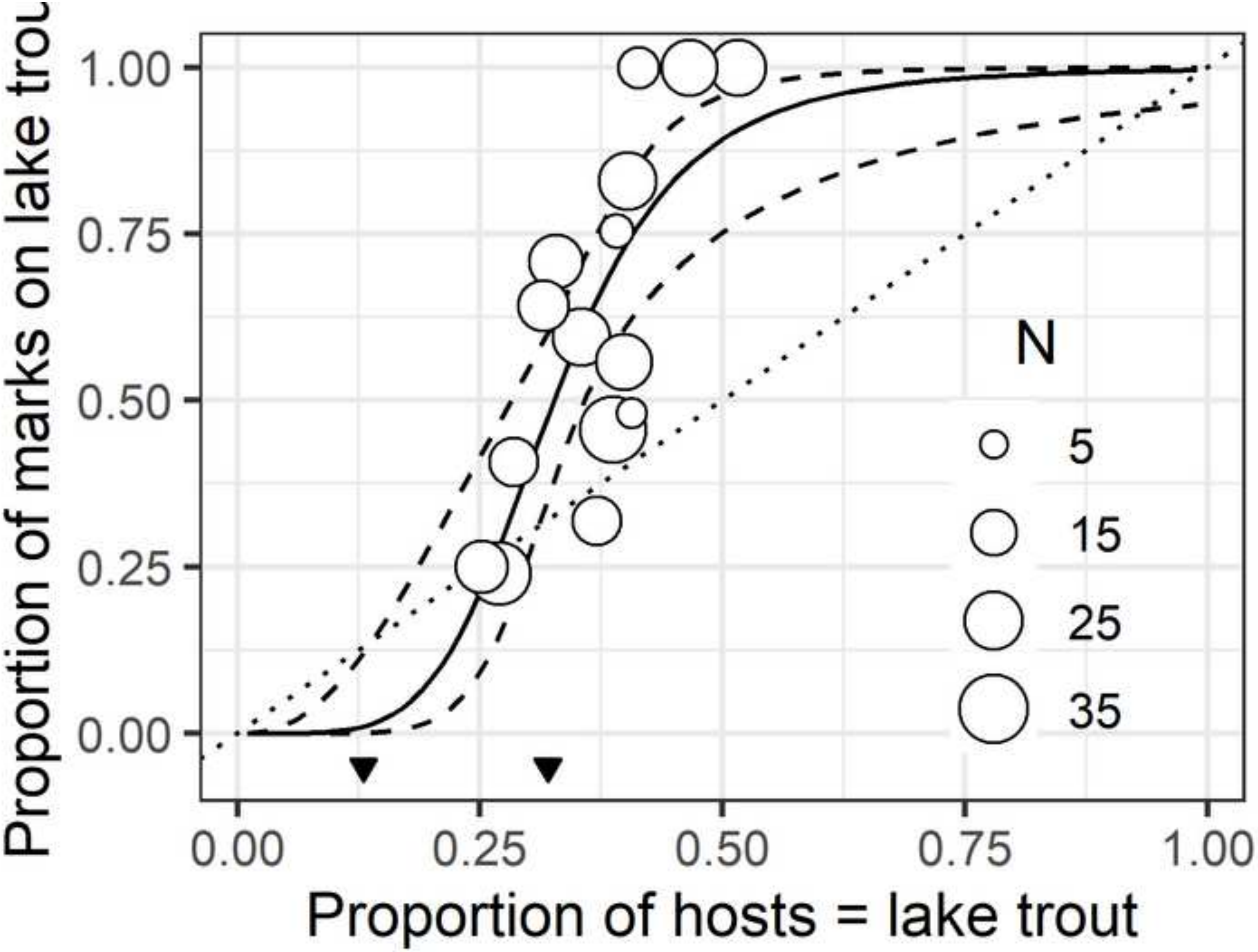

Proportion of marks on lake trou
1.00
0.75
0.50
0.25
0.00
0.00
0.25
0.50
0.75
1.00
Proportion of hosts = lake trout
N
5
15
25
35

Figure 3

Click here to download high resolution image

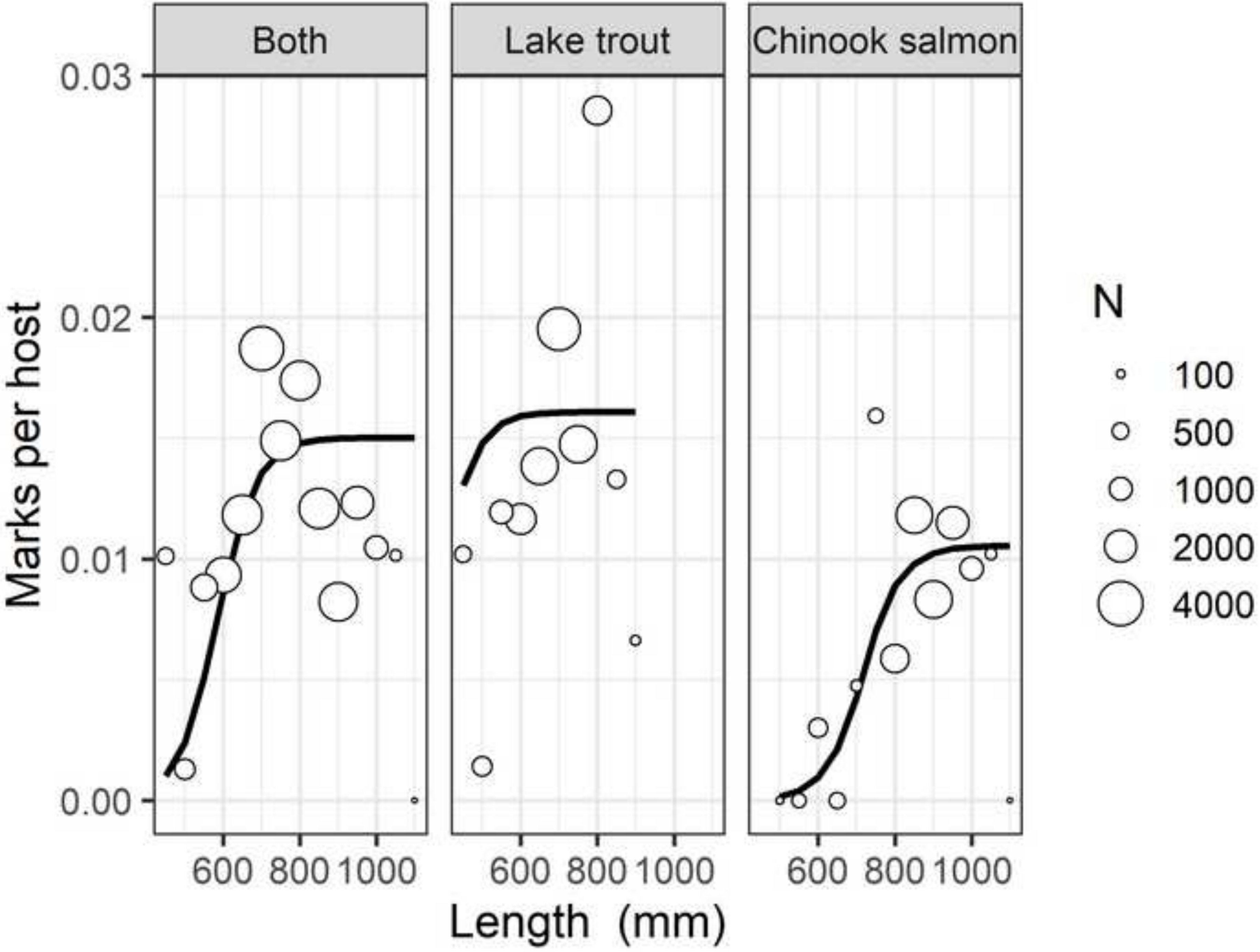


Figure 4

Click here to download high resolution image

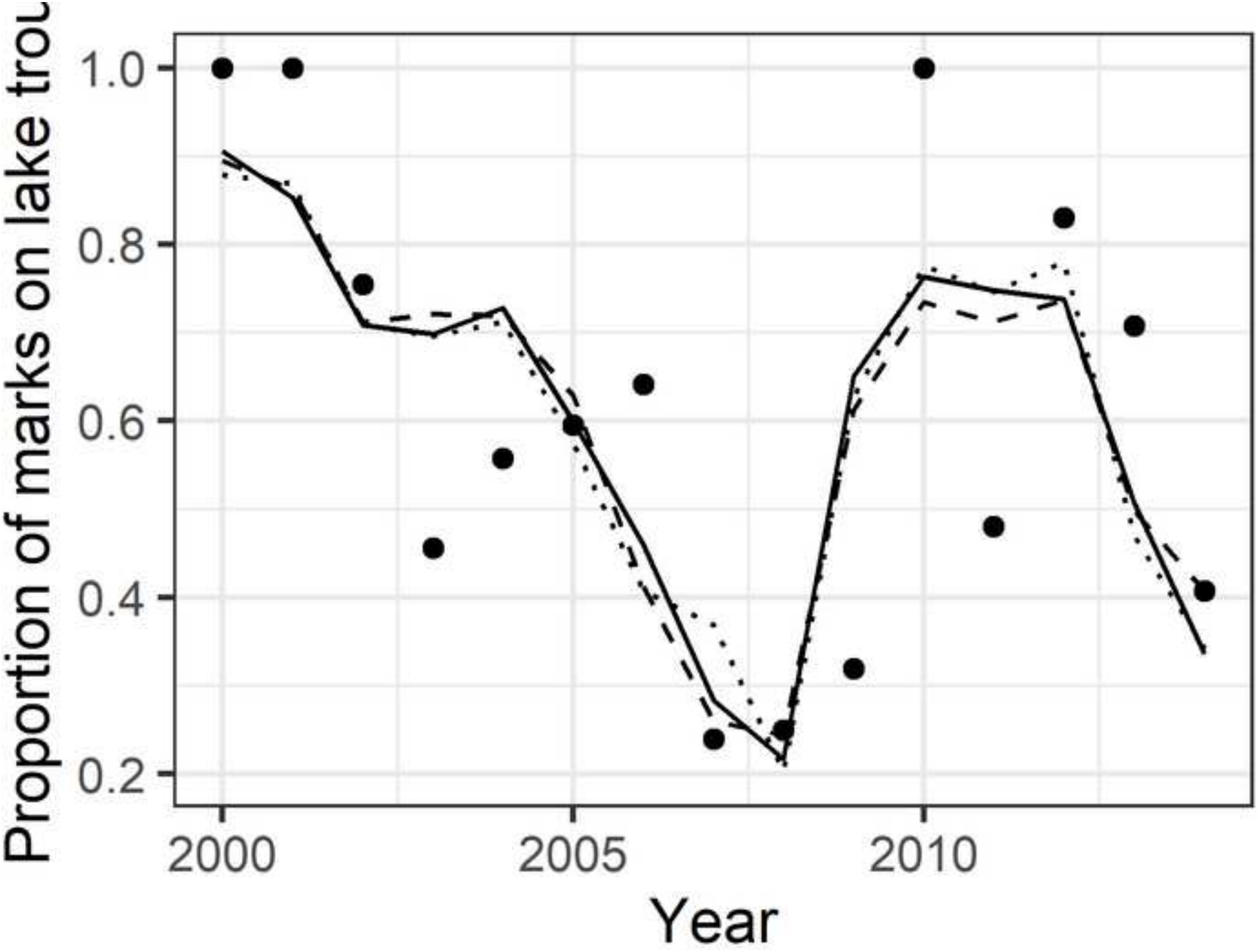


Figure 5

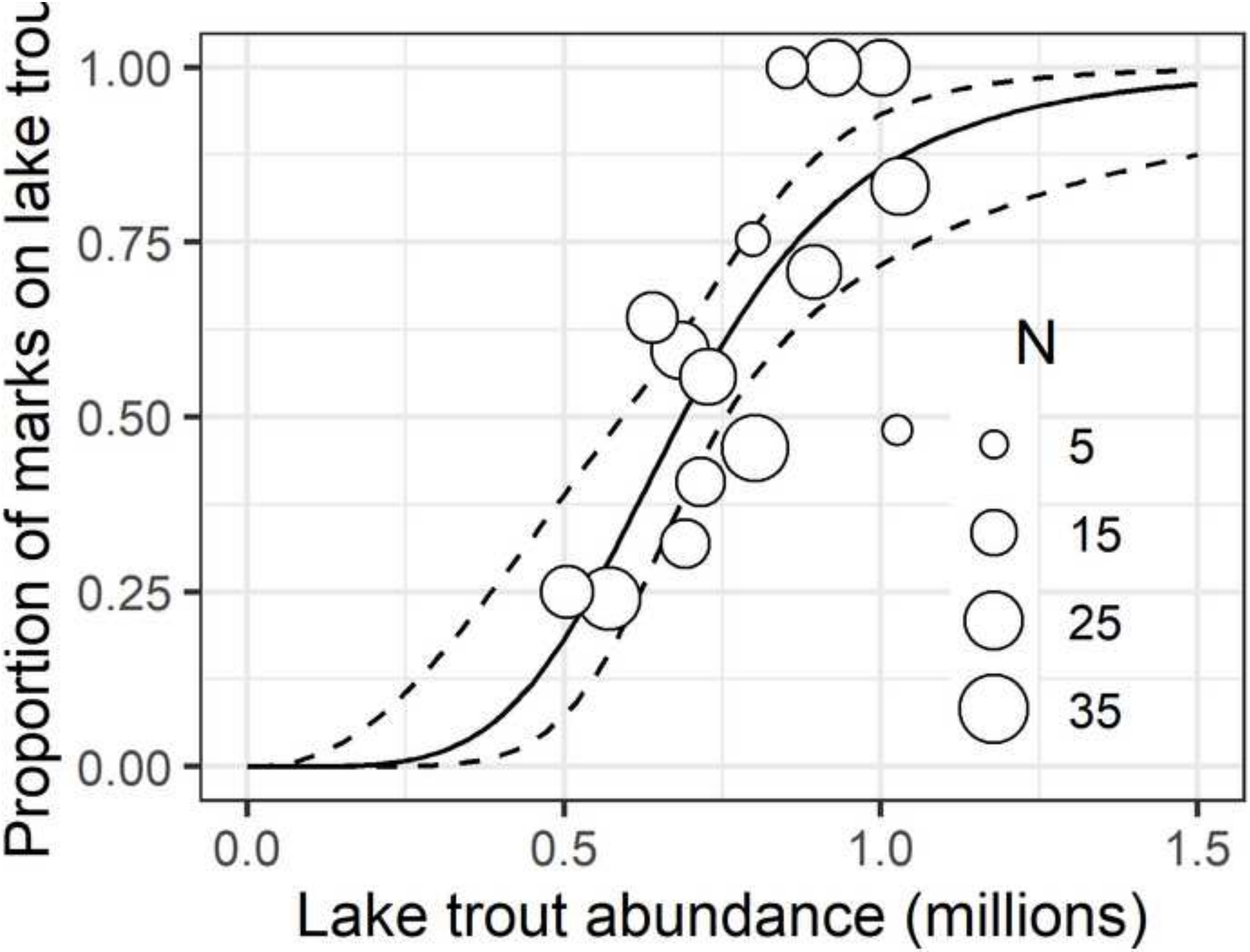
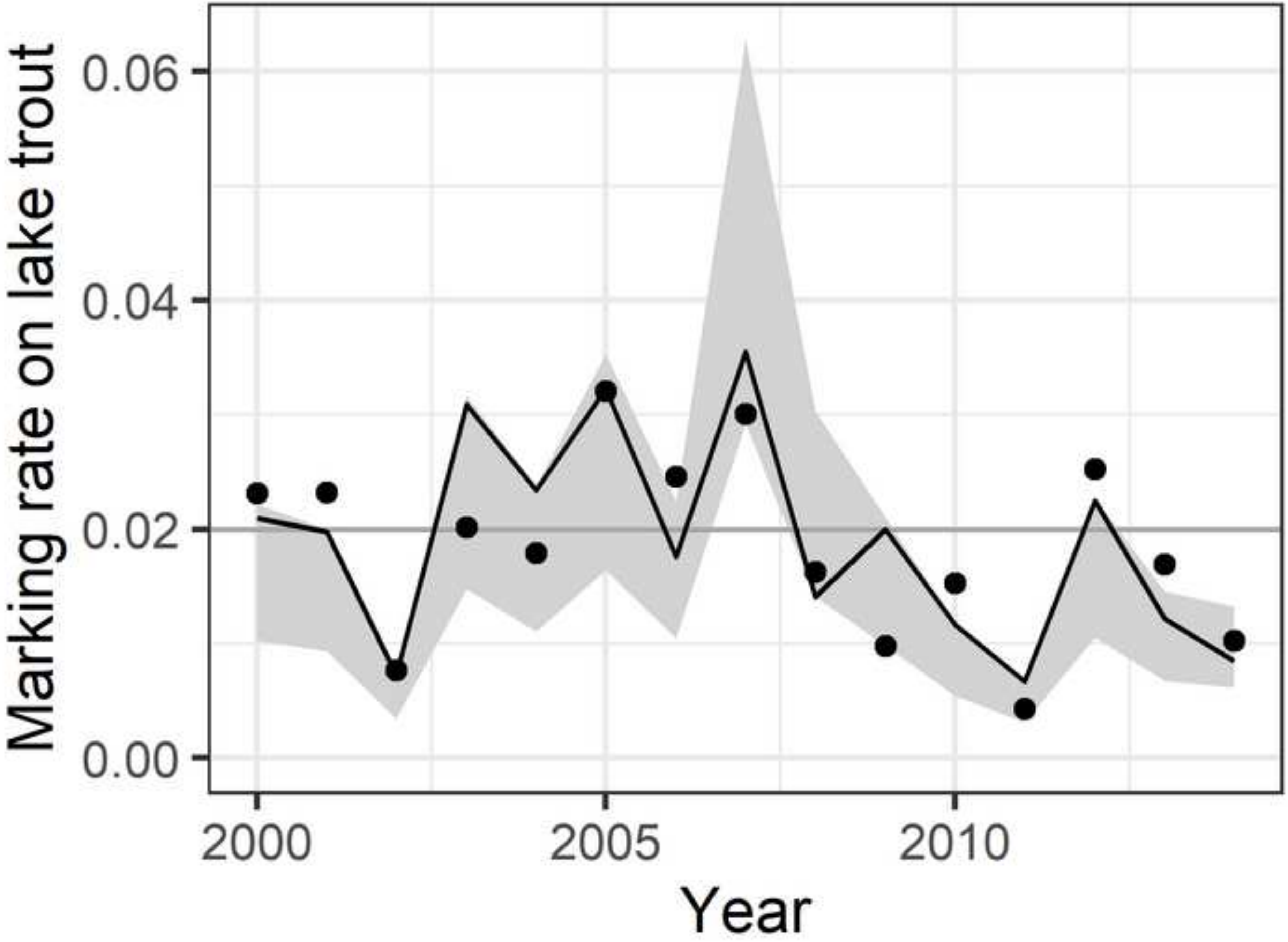

Proportion of marks on lake trou
1.00
0.75
0.50
0.25
0.00
0.0
0.5
1.0
1.5
Lake trout abundance (millions)
N
5
15
25
35

Figure 6


Marking rate on lake trout
0.06
0.04
0.02
0.00
2000
2005
2010
Year