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Oncorhynchus mykiss escaped from commercial freshwater aquaculture pens in Lake Huron, Canada

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ABSTRACT: The fate of farmed fish after escape from aquaculture operations, and their potential ecosystem impacts, remains a primary concern for the sustainable development of this industry. We simulated small- (<50 fish) and large-scale (500 fish) escape events of rainbow trout *Oncorhynchus mykiss* from 2 commercial operations in the North Channel of Lake Huron, the site of greatest freshwater production in Canada. Individual fish were either implanted with telemetry transmitters (n = 120) or marked with external tags (n = 1000) to monitor their movements and estimate survival and growth upon recapture. Rainbow trout dispersed quickly from the farms, and overall showed variable levels of site fidelity (2 to 40% after 3 mo), with most fish returning to the farm sites on multiple occasions after departure. Released fish were often detected in near-shore areas or at neighbouring commercial operations, but escapees were capable of long distance movements (>350 km), where they were located in rivers, open waters and in an adjacent Great Lake. Rainbow trout maintained high specific growth rates (average 0.33% d^{-1}) in the wild, both at and away from the farms. Known survival of escaped fish after a 3 mo period following release was ~50%, with some fish recaptured up to ~2.5 yr after release. Angling and avian predation accounted for the majority of mortalities. The ability of farmed fish to survive, successfully forage near and far from aquaculture operations and their preponderance to occupy near-shore habitats provide a strong basis for understanding the potential risks that escaped fish may pose to the fish community of Lake Huron.

KEY WORDS: Open-pen aquaculture · Escapee · Rainbow trout · Site fidelity · Dispersal · Survival · Growth

INTRODUCTION

Commercial open-pen farming of salmonid fishes (salmon, trout, charr) has seen unprecedented growth in the past half century, and, although husbandry practices and cage design strive to minimize losses, the escape of farmed fish to the wild remains a serious ecological concern associated with the aquaculture industry (Naylor et al. 2005, Weir & Fleming 2006, Jensen et al. 2010). Selection for high growth rate coupled with constant food availability and absence of predators, standard in aquaculture hatcheries, have resulted in farmed fish being maladapted to the wild environment (Gross 1998). Subsequently, salmonid escapees pose a number of potential negative ecological impacts to wild populations, including reduced fitness as a result of hybridization (McGinnity et al. 2003, Araki et al. 2007), as well as transfer of disease and competition for resources (Lura & Saegrov 1993, Bjørn & Finstad 2002). The escape of farmed fish therefore presents a significant challenge for the conservation of wild stocks of salmonids and the expansion of the aquaculture industry.

Much of what we know regarding the potential ecological impacts of escaped salmonids is from studies conducted on Atlantic salmon *Salmo salar* in the marine environment (e.g. Naylor et al. 2005, Rikardsen et al. 2008, Roberge et al. 2008, Jensen et al.

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2010). Yet, in Canada intensive open-pen aquaculture of rainbow trout *Oncorhynchus mykiss* has been occurring in freshwaters for the past 30 yr, with most production based in the North Channel and Georgian Bay of Lake Huron (Moccia & Bevan 2007, DFO 2009). Much like its marine counterpart, growth of the freshwater aquaculture industry has garnered concern regarding impacts on the local environment, focused largely on nutrient inputs, benthic impacts and escape of farmed fish (reviewed in Yan 2005, Podemski & Blanchfield 2006). However, unlike salmonid aquaculture in most other places, interbreeding between escaped farmed and wild fish is thought to be of limited concern as Lake Huron contains 'naturalized' rainbow trout populations from intentional stocking that has taken place since the late 1800s with a species that is not native to the area (OMNR 2006). Instead, concerns regarding escaped rainbow trout center on their potential impact on native fish communities through habitat and dietary overlap with other top predators. Oligotrophic freshwater systems, like Lake Huron, have low annual production; therefore, heightened concern exists about escape events that result in an influx of farmed fish with increased growth rates, because of the potential for increased foraging pressure on limited resources (Podemski & Blanchfield 2006, Arismendi et al. 2009).

The extent to which escaped fish might result in ecological perturbation is dependent upon a host of factors that include, among others, dispersal, growth and survival. High levels of fidelity to farm sites and consumption of waste feed are believed to minimize the impact of escaped fish by reducing competition with local fish for food and habitat (Phillips et al. 1985) and by increasing the potential for their subsequent recapture if fish are targeted promptly (Skilbrei & Jørgensen 2010, Chittenden et al. 2011). Alternatively, long-distance dispersal of farmed salmonids widens the area of possible impact, and hence risk associated with escapees (e.g. Jonsson et al. 1993, McKinnell et al. 1997, Whoriskey et al. 2006). The presence of large numbers of escaped farmed Atlantic salmon in the wild indicates that at least some are able to successfully forage and live outside of the aquaculture environment (Hansen et al. 1997, McKinnell et al. 1997), in spite of lower survival rates compared to their wild conspecifics (Einum & Fleming 2001).

At present, we lack even the most basic data on the behaviour, dispersal and survival of escaped farmed rainbow trout from freshwater commercial aquaculture operations in Canada. In a recent whole-ecosystem study, rainbow trout released from a model open-pen farm in a boreal lake showed high fidelity to the cage site, low survival and high growth rates in the wild (Blanchfield et al. 2009). The small size of the lake, a single aquaculture operation, no angling pressure and few avian predators may limit the applicability of this research to understanding the fate of escaped farmed fish from commercial freshwater aquaculture operations. Whereas, steelhead (anadromous form of *Oncorhyncus mykiss*, herein referred to as rainbow trout) released from a commercial marine aquaculture operation off the east coast of Canada showed high initial attraction to the farm site; after this initial period escaped fish were found at other aquaculture operations and showed directed movement towards a nearby hatchery (Bridger et al. 2001). The geographical size of Lake Huron (59 596 km^2 surface area) and the presence of multiple spatially distinct aquaculture operations indicate that the dispersal and behaviour of escaped farmed rainbow trout may be most similar to findings from marine systems. We simulated small- and large-scale escape events of rainbow trout from commercial freshwater aquaculture operations to determine the dispersal, survival and growth of farmed fish in the wild. Our specific objectives were to determine fidelity to cage sites, timing and magnitude of dispersal and the growth and survival of farmed rainbow trout within the North Channel and greater Lake Huron system.

MATERIALS AND METHODS

Study area

Lake Huron is connected with the other 4 Laurentian Great Lakes — Superior, Michigan, Ontario and Erie — together representing the largest freshwater ecosystem on earth (Abell et al. 2000). Manitoulin Island separates Lake Huron, Canada, into 3 distinct basins: the North Channel to the north, Georgian Bay to the east and the main basin to the south (Fig. 1a). The North Channel has a maximum length of 150 km and is 35 km at its widest, with a surface area of 3950 km^2 and a mean depth of 22 m, while Georgian Bay is roughly 4-fold larger at 15 111 km^2, with a mean depth of 44 m (Sly & Munawar 1988). Water temperatures around Manitoulin Island average 5°C, but can reach 20°C in the summer months to depths of 15 m (K. Patterson unpubl. data).

We conducted this study at 2 open-pen aquaculture operations in the North Channel, where all but

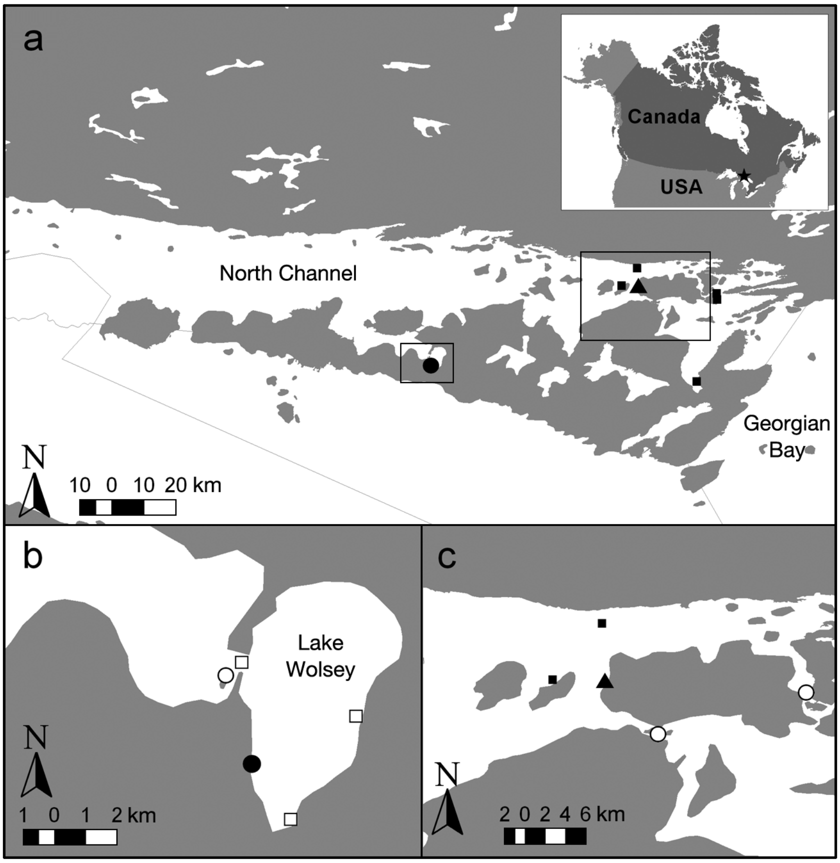

Fig. 1. (a) Study area showing the location of active aquaculture operations around Manitoulin Island (45° 48′ N, 82° 14′ W) in the North Channel of Lake Huron, Canada. The 2 farms where rainbow trout *Oncorhynchus mykiss* were released (Farm 1: black triangle; Farm 2: black circle) and nearby aquaculture sites (black squares) are noted. Boxes around farm locations indicate areas shown in detail in lower panels. Locations of radio or acoustic receivers in the vicinity of Farm 2 (b) and Farm 1 (c) are noted (Lotek: open circles; Sonotronics: open squares)

1 of the ~10 commercial farms in Lake Huron are located (Fig. 1). Both study farms have been active for the past 2 decades and annually produce ~350 to 400 t of rainbow trout. Farm 1 is located in a deep (Z_{max} = 50 m), open (~1.5 km wide) channel with minimal geographical restrictions to Georgian Bay and the main basin of Lake Huron, and is representative of most commercial operations in the area. Several other aquaculture operations are located within 5 to 26 km of Farm 1 (Fig. 1a). Farm 2 is located in a distinct lake (Lake Wolsey; area = 23.2 km^2, Z_{max} = 26 m), which connects to the North Channel through a narrow (~0.1 km wide), 5 to 7 m deep channel (Fig. 1b). Both operations raise diploid all-female and regular stock (male and female) domestic rainbow trout from fingerlings (Spring Valley or Trout Lodge strains) to market size (~1 kg) year round, with most production occurring between May and October.

Fish tagging

In July 2008 and May 2009, we implanted 120 farmed rainbow trout with telemetry transmitters (Table 1). Fish were approximately 1 yr of age, having been raised from fingerlings in the year prior to release. Rainbow trout were randomly selected from commercial operations with the requirement that transmitter weight be <2% of body weight (Winter 1983). In 2008, we surgically implanted 20 trout at each farm with equal numbers of 2 types of transmitters: radio transmitters (R) (Lotek, Model MCFT-3A, 16 × 46 mm, weight in water: 6.7 g) and combined acoustic-radio transmitters (CART) (Lotek, Model CART 16-1, 16 × 60 mm, weight in water: 13.5 g). In 2009 we implanted a total of 80 rainbow trout, 40 at each farm, but because we encountered difficulties detecting signals from radio transmitters, we limited our use of this transmitter type. At Farm 1 in 2009, we implanted 10 radio transmitters that incorporated pressure and temperature sensors (Lotek, Model SR-TP-16-25, 11 × 55 mm, weight in water: 8.0 g, depth accuracy: 0.21 m, temperature accuracy: 0.8°C) and 30 CARTs (Lotek, Model CS-16-25, 16 × 57 mm, weight in water: 14.0 g). At Farm 2, we implanted 30 rainbow trout with acoustic transmitters (A) (Sonotronics, Model CT-82-2-1, 15.6 × 53 mm, weight in water: 9.0 g) and 10 with pressure-sensing acoustic transmitters (A-P) (Sonotronics, Model DT-97-L, 15.6 × 80 mm, weight in water: 11.0 g, depth accuracy: 0.35 m) (Table 1). Acoustic signals were transmitted every 3 s (Sonotronics) or 4 to 6 s (Lotek).

Rainbow trout were seined by farm staff into the corner of a net pen the day of surgery and transferred to a pre-surgery holding container. Fish were individually dip netted and placed into an anaesthetic solution of 60 mg l^{-1} tricaine methanesulfonate (TMS) buffered with sodium bicarbonate in ambient temperature lake water. Once anaesthetized, fork length (mm) and weight (g) of each fish were determined before they were placed ventral side up in a V-shaped surgical apparatus; surgeries followed standard protocols (see Blanchfield et al. 2009, Patterson 2010). For radio and CART transmitters, an exit site for the antenna wire was made with a 16 gauge needle, posterior to the incision site, at a slight angle to the body to reduce irritation during movement. The antenna wire (44 cm) was fed through the needle and out the body cavity. Incisions were closed with 3 monofilament sutures (Monocryl). Fish were immediately transferred to a recovery bath of fresh lake water and, once upright and active, were placed in a sectioned off corner of a net pen where they remained for ~24 h. All fish exhibited normal swimming behaviour and were individually released to the wild by dip net the day following surgery (Table 1).

In 2009 an additional 1000 rainbow trout, 500 at each farm, were tagged with an individually labelled external T-bar anchor tag (Floy Tag) to simulate a large-scale escape event (Table 1). Tags were inserted in the muscle tissue below the base of dorsal fin and rotated 90° so that the tag anchored between bony supports of the dorsal spines. Each external Floy tag and telemetry transmitter had a contact e-mail, telephone number, reporting details (location, weight and length) and 'reward' inscribed on it.

Telemetry data collection

Prior to the release of rainbow trout, receiving stations (Lotek) were installed to detect fish presence at each farm site. These systems consisted of a radio antenna (6-element Yagi) placed on shore central to the farm site, an omni-directional hydrophone submerged 1.8 m below the surface and a receiver (Model SRX_400). Transmitters were detected to a distance of 400 m for range tests conducted away from the cages (Patterson 2010). We confirmed that transmitters were detectable across the entire area of each farm, although the distance from receiver to the outer edge of the most distant cages was 2-fold greater at Farm 2 (144 m) than at Farm 1 (64 m). Because the various telemetry systems and transmitters had similar capabilities, we assumed that fish detection distance (400 m) was comparable at each farm site between years. Three additional radio-only receiving stations ('gate' stations) were strategically placed in narrow areas (167 to 409 m width) to monitor the movement of fish into larger bodies of water (Fig. 1). The receivers monitored fish presence from 2 July to 18 October 2008 (108 d) and from 12 May to 19 September 2009 (130 d).

In 2009, 4 submersible ultrasonic receivers (Sonotronics Model SUR-2) were hung 1 to 3 m below anchored surface buoys in the waters at and around Farm 2 to monitor fish presence within the lake and fish moving out of the lake (Fig. 1b). All receivers recorded the transmitter identification code, as well as the date and time of detection. Lotek receivers recorded a power value of each tag reading, and, when sensor transmitters were detected, the water depth (m) or temperature (°C) was recorded on both receiver types. Receivers were downloaded at least once every 7 to 14 d.

Manual location of telemetry fish (termed 'tracking') was undertaken to locate escaped rainbow trout once they had dispersed from the farm. The system (Lotek) was comprised of a 5-element Yagi antenna, a tethered directional hydrophone, a sonic upconvertor to convert acoustic signals to SRX compatible radio frequency, a SRX_400 receiver, and a 12 volt battery. Manual tracking followed standard methods (Blanchfield et al. 2005) and consisted of 10 and 14 efforts around Farm 1 in 2008 and 2009, respectively, and 8 efforts around Farm 2 in 2008. Generally, listening points were separated by 1 km (500 m range tag) unless an obstruction (e.g. a cove) required more frequent scans to ensure an area was covered. In order to contact as many dispersed individuals as possible in a large system the areas scanned were not consistent among surveys, but contingent on factors such as daily weather and previous locations

Table 1. *Oncorhynchus mykiss*. Mean (±1 SE) fork length and weight, and numbers of individually marked farmed rainbow trout released (n) into Lake Huron, Canada, from 2 commercial aquaculture operations, Farm 1 and Farm 2. The number (percentage in parentheses) of tagged fish reported recaptured through recreational angling is noted. Fish were implanted with a telemetry transmitter or Floy tag in both study years. CART: combined acoustic radio transmitter; R: radio; A: acoustic; A-P: acoustic with pressure sensor

Release site	Release date	Tag type	n	Recaptured (no. [%])	Fork length (mm)	Weight (g)
Farm 1	2 Jul 2008	CART, R	10, 10[a]	1 (10)	387 ± 4	884 ± 30
	12–13 May 2009	CART, R	30, 10[a]	4 (13)	354 ± 2	775 ± 14
	25–26 May 2009	T-bar	500	43 (9)	344 ± 1	732 ± 7
Farm 2	4–12 Jul 2008	CART, R	10, 10[a]	1 (10)	434 ± 7	1384 ± 69
	15–16 May 2009	A, A-P	30, 10	9 (23)	389 ± 3	960 ± 25
	27–28 May 2009	T-bar	500	51 (10)	351 ± 1	710 ± 8

[a]10 rainbow trout implanted with radio transmitters were not consistently detected by receiver stations and removed from dispersal and fidelity data analyses (see 'Materials and methods')

of individuals. Tracking was carried out up to 30 km from the release farm.

Reward notices were posted in localities with high angler traffic, such as local resorts, bait shops and boat launches prior to the release of fish, and interviews with regional newspapers were conducted throughout the study. A shore-based creel survey occurred in close proximity to each farm site (Farm 1: 6.4 km; Farm 2: 3.6 km) 1 d wk^{-1} from June to September 2009. Interviews were conducted with all anglers accessing these points to gather information about target species, gear used, catch and areas fished. Surveys were designed and implemented to obtain information on fishing effort around each farm site and body size information of any tagged rainbow trout. The same questions were applied to anglers via phone or e-mail when reporting a tagged fish. We also documented fishing effort at each farm with remote cameras (Cuddeback®) that took photographs hourly for the duration of the study.

Data analysis

To exclude false detections, an individual fish was considered to be present at a farm site only if it was detected twice by a farm receiver within a specified amount of time (Sontronics: 3 min; Lotek: 15 min) determined by transmitter trials and consultation with telemetry equipment manufacturers. The date of release was set as Day 0 for all released fish to standardize the data sets.

We quantified time to initial dispersal for individual rainbow trout with telemetry transmitters as the number of days before a fish departed a farm for a period >24 h. Individual fish were considered to exhibit site fidelity if detected at the release site (i.e. present) at any time during 24 h of a single day. Fish tagged with external Floy tags were considered to demonstrate site fidelity if they were reported angled within 500 m of the release farm. Dispersal distance was calculated as the maximum linear distance (km) an individual was located away from the farm via manual location, gate station detection, or angler recapture of both telemetry- and Floy-tagged fish.

We considered the following instances as evidence of mortality of released rainbow trout: (1) angler return of tagged fish, (2) lack of movement of a telemetry transmitter, or (3) recovery of a transmitter (e.g. on shore or in shallow waters). Any fish detected after the monitoring period was considered alive in our monitoring period. Size information gathered from angler returns of Floy-tagged fish was compared to fork length and weight at initial tagging. A single outlier (unrealistic change in weight over time) was removed from all growth analyses. Measurement of length (methodology unknown) reported by anglers was assumed to be total length (TL) and was converted to fork length (FL) as follows: FL = TL × 1.071^{-1} (Carlander 1969).

Statistical analysis

Data analyses were completed with Statistica V. 6.1 (Statsoft) software using a combination of parametric and non-parametric tests (specified in 'Results') depending on data normality (Shapiro-Wilk's test) and homogeneity of variances (Brown-Forsythe test). Fish mass was log transformed, and initial fish size between study years and cage sites was tested with a 2-factor ANOVA. Fidelity of escapees to cage sites was compared between years (summer 2008 vs. spring 2009), at 1 wk, 1 mo and 3 mo, using Mann-Whitney *U*-test. We compared whether there was evidence of directionality in dispersal locations of released rainbow trout from manual tracking and angling recapture datasets using Rayleigh's test, which calculates the probability that the data are uniformly distributed. If the null hypothesis is rejected, the dispersal of fish exhibits significant directional orientation. We examined differences between farms in numbers of captures (Chi-squared analysis) and dispersal distances (*t*-test) of Floy-tagged rainbow trout. The influence of time at large on dispersal distance was determined with linear regression. We tested for the influence of body size on fidelity and survival by comparing the initial mass of rainbow trout known to stay at the farm versus those that dispersed, and those known to survive versus confirmed mortalities, respectively (*t*-test). Lastly, we examined whether initial size at stocking related to the growth rate of escaped fish (Pearson's correlation coefficient) and whether growth rates of recaptured rainbow trout differed when found in close proximity to cage sites versus when captured away from the influence of aquaculture operations (*t*-test).

RESULTS

We determined that the ability to detect radio transmitters was limited in our study system (Patterson 2010), and therefore data collected from *Oncorhynchus mykiss* with this transmitter type implanted (n = 30) were excluded from analyses of site fidelity and dispersal, but included in survival estimations (Table 1). Three of the remaining 90 fish released with telemetry transmitters were never detected and were also excluded from all analysis (n = 87). Rainbow trout released from both farms were significantly larger in 2008 than 2009 (2-factor ANOVA; year: $F_{1,86} = 43.8$, $p < 0.001$). Due to different release dates between years, July 2008 versus May 2009, the fish would have been 2 to 3 mo older in 2008 (Table 1). Rainbow trout from Farm 1 were significantly smaller than fish released from Farm 2 in both years (farm: $F_{1,86} = 69.0$, $p < 0.001$: honestly significant difference [HSD] post hoc; $p < 0.001$), although there was no significant difference in fish size between years at Farm 1 (HSD post hoc; $p > 0.05$).

Fidelity to aquaculture sites

Initial dispersal of acoustically tagged rainbow trout away from commercial farms in Lake Huron ranged from hours to months (mean ± 1SE: 6.3 ± 1.8 d; range = 0.001 to 88.5 d). Except for Farm 2 in 2008, almost all (>90%) rainbow trout had departed the vicinity of the farms for a period of at least 24 h within the first 3 wk of being released (Fig. 2). Once initially dispersed, 18% of fish never returned, while all other fish remained at large from 1 to 102 d (mean ± 1SE: 12.4 ± 3.4 d) before returning to their release site. As a result, fidelity to the farm sites was variable over time. The number of tagged fish remaining at the farms steadily declined with 10 to 72% present 30 d post release (Fig. 2). Over the next 60 d a resident population of escaped rainbow trout appeared to become established that consisted of 2 to 47% of released fish depending on the farm site and year of release (Fig. 2). After 90 d in the wild, site fidelity of escaped fish ranged from 2 to 40% (year- and site-specific averages for the final week in which fish were monitored; 2008: Farm 1 = 17%, Farm 2 = 40%; 2009: Farm 1 = 2%, Farm 2 = 18%). Variability in the daily numbers of released rainbow trout observed at each of the farm sites within a specific year was a result of departed fish intermittently returning to sites of release after a period of absence (e.g. Fig. 3). Only at Farm 1 did we observe long-term reliance upon the cage site, whereby 2 rainbow trout (20%) released in 2008 were frequently present at the cage in the following year (Fig. 3).

Differences in site fidelity of released rainbow trout were apparent between study years at individual farm sites (Fig. 2). Fish released in summer (July 2008) demonstrated greater reliance on the farm at 1 wk, 1 mo and 3 mo following release than those released in spring (May 2009) (Mann-Whitney *U*-tests, Farm 1: $Z = 2.87$ to 3.13, $p < 0.01$; Farm 2: $Z = -3.13$, $p < 0.01$).

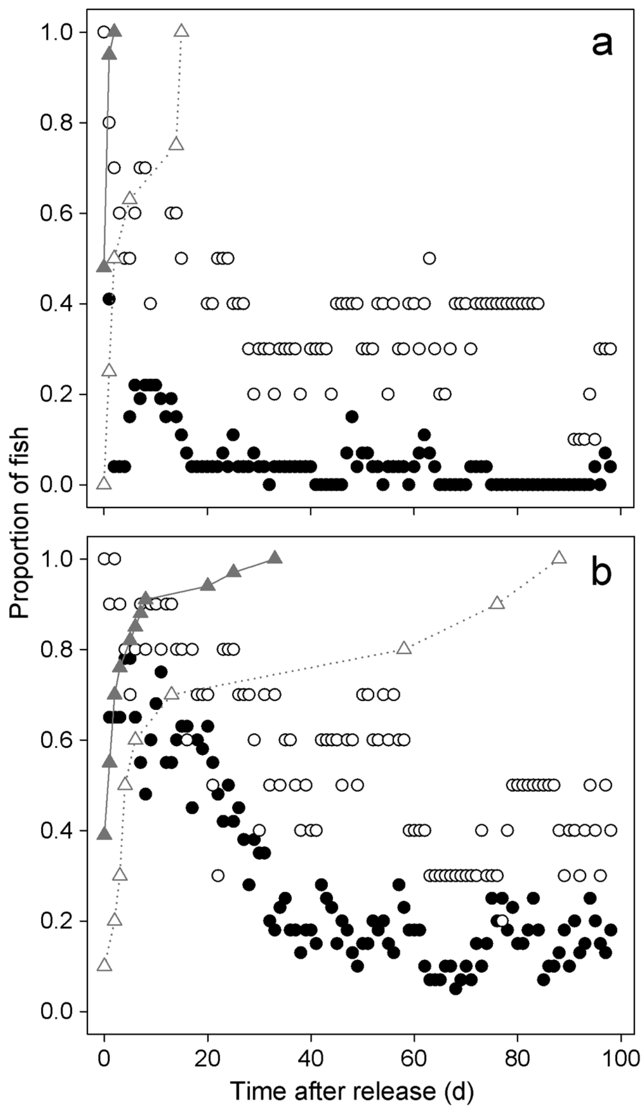

Fig. 2. *Oncorhynchus mykiss*. Daily proportion of acoustically tagged farmed rainbow trout present at 2 commercial aquaculture sites in Lake Huron, (a) Farm 1 and (b) Farm 2, from which they were released. Fish were monitored for 14 wk in 2008 (open circles; 2 July to 19 October) and 2009 (solid circles; 15 May to 20 September). Also shown is the cumulative time required for all rainbow trout to initially disperse from release sites (defined as not detected by the farm receiver for a period of 24 h) in 2008 (open triangle, dashed line) and 2009 (solid triangle, solid line)

The mean depths of individual rainbow trout when present at the farm sites ranged from 0.3 to 3.0 m at Farm 1 (n = 10 fish, n = 3442 detections) and 0.1 to

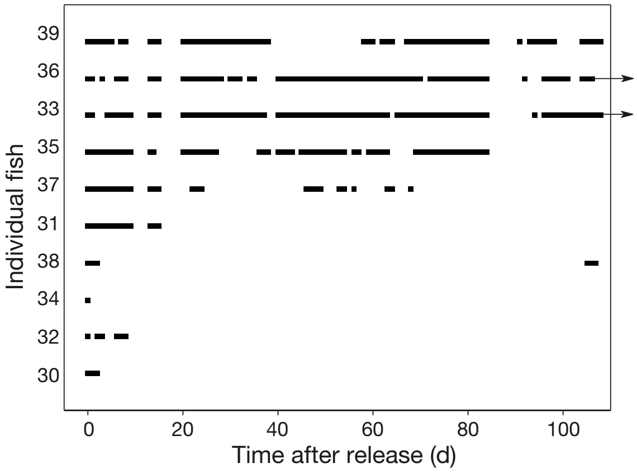

Fig. 3. *Oncorhynchus mykiss*. Patterns of site fidelity for 10 rainbow trout released from Farm 1 and monitored by radio-acoustic telemetry for 14 wk in 2008. Each block represents the daily presence of an individual based on detection by the farm receiver. Two rainbow trout (arrows) were detected at Farm 1 the following year (2009)

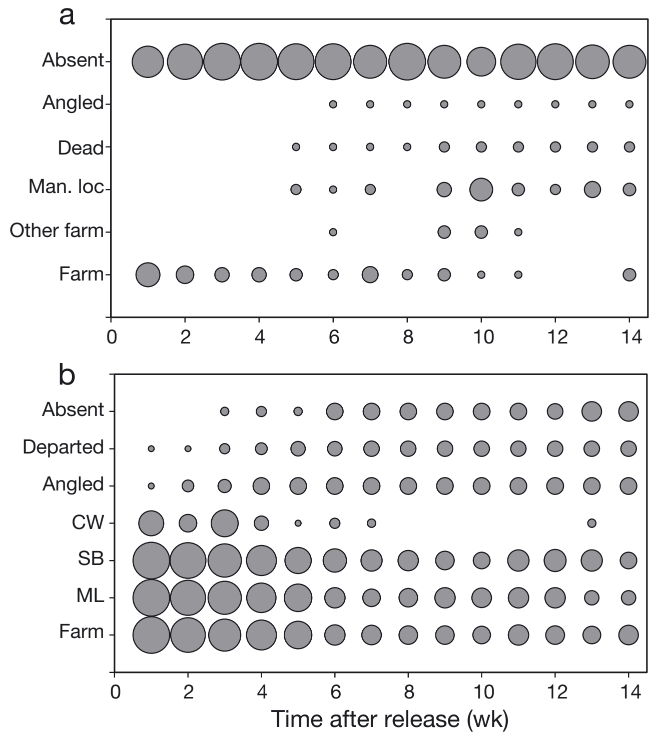

Fig. 4. *Oncorhynchus mykiss*. Fate and movement of telemetry-tagged rainbow trout released from 2 farms, (a) Farm 1 and (b) Farm 2, in the North Channel of Lake Huron in 2009. The size of the circle shows the proportion of fish observed in each category; the smallest circle indicates a single fish, while the largest circle represents 26 of 30 fish at Farm 1 and 39 of 40 fish at Farm 2 in 2009. Absent: fish was not located within the week by any means; departed: a fish was detected moving out of the system via a receiver; man. loc.: manually located; farm: release site. At Farm 2, 3 additional receiving stations monitored fish movement (refer to Fig. 1b) — CW: gate station from Lake Wolsey to the North Channel; SB: south basin; ML: mid-lake

10.1 m at Farm 2 (n = 10 fish, n = 43 146 detections) for fish fitted with pressure-sensing transmitters. The proportions of fish detections in the upper 1 m of the water column were 7 and 37 % at Farms 1 and 2, respectively. At Farm 1 maximum fish depth (10 m) was less than the lake bottom depth at the cage site (20 m). At Farm 2, 1 % of all fish detections were at or near the lake bottom under the cages (13 m). Fish manually located away from Farm 1 were detected at depths of 0.4 to 3.4 m, (mean: 2.0 m, n = 19). Fish detected away from Farm 2 in Lake Wolsey (n = 10) were at depths of 0.1 to 8.2 m, and in total 36 and 73 % of fish detections (n = 93 058) were in the upper 1 m of the water column at the south basin and mid-lake receivers, respectively (Fig. 1b). Mean temperatures of individual fish detected at Farm 1 ranged from 9.4 to 27.6°C.

Patterns of escapee dispersal

Rainbow trout released from Farm 1 rapidly dispersed outside of the monitoring range in each year of the study (Fig. 2). In particular, in 2009, a large proportion of tagged fish were absent (i.e. dispersed) over the 14 wk period (Fig. 4), of which, 44 % never returned to the farm site. A quarter of the released fish (7 of 27) were never detected by any means once they left the farm. Rainbow trout released from Farm 2, the semi-enclosed aquaculture operation, were slow to initially disperse (absent from farm for >24 h) in both years, remaining at the farm site for up to 1 to 3 mo post release (Fig. 2). In 2009, tagged rainbow trout released from Farm 2 made movements throughout the lake in the first few weeks, being detected on all receivers within Lake Wolsey, but were also always detected daily at the farm site and not considered dispersed. This pattern continued for the majority of fish from Farm 2 throughout the monitoring period. In total, 18 % (7 of 40) of rainbow trout were detected 'departing' from Lake Wolsey 2 to 36 d post release in 2009 (Figs. 1b & 4b), while none were detected moving into the North Channel when released in July 2008.

Manual locations of rainbow trout dispersed from Farm 1 in 2009 showed that fish displayed directional preference, moving west more often than east of the release site (Rayleigh's test, $z = 5.87$, $p < 0.05$). Escapees were detected up to 23 km from the release site, with a maximum distance of 16.2 km between detections of an individual. Based on manual fish locations (n = 56), a majority of fish (56%) were detected in near-shore areas (<1 km from shore), while roughly a quarter of detections (22%) included both off-shore habitat and other commercial farms (Fig. 5a). Three individuals were detected at 2 different fish farms located within 6 km of Farm 1 (Fig. 4a). One of these escapees displayed a degree of site fidelity to a foreign farm, being detected there on 3 different occasions. An additional fish was angled at a neighbouring farm 36 d post release.

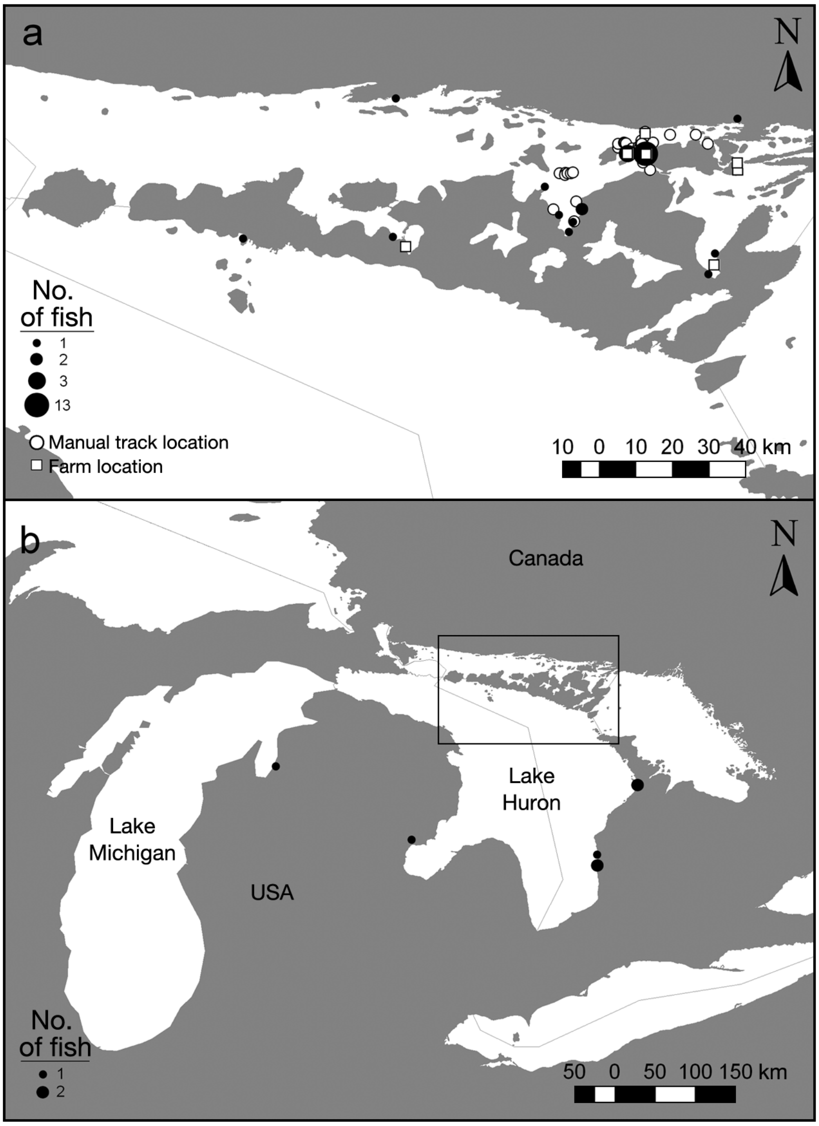

Fig. 5. *Oncorhynchus mykiss*. Locations of telemetry- (open circles) and Floy-tagged (solid circles) rainbow trout released from Farm 1. Open squares indicate farm locations. The number of escapees are represented by the size of the symbol for fish detected or captured (a) in the Manitoulin Island region and (b) the extent of the range over which Floy-tagged fish were caught, including the south end of Lake Huron and Lake Michigan

Dispersal of Floy-tagged fish

A total of 97 (9.7%) externally tagged farmed rainbow trout had been reported as captured by anglers within 31 mo (December 2011) of their release. Roughly equal numbers of fish from each farm were recaptured; 43 and 51 fish from Farms 1 and 2, respectively (3 returns did not indicate Floy tag number). Where location data were available (n = 82), greater than one-third (39%) of the tagged fish were recaptured within close proximity (500 m) of the commercial aquaculture release sites, 31% were angled within 5 km of the farms and the remaining fish (30%) were roughly equally captured at medium (5 to 50 km) and far (>50 km) distances away from the farm sites, ranging as far away as 360 km (Fig. 5). Almost all recaptured fish from Farm 2 (91%) were angled within a 5 km radius of the release site, with almost half (47%) caught within 500 m of the farm. In contrast, 29% of rainbow trout recaptures from Farm 1 occurred at the site, although the difference in capture rates between farms was not significant (χ^2 = 3.02, p = 0.082). We observed significantly greater angling pressure in close proximity to Farm 2, where 278 boats with an estimated 550 anglers (~17 boats or 34 anglers wk^{-1}) were observed in 115 d by automated cameras at each farm. At Farm 1, 18 boats with an estimated 23 anglers (~1 boat or 1 angler wk^{-1}) were observed over the same period.

Floy-tagged rainbow trout not captured in close proximity to farm sites and not within 2 wk of initial release (n = 41) were angled significantly farther away from Farm 1 (mean ± 1SE: 93.6 ± 25.1 km; maximum = 360 km) than fish released from Farm 2 (26.5 ± 15.4 km; maximum = 200 km) (t-test: t_{39} = 3.12, p = 0.0034). Distance away from site of release upon recapture was positively related to time at large (linear regression: $F_{1,39}$ = 8.75, p = 0.0052, R^2 = 0.16). Rainbow trout recaptured away from Farm 1 showed no directional preference in their movements (Rayleigh's test, $z = 0.93$, $p > 0.05$). Two-thirds of angled escapees from Farm 1 (n = 36 with precise recapture location) were equally captured at the farm site or in near-shore habitats (<1 km from land), with the remaining captures at other aquaculture operations (11%) or in rivers (22%). Rainbow trout were caught between the mouth and 12.5 km upstream in rivers located 23 to 360 km from Farm 1, with 2 instances of 2 fish being captured in the same river on separate occasions (Sauble River, Ontario, 192 km away, and Maitland River, Ontario, 280 km away) (Fig. 5b). Angling captures of fish released from Farm 2 were split evenly between the farm site and near-shore areas. There was no difference in initial body weight between fish that dispersed from the farm compared to those that exhibited site fidelity at either farm (t-test: Farm 1, $t_{33} = -0.57$, p = 0.58; Farm 2, t_{25} = 0.016, p = 0.99).

Survival and growth

The fate of all telemetry-tagged rainbow trout (n = 117) released into Lake Huron from commercial farms at the end of each 3 mo monitoring period was as follows: 52% of fish were alive, 15% were dead and the remaining fish (33%) were unaccounted for. The majority of mortalities (n = 10) were attributed to angling; 5 fish died due to unknown causes and 2 deaths were by avian predation. Beyond the monitoring period (>3 mo) there were 7 further angling mortalities and 1 unknown cause of death. Overall, known mortality of telemetry-tagged fish was 21% at the end of the study (December 2011). Telemetry-tagged fish were captured by angling between 6 and 901 d post release. Predation on farmed rainbow trout occurred in each year, with tags recovered from the nests of an osprey *Pandion haliaetus* and a double-crested cormorant *Phalacrocorax auritus*, first detected 7 and 54 d after release, respectively. Overall, body size at release did not appear to influence survival. There was no difference in initial fish size between fish that survived (n = 53) and those known to have died (n = 25) (t-test, FL: $t = 0.93$, p = 0.35; weight: $t = 0.96$, p = 0.34).

Floy-tagged fish angled outside of the acclimation period (2 wk post release) and with full information (date, mass, length; n = 58) showed positive mean specific growth rate for fork length (mean ± 1SE: 0.12 ± 0.02% d^{-1}) and mass (0.33 ± 0.05% d^{-1}). The period of greatest growth occurred during the first 3 mo after release, at which time some fish achieved specific growth rates as high as 1.2% d^{-1} (Fig. 6). As an extreme example, a rainbow trout angled 478 d post release exhibited an 8-fold increase in mass, from 550 to 4636 g. Nonetheless, growth was highly variable, and some fish did not grow or even lost weight (Fig. 6). Initial size at stocking was not strongly correlated to growth rate of escaped fish (Pearson's correlation coefficient, r = –0.09), and there was no significant difference in growth rates of fish angled at the farm sites and those dispersed from the release location ($t_{1,53}$ =0.46, p = 0.32) (Fig. 6).

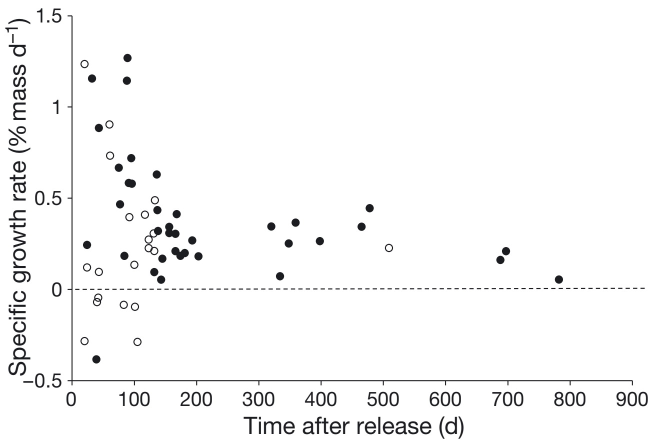

Fig. 6. *Oncorhynchus mykiss*. Specific growth rate of Floy-tagged rainbow trout released from 2 commercial aquaculture operations that were recaptured by angling at the farm sites (open circles) or >500 m away from the farm sites (i.e. dispersed) (solid circles). The dashed line on the y-axis at 0 separates fish with positive (above line) and negative (below line) specific growth rates

DISCUSSION

Simulated small- and large-scale escape events of tagged farmed rainbow trout *Oncorhynchus mykiss* from commercial aquaculture operations in the North Channel area of Lake Huron, the site of most freshwater production in Canada, revealed variable levels of site fidelity over time that were a result of frequent return visits to cage sites after rapid initial dispersal. Farmed rainbow trout were capable of long-range movements and high growth rates in the wild, but were susceptible to avian predation and to angling, especially at the aquaculture site where fidelity was greatest.

We observed year- and site-specific variability in numbers of rainbow trout exhibiting long-term (3 mo) site fidelity (2 to 40%) to commercial farms. In general, an initial rapid dispersal of farmed fish, with half departing in the first week, was followed by a steady decline in fish presence over the next 3 mo until

<40 % of fish remained, although at no time throughout the study did 100 % of fish disperse. Specific factors influencing site fidelity of escapees to commercial farms are poorly understood, although it is generally believed that farm processes, especially feeding regime may attract escaped and native fish (Bridger et al. 2001, Blanchfield et al. 2009). Despite the fact that in Lake Huron, large aggregations of native prey and top predator fishes have been found at cage sites (Johnston et al. 2010), we did not observe strong attraction by escaped rainbow trout.

Our finding of limited site fidelity by escaped rainbow trout is consistent with other studies that have simulated the release of adult farmed fish from commercial operations. For example, rainbow trout initially exhibited a high degree of site fidelity to a marine farm located in a secluded bay that decreased to <10 % of fish remaining within months (Bridger et al. 2001). In contrast, complete dispersal of salmonids occurred within days of release at an open marine site and at a lake site, with no continual use of the farms (Whoriskey et al. 2006, Lindberg et al. 2009). Likewise, dispersal of all but a small proportion (~20 %) of escaped Atlantic cod *Gadus morhua* occurred within 1 to 2 wk from fish farms in a Norwegian fjord (Uglem et al. 2008, Serra-Llinares et al. 2013). Similar to the present study, however, 40 % of released cod returned to the farm, with some individuals remaining at the farm site until the end of the 12 to 13 wk monitoring period (Uglem et al. 2008). Although we found higher site fidelity of fish at the more enclosed site (Farm 2), long-term site fidelity was only observed at Farm 1, the more open site. Blanchfield et al. (2009) found escapee rainbow trout incorporating the cage site into their home range up to 3 yr after release from an experimental farm into a small lake. However, the present study is the first to report long-term site fidelity at commercial freshwater operations.

An important finding from our study is that most escaped rainbow trout returned to the site of release after their initial dispersal. Thus, our evaluation of site fidelity underestimates the total number of escapees present at freshwater aquaculture operations because different individuals were present over time. The majority of trout (63 to 75 %) returned to the open site (Farm 1) after initial dispersal, while even greater numbers of dispersed fish (97 to 100 %) returned to the enclosed site (Farm 2). Further, some rainbow trout individuals at both farms returned to their release sites after spending >3 mo away. A similarly high percentage of rainbow trout returned to the cage site in a small lake (Blanchfield et al. 2009), whereas 40 % of farmed cod released in an open fjord returned to the cage site (Uglem et al. 2008); yet in other studies, none of the escaped fish returned to farm sites (Whoriskey et al. 2006). It is generally thought that return rates of escapees decline as the size of the water body increases (see Whoriskey et al. 2006, Uglem et al. 2008, Blanchfield et al. 2009). The present study was carried out in a large freshwater system, the Laurentian Great Lakes, yet a minimum of ~60 % of escaped fish returned to their release site. We suggest that dispersal is likely more complex than water body size alone and that a suite of factors can influence attraction to aquaculture operations.

The presence of other fish farms, hatcheries, or rivers has been shown to influence patterns of movement by escaped fish (e.g. Carss 1990, Bridger et al. 2001). In the present study, rainbow trout released from Farm 1 were occasionally detected (20 %) or angled at neighbouring commercial operations. Acoustic telemetry studies have shown that escaped farmed fish are present around spatially congregated sites of commercial aquaculture (Bridger et al. 2001, Uglem et al. 2010, Skilbrei 2012), potentially driven by the abundance of waste feed (Dempster et al. 2009), by high densities of natural prey items (Dempster & Taquet 2004), or because a farm may provide shelter from predation (Bridger et al. 2001, Dempster & Taquet 2004). The nearest commercial operation to Farm 2 was 90 km away and may, in part, explain the greater fidelity to this site. In addition, the lower dispersal and greater fidelity of fish released from the enclosed farm site (Farm 2) may have been a result of limited opportunity to disperse because of the potential barrier that the shallow channel, which connects the lake to large open water areas of the North Channel, poses relative to the open site (Farm 1).

Large-scale releases of externally tagged rainbow trout, particularly those released from Farm 1, revealed a much more widespread distribution than could be determined through telemetry. Escaped fish were found to occupy habitats similar to those of naturalized rainbow trout in the area. Over half (55 %) of the fish released from Farm 1 were angled in near-shore habitats, including numerous recaptures (>20 %) in rivers along the north shore and main basin of Lake Huron, as well as in Lake Michigan, away from any aquaculture operations (Fig. 5). Studies of naturalized rainbow trout movement in the Great Lakes found fish travelling up to 290 km in 94 d in Lake Ontario (Haynes et al. 1986) and 20 to 201 km in Lake Erie (Wegner et al. 1985). The distance over which fish were angled (0 to 360 km) demonstrates the ability of escapees to undertake long-distance movements on the same scale as naturalized populations. The rapid ability of farmed rainbow trout to pervade the lacustrine and riverine habitats of wild fish increases the likelihood of interaction and competition within the Lake Huron fish community and beyond into Lake Michigan.

Dispersal rates of escaped farmed fish provide the basis to estimate recapture potential should a large-scale escape of aquaculture fish occur. Recent studies have shown that for some farmed species, low initial dispersal would allow for high recapture of escaped fish if prompt action were taken (Skilbrei & Jørgensen 2010, Uglem et al. 2010, Chittenden et al. 2011). Variability in dispersal rates by farmed rainbow trout in the present study makes it difficult to predict the effectiveness of a targeted recapture program (commercial or recreational) for escapes in Lake Huron. In general, the relatively quick movement of fish away from farms would require an immediate recapture effort as fish, once dispersed, are capable of long-distance movements. Because there is not a commercial fishery for rainbow trout in Lake Huron, recapture of escapees would primarily occur through line and pole recreational fishery, which in our study returned a small proportion of escaped fish (10 %), even with high angling pressure (~34 anglers wk^{-1}) at the site with the greatest site fidelity (Farm 2). Therefore, recapture efforts may yield substantially lower returns in Lake Huron than the aforementioned studies, which showed high potential for the recapture of escapees through commercial and/or recreational netting or angling.

Estimating the survival of escaped farmed fish is critical for any assessment of potential risk these fish pose to native ecosystems. Known survival of rainbow trout after a 3 mo period following release was ~50 % in this study; however, this is likely an underestimate because we were unable to determine the fate of one-third of tagged fish that had moved outside of the telemetry array. Survival of <3 yr was observed for the same strains of rainbow trout when released into a small boreal lake closed to angling (Blanchfield et al. 2009), which is lower than the 3 to 7 yr life span of naturalized populations of rainbow trout in the Great Lakes (MacCrimmon & Gots 1972). Recreational angling was the major source of mortality of telemetered fish (15 %), of which a large portion occurred directly at the release sites, which attract anglers due to the presence of large numbers of native and escaped farmed fish (Carss 1990, Dempster et al. 2009, Johnston et al. 2010). Overall, rainbow trout removal through angling was comparable to that of farmed fish in other studies (21 to 52 %; Uglem et al. 2008, 2010, Lindberg et al. 2009). Direct estimates of escapee survival are often difficult to derive, especially in the large systems where marine and freshwater aquaculture occurs, yet the present findings are consistent with the general observation that farmed fish have lower survival rates than their wild conspecifics (Einum & Fleming 2001, Saloniemi et al. 2004).

Avian predation was the other source of mortality to farmed rainbow trout in this study. Telemetry transmitters were found in osprey and cormorant nests, and cormorants were observed to consume rainbow trout at farm sites (P. Blanchfield pers. obs.). Decreased swimming ability (Reinbold et al. 2009), reduced anti-predator behaviour (Jörgen et al. 1991, Einum & Fleming 1997) and selection of riskier foraging habitats in the wild result in higher mortality of domestic salmonids relative to wild conspecifics (Jörgen et al. 1991, Biro et al. 2004). Rainbow trout implanted with pressure-sensing transmitters in our study consistently occupied the upper 1 m of the water column (45 % of detections). Selection of risky, shallow-water habitats would make farmed rainbow trout highly susceptible to avian predation, which has been observed for rainbow trout in other studies (Warner & Quinn 1995, Blanchfield et al. 2009). Only radio transmitters can be detected in air, so it is probable that we have underestimated avian predation in our study, and most likely a proportion of farmed fish unaccounted for were prey for aquatic birds.

Counter to the idea that farmed fish are maladapted to feed in the wild (Rikardsen & Sandring 2006, Skilbrei 2012), escaped rainbow trout maintained high specific growth rates (average: 0.33 % d^{-1}) in the first 3 mo after release. This rate of growth was similar to that of conspecifics reared in commercial cages, and was achieved regardless of habitats occupied in Lake Huron. Similar growth has been seen in adult farmed rainbow trout released into a small boreal lake (Blanchfield et al. 2009). Fish farms have been considered optimal feeding habitats (Tuya et al. 2006, Uglem et al. 2008), yet based on the shallow depth distribution when present at the cages, it appears unlikely that rainbow trout were feeding on waste feed and faeces accumulated on the lake bottom. Instead, escaped fish most likely took advantage of the greater numbers of prey fish associated with cage sites in Lake Huron (Johnston et al. 2010), as well as any waste feed pellets that may have made their way outside of the net-pen. The fact that dispersed escaped rainbow trout maintained a comparable growth rate to those showing fidelity to cage sites suggests that they are capable of quickly adapting to forage on wild prey.

Our study is the first to examine the fate of escaped farmed rainbow trout from Canadian commercial freshwater aquaculture operations and provides a framework for understanding the potential risks that farmed fish may pose to the Lake Huron fish community and ecosystem. Based on the findings of this study, low escape rates (1 to 3%) of farmed fish would result in ~50 000 to 150 000 farmed rainbow trout introduced annually into the Lake Huron ecosystem at the current level of production. Annual stocking of salmonids into the Canadian waters of Lake Huron over the past decade has averaged ~2.8 million fish, the majority (~70%) of which were lake trout *Salvelinus namaycush*, a cold-water pelagic species (Hunt et al. 2009). While escaped rainbow trout would constitute a small portion of introduced salmonids to the region, our findings suggest that their observed high growth rate and preponderance for near-shore areas could exert disproportionate pressure on available resources in these habitats. We advocate continued stringent escapee reporting by commercial operators and recommend the inclusion of escapees in population monitoring programs used in stocking density decisions by provincial agencies to minimize any potential impacts of escaped farmed fish to Lake Huron. Such an approach is warranted given the impending expansion of the freshwater aquaculture industry in this region. Future research should include extensive monitoring of fish movements, fine-scale habitat assessments and dietary analyses to further understand the potential for interactions between escaped farmed rainbow trout and native species in the Great Lakes.

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