POPULATION DEMOGRAPHICS AND HABITAT USE OF THE AMERICAN EEL, *Anguilla rostrata*, IN A PROTECTED WATERSHED IN NOVA SCOTIA

by

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Abstract

The American eel, *Anguilla rostrata*, is designated by COSEWIC as a threatened species prompting an increased need for more information about the species' habitat use and abundance. Very little information is known about American eels in local populations. To address this information gap, a long-term eel monitoring program was implemented in a small protected watershed in Nova Scotia. American eel habitat use, demographics, abundance and trap efficiency was investigated from 2009 – 2012 using capture-mark-recapture (CMR) techniques. Eels were captured in traditional eel traps and minnow traps, and tagged in Oakland Lake. Catch-per-unit-effort (CPUE) was calculated and related to habitats characterized by temperature, dissolved oxygen, pH, vegetation type, substrate composition, depth, and underwater and shoreline slope. Other factors including eel age, length, mass and home range were examined. In total, 842 eels were captured and 368 Passive Integrated Transponder (PIT) tags were implanted. Eels were found in all habitats, but in different habitat areas depending on date of capture (month), but not time of capture (day vs. night). Acoustically tagged eels used all water depths (m), but no eels were captured at depths >3 m. Closed population estimates were calculated using the Schnabel method. Yearly baseline population estimates ranged from 87 to 161 eels. A simulation of variable and fixed capture event durations showed that population estimates are sensitive to the number of traps deployed and timing of trap checks. As well, changes in sampling protocols can affect population estimates. Traps were found to be efficient at catching larger eels. Gaining a better understanding of local American eel populations over time will provide valuable information to aid in habitat conservation and inform eel conservation and management efforts.

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Chapter I

An introduction to the life history, importance, status, and population analysis of the American eel, *Anguilla rostrata*

Taxonomy and Genetics

The American eel, *Anguilla rostrata* (Lesueur, 1817), belongs to the family Anguillidae and is one of 16 species in the genus *Anguilla* (Teng et al., 2009). The majority of speciation occurred 45 – 35 million years ago near present day Indonesia (Tsukamoto and Aoyama, 1998) when new species evolved from the ancestral form. As the continents drifted apart, species followed different oceanic currents and it is proposed that the larvae of two eventual Atlantic species spread eastward into what is now known as the North Atlantic Ocean (Palstra and van den Thillart, 2010). These two Atlantic species, the American eel and the European eel, *Anguilla anguilla* (Linnaeus, 1758), evolved much later than other species at about 10 million years ago (Tsukamoto and Aoyama, 1998).

Distinguishing between American and European eels is possible, but not easily accomplished morphologically. All Anguillid eels have long cylindrical-shaped bodies, well-developed pectoral fins, and a dorsal fin that is continuous with the caudal and anal fins. Both North Atlantic species are basically indistinguishable using these external morphological characteristics, but it is possible to differentiate between them by counting the number of vertebrae. Vertebral counts were first used to separate these two species by Schmidt (1923). On average, American eels have 107 (range 103 – 110) whereas European eels have 115 (range 110 – 119) vertebrae (Mank and Avise, 2003). Recently, it has become easier, and more practical for scientific purposes, to distinguish species molecularly.

The issue of species differentiation between American and European eels is an on-going research area, but significant gains have been made using molecular techniques. For example, Avise et al. (1986) showed species distinction using mitochondrial DNA (mtDNA) from the heart and liver; 11 of 14 (79%) restriction endonucleases from eels taken in continental waters were sufficient to distinguish between the two species. However, depending on environmental conditions and life history, species that are geographically widespread often show genetic differences throughout their distribution and animals can exhibit wide differences in genetic differentiation across spatial scales (Williams et al., 1972; Hamrick and Godt, 1996; Waples, 1996, 1998). Neilson et al. (2009) reported that marine animals in particular, which exist in areas without barriers to gene flow, typically show low but statistically significant genetic variation. If no genetic differentiation is noted, the population may be panmictic. A panmictic population is one in which all individuals are potential partners with no mating restriction and thus all genetic combinations are possible. Because of random mating, genes are randomly distributed throughout the population and genetic differentiation is not strong enough to form distinct groups.

Avise et al. (1986) found American eels to exhibit no genetic divergence over a 4 000 km stretch of North American coastline, supporting the idea of panmixia. Both Daemen et al. (2001) and Wirth and Bernatchez (2001) found weak but significant isolation by distance of European eels using microsatellites and their results suggest geographical genetic differentiation within that species. Geographical differentiation was called into question by Dannewitz et al. (2005) and Maes (2006) who found temporal differentiation between samples of glass eels arriving at different times at the same locales, but not on a geographical scale. Similarly, Palm et al. (2009) found slight temporal variation between cohorts of adult eels but no geographical variation. Recent, and more sophisticated, studies support panmixia in both species. Côté et al. (2013) found no genetic differentiation among 32 sampling sites of American eels using 18 microsatellite markers. As well, Als et al. (2011) undertook the first molecular population genetics study of both Atlantic eel species on their spawning ground. They analyzed mitochondrial cytochrome b genes, 5S rRNA genes, and 21 microsatellite markers of larvae for genetic differentiation, isolation by distance, and isolation by time, and found strong evidence in support of panmixia – and found only one apparent hybrid (offspring of American and European eel) in a total of 388 larvae. Further, a total of 1 010 European glass eels (post-larval stage) were sampled across 14 locations ranging from Iceland to Morocco and no significant differences were found in genetic differentiation or isolation by distance (Als et al., 2011). These most recent results provide strong evidence for panmixia from both breeding ground and continental samples.

Als et al. (2011) suggested the existence of a potential breeding area in a specific region of the Sargasso Sea followed by non-random movement of hybrids to Icelandic waters. A total of 1 127 larvae and glass eels from 14 geographical locations from both continents, and several Icelandic locales were genotyped and 15.5% of these were determined to be hybrids found in Icelandic waters, with values ranging from 6.7 – 100% depending on life stage and locale (Als et al., 2011). Hybrids have been determined to exist after the first generation. Nonrandom geographic distribution of hybrids has been shown in the North Atlantic, a higher proportion of hybrids has been found in first and later generations of yellow-phase eels compared to glass eels and, finally, a significant latitudinal gradient in the proportion of hybrids has been shown in Icelandic freshwater (Avise et al., 1990; Albert et al., 2006; Als et al., 2011). It is estimated that 2 – 4% of the Icelandic eel gene pool has evolved from American eel ancestry (Avise et al, 1990). Similar to American eels, vertebral numbers found in Icelandic eels tend to be lower than those of European eels (Avise et al., 1990).

Species Range

The species range of the American eel extends from Southwestern Greenland to northern South America (Figure 1). Although rare in Greenland and Labrador (Cairns et al., 2014) their northernmost continental range is the Hamilton Inlet-Lake Melville estuary of Labrador. Eels are found southward from Newfoundland along the Atlantic coast of Canada and the United States continuing to the Gulf of Mexico, Panama and the West Indies and to Guyana in northern South America (Department of Fisheries and Oceans, 2010). The American eel is capable of inhabiting all marine, estuarine and freshwater habitat connected to the Atlantic Ocean. Their native habitat extends inland as far as Niagara Falls in the Great Lakes and up the Mississippi River (COSEWIC, 2012). Eel presence is uncommon in Lakes Erie, Superior and Huron, and rare occurrences are the result or stocking and/or dispersal through the Erie and Welland Canals (Scott and Crossman 1973; Trautman 1981; COSEWIC 2006). Aoyama et al. (2001) originally found American eels to be absent in Central America but present in Venezuela. More recently, Aoyama (2009) found a continuous distribution of American eels from Mexico through Central America and across South America.

Life Cycle, Sex and Diet

The American eel life cycle begins after spawning which occurs in the Sargasso Sea. The Sargasso Sea is surrounded by ocean currents and is bounded on the west by the Gulf Stream, north by the North Atlantic Current, east by the Canary Current and on the south by the North Atlantic Equatorial Current. American eels share this spawning ground with European eels (Avise et al., 1986; Aarestrup, 2009) in partial sympatry, thus, partly occupying the same geographical location during reproduction (Miller et al., 2014). Despite this common spawning area and spawn timing, American and European eel larvae return to their respective continental habitats. This separation suggests that the larvae of both species either have different drift routes or similar current drift routes, but of different drift duration (Munk, 2010). Investigation into larvae drift has shown larvae presence in the Antilles Current, Gulf Stream and North Atlantic Drift suggesting an earlier separation, a shorter migration time and a shorter larvae phase for the American eel (Bonhommeau et al., 2009).

After eggs hatch, the early American eel larvae are called leptocephali. This flat and transparent larval form is morphologically shaped like a willow leaf (Figure 2). During early development, leptocephali passively migrate up the west coast of the North Atlantic following the Gulf Stream current and coastal eddies that transport larvae towards the coast, and, through the Gulf of Mexico, Caribbean, and south to the northern coast of Venezuela, on southern currents (Tesch, 2003). The diet of leptocephali remains controversial, but it has been suggested that they feed primarily on organic matter and particulates (Otake et al., 1993; Mochioka and Iwamizu, 1996; Pfeiler 1999). When leptocephali move closer to the coast, they metamorphose into unpigmented glass eels

(Haro and Krueger, 1988). Eventually glass eels metamorphose into elvers nearer to the coast or when they reach estuaries and fresh water outflows (Miller, 2005). At this stage, these young eels begin to feed and grow, and some migrate into fresh water habitats (Haro and Krueger, 1988). Because American eels are a facultatively catadromous species, an unknown proportion remain in saline waters and some may migrate periodically between fresh and saline habitats (Jessop et al., 2002; Daverat et al., 2006; Jessop, 2010). Dutil et al. (1989) analyzed the stomach contents of elvers from the Petite Trinité River on the north shore of the Gulf of St Lawrence and found that they primarily fed on insect larvae. After reaching about 100 mm in length, elvers are fully pigmented and enter the yellow eel phase (Hammond, 2003). American eels stay in the yellow eel phase for the majority of their life and during this phase some eels undergo extensive upstream migrations into rivers and lakes (Hammond, 2003), while others remain in saline waters (Jessop et al., 2002; Daverat et al., 2006). Sexual maturity occurs variably between seven years and 40 years in freshwater depending on food resources, growth rates, and sex (Miller, 2005). Sexual maturation occurs earlier in saline waters because of more rapid growth there (Cairns et al. 2009). At the end of the growth phase, yellow eels change into silver eels through a series of physiological changes that prepare them for ocean migration. In addition to acquiring a white belly colour, changes include increased eye diameters, development of a lateral line, changes to the morphology and physiology of the swim bladder, and feeding cessation (Hammond, 2003; Van den Thillart et al., 2004) These silver eels migrate toward their breeding ground in the Sargasso Sea (Oliveira, 1999). Yellow and silver-phase eels are carnivores that feed on insects, fish,

fish eggs, crabs, worms, clams and frogs (Ogden, 1970; Facey and LaBar, 1981; Lookabaugh and Angermeier, 1992; Denoncourt and Stauffer, 1993; Stacey, 2013).

Female eels mature at greater lengths than male eels, so length is often an indicator of sex at the silver eel phase and often can be applied to larger yellow eels (Oliveira, 1999). Many contradicting theories have been proposed as to why sex ratios of American eels are highly variable. Vladykov (1996) hypothesized female eels should be found in greater proportions in higher latitudes while a greater proportion of males should be found in lower latitudes. Winn et al. (1975) found 90% males in Rhode Island streams, but Krueger and Oliveira (1997) found males outnumbered females 3 to 1 in the Annaquatucket River, Rhode Island. Another hypothesis states that females should be found predominately in freshwater and males predominantly in estuarine waters (Vladykov, 1966; Tesch, 1977). The highly productive saltwater environment may increase growth among males where freshwater habitats would lead to slower growth and increased fecundity in females (Helfman et al., 1987). Winn et al. (1975) found the opposite trend in Rhode Island streams where males predominated and females remained in estuaries. Similarly, Facey and Helfman (1985) found that 91% of mature eels from freshwater areas in Georgia were males. A recent compilation of American eel sex ratios from 65 sites found no significant difference in percent of males in fresh (18.7%) and saline (19.4%) waters (Cairns et al., 2014).

More recent research suggests density plays an important role in determining sex with males produced when eels are in higher densities and females produced in lower densities (Krueger and Oliveira,1999). They hypothesized that density is the primary biological factor influencing the sex ratio of eels in rivers. Females would therefore be found further upstream where density is lowest and where they can utilize all suitable habitat to grow larger and slower (Krueger and Oliveira, 1999; Goodwin and Angermeier, 2003). Males, on the other hand, predominate where crowding tends to occur which is often further downstream closer to saline waters (Helfman, 1987; Oliveira et al., 2001).

Importance to Aboriginal Peoples

Eels are important to Aboriginal people as food, for spirituality and medicine, and for decoration. Traditionally, American eels were an extremely important and nutritious food source for Aboriginal people because of their high fat and protein content and ability to preserve well. Because eels are considered sacred among Aboriginal people the entire fish is always used, often for non-food purposes (Allen, 2007a; Allen, 2007b). Eel skin is thick, tough and able to tighten making it ideal for binding, tying, wrapping, sewing and mending thus traditionally providing Aboriginal people with fishing and hunting gear, clothing, bandages and even sporting equipment. Internal organs were often buried as offerings after successful hunting or fishing expeditions (Prosper and Paulette, 2002).

In Nova Scotia, eel fisheries by native peoples are known from 3 000 years ago. Mi'kmaq people have fished eels (kat) with various types of traditional gear including stone weirs, eel pots and spears. Currently, many Aboriginal groups (First Nations and Native Councils) have eel licenses for yellow and silver-phase eels for food, social, ceremonial (FSC) and commercial purposes. A minimum size limit of 35 cm applies in all cases. One Nova Scotia First Nation Band has a license to fish elvers for commercial purposes.

The legal rights to catch and sell eels was contested in 1993. After being charged for fishing and selling eels out of season, a Nova Scotian Mi’kmaq, Donald Marshall Jr., launched a legal battle which reached the Supreme Court of Canada (Wicken, 2002). The essence of the claim was that Mi'kmaq are allowed to catch and sell fish by virtue of a treaty signed with the British Crown. In September, 1999 it was confirmed that Donald Marshall Jr. had a treaty right to catch and sell fish to make a moderate livelihood (Aboriginal Affairs and Northern Development Canada, 1999). In November, 1999 the Supreme Court of Canada provided clarification stating that justified fishing regulations could be implemented for conservation or other public objectives (Aboriginal Affairs and Northern Development Canada, 2010). In total, 34 First Nations in Nova Scotia, New Brunswick, Prince Edward Island and the Gaspé region of Quebec were positively affected by the Marshall case (Aboriginal Affairs and Northern Development Canada, 1999).

Fishing and Commercial Importance

The most inland American eel range in Canada occurs in Ontario (Casselman, 2003) where baited setlines, hoopnets (fyke nets), trapnets and electro-fishing boats have been used by fishers to catch yellow and silver-phase eels. The inland Quebec fishery used trap nets while weirs are used along the St. Lawrence. Fishers in the Atlantic Provinces use baited pots, spears, dipnets, hoopnets (fyke nets) and weirs (Department of Fisheries and Oceans Canada, 2013). In the late 1980s when eel prices were on the rise, sometimes over 100 people would gather in Antigonish Harbour to spear eels. Spearing occurred year round except in the spring as the ice was melting. Buyers would purchase the eels for \$5.50 – \$7.70 per kilogram which was considered a good profit because the spear would cost no more than \$50.00 (Prosper, 2001).

All continental life stages of American eels are fished in at least some regions of Canada (COSEWIC, 2012). The most historically successful commercial eel fisheries occurred in Ontario and Quebec, specifically Lake Ontario and along the main stem of the St. Lawrence River and estuary where yellow and silver-phase eels were fished (Department of Fisheries and Oceans Canada, 2013). In the 1980s and early 1990s yellow and silver-phase American eels was one of the top three most economically valuable fish species in Ontario, valued in some years at $600 000 (Ministry of National Resources Ontario, 2007). Other important commercial eel fishing currently occurs in the Saint John River, along the Eastern shore of New Brunswick, on Prince Edward Island, along the Southern coast of Nova Scotia and on Cape Breton (COSEWIC, 2006) but only in a minority of the habitat they occupy (Cairns et al., 2012). There is also a small yellow and silver-phase fishery in Newfoundland (Department of Fisheries and Oceans Canada, 2013). Since 1965 annual commercial harvests of yellow and silver-phase eels varied widely among saline water fishing regions (Figure 3). In Ontario, in the 1970s an unprecedented 228 tonnes representing approximately 20% of total Canadian eel harvest was caught (Department of Fisheries and Oceans Canada, 2013). The 228 tonne catch was substantially greater than the mean catch of 80 tonnes per year between 1950 and 2003. Prices for yellow and silver-phase eels have varied regionally, increasing over time but have recently been about $3 – 5 per kilogram (Department of Fisheries and Oceans Canada, 2013). Commercial North American harvests began to decline in the early 1990s (Casselman, 2003; COSEWIC, 2012) most drastically in Ontario and Quebec. Ontario closed all commercial eel fisheries in 2004 (COSEWIC, 2006). The onset of major declines of yellow and silver-phase eel landings show temporal differences across regions, but the general trends show that the Ontario harvest paralleled those in the United States and elsewhere in Canada (Casselman and Marcogliese, 2007) which has been interpreted as a cosmopolitan reduction in spawning biomass.

A high portion of the recent (post 2004) fishery value is from the commercial elver fishery which began in 1989 in Scotia-Fundy waters due to an increased demand for elvers in Japan and other Asian countries (Department of Fisheries and Oceans Canada, 1998). In 1997, the total Canadian eel harvest of all stages reached around 700 t, worth approximately $6.3 million (Department of Fisheries and Oceans Canada, 2013); however, a high proportion of this value was from elvers. This increased demand is due to a shortage of Japanese eels, *Anguilla japonica* (Temmink and Schlegel, 1846) and European eel elver export restrictions in Europe (Canfield, 2013) leaving North America with an increasing role as a supplier to these markets. Elver fishing occurs in the spring, typically between April and the beginning of June near the head of tide along river mouths. A set of provisions is attached to each licence indicating geographic area limitations and permitted gear type, and licence holders are generally not permitted to fish on rivers that have established adult eel fisheries (Department of Fisheries and Oceans Canada, 1998). Elvers are caught and shipped live, and used to stock eel farms, where they ultimately grow to market size and provide a meat source, particularly for the popular Japanese “Kabayaki” (marinated and grilled eel) market (Burden, 2012). Canadian elver prices have ranged from $60 per kilogram in 1989 (Department of Fisheries and Oceans Canada, 1998) to, periodically, over $5 000 per kilogram (Canfield, 2013). The total elver catch has increased from 26 kilograms in 1989, when the Canadian elver fishery began (Jessop, 1997), to 1.6 tonnes in 1994 (Jessop, 1995). Preliminary reported elver landings from 2012 and 2013 totalled 4 193 and 5 069 kilograms, respectively (Department of Fisheries and Oceans Commercial Data Division).

Recreational Importance

In Canada, eels are fished for leisure and personal food. Unlike most sport fish in Canada, eels do not have a significant economic value as a recreational species. Depending on the province, eels are typically fished using spears, pots, traps and through recreational angling. Angling eels is allowed incidentally on provincial angling and/or sportfishing licenses with the exception of Ontario. Following the 2004 closure of the Ontario commercial fishery, in 2005 the Ontario recreational fishery was also closed due to eel declines in this region (Mathers and Pratt, 2011). In other provinces recreational fisheries target yellow and silver-phase eels and may be restricted by bag and size limits depending on location and gear type. A Federal license to recreationally fish eels may be required in some provinces or locales such as inland waters or if certain gear types are used such as eel pots or traps. Provincial licenses may also be required. In DFO's Maritime Region, no new recreational eel licences for using eel pots and eel traps are available and existing licenses are terminal meaning they cannot be transferred to another person.

Population Decline and Conservation

Fisheries management is controlled by the provinces in Ontario and Quebec, and by Regions (Newfoundland and Labrador, Maritimes, Gulf) in the Atlantic provinces (Chaput et al., 2013). Human impacts that have the potential to influence American eel conservation in Canada are highly varied, and can be under the jurisdiction of provincial governments, the federal government or both. For example, in Ontario and Quebec the federal government has a role, even though it doesn't directly control eel fisheries (David Cairns, pers. comm., 2015). Commercial North American harvests began to decline in the early 1990s (COSEWIC, 2012) most drastically in Ontario and Quebec. This decline contributed to the decision by Ontario to close commercial eel fisheries in 2004 (COSEWIC, 2006). Previously high abundances of eels in Lake Ontario, St. Lawrence River and Ottawa River watersheds (MacGregor et al., 2009) have declined by more than 90% (MacGregor et al., 2011). Declines are monitored, in part, through four on-going abundance indices for the St. Lawrence and Lake Ontario region (COSEWIC, 2012). These indices include juvenile eel counts (1974 – 2010), trawl surveys (1972 – 2010), electrofishing surveys (1984 – 2010) and dam tailwater surveys (2000 – 2010). These indices show that over the past 10 – 36 years there have been significant eel declines in this part of the species range. It is estimated, from Ontario abundance indices, that eels are at approximately 3% of their mid-1980 abundance in that area (Mathers and Pratt, 2011). Nevertheless, the American eel remains widely distributed in eastern North America with various abundance indices showing variable trends (COSEWIC, 2012).

The American eel was assessed by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) in 2006 as Special Concern (COSEWIC, 2006). Population declines in the upper St. Lawrence River and Lake Ontario system had a major influence on this assessment. In 2012, the assessment of the American eel was changed to the higher risk category of Threatened, primarily because of the addition of the effects of turbines and hydroelectric dams. Turbines of hydroelectric dams cause substantial mortalities (up to 40%) to downstream migrating silver eels in the St. Lawrence River. The majority of dams are small and contain smaller turbines and therefore have higher mortality rates than larger dams because the blades are closely spaced. Upstream passage is provided at two large dams in the St. Lawrence River but in Canada, no upstream passage is required for most hydroelectric dams (COSEWIC, 2012). Other factors contributing to American eel decline are considered to be of medium or high level of concern (Chaput et al., 2014) and include commercial fisheries (overharvesting), physical obstructions (hydro electric dams, dams and barriers), habitat alteration and loss, changes in oceanic conditions and circulation, parasitism, and biological and chemical contamination (COSEWIC, 2012, Chaput et al. 2014, Cairns et al. 2014).

The coincidence of declines in American, European and Japanese eels has prompted a search for a common mechanism. For example, Kettle et al., (2010) suggested a possible link between the North Atlantic Oscillation (NAO) and decline in eel populations. The NAO index indicates strengths in low and high surface pressure differentials near Iceland and the Azores. As the pressure gradient increases between the Icelandic low and the Azores high, westerly wind strength increases, affecting oceanic currents and precipitation patterns around the North Atlantic. Glass eel recruitment depends on favourable speed and direction of currents for transport. These oceanic changes may be a possible factor for explaining variation in recruitment to coastal rivers (Knights, 2003). However, it is important to explore all possibilities including local disturbances that may lead to local declines in eel abundances (Kettle et al., 2010).The effects of fishing on the American eel life cycle are not well known. All life stages, excluding leptocephali, are subject to fisheries removals. Eels are semelparous (only spawn once); therefore, all fishing occurs before spawning (Richkus and Whalen, 1999).

For example, it was estimated that fished areas in tidal waters in Prince Edward Island (PEI) reduced spawning escapement by 90%, below what it would have been without fishing (ICES, 2001), but not all coastal areas are fished for eels in PEI so this estimate does not represent a provincial estimate of fishing impact on spawning escapement. Exploitation rates of silver-phase eels in the St. Lawrence estuary was determined to be 19% in 1996, 24% in 1997 (Caron et al., 2003) and 11% in 2005 (Verreault, MRNF, pers. comm., 2011) thereby reducing spawning biomass.

Although yellow and silver-phase fishing has occurred for a long period and decreases in pre-spawning biomass of local populations (in fished areas) documented, the great majority of eel habitat is not fished, suggesting other factors may contribute to population declines. Glass eel and elver harvesting is a recent development in North America and there is no firm understanding of how it affects population dynamics of local populations. Because the mortality rate of eels transitioning from elvers to yellow and silver phase is high (upwards of 95 %) (Department of Fisheries and Oceans, 1998), it is thought that harvesting elvers should not greatly impact local populations because the vast majority of elvers never reach the silver-phase under natural conditions (Department of Fisheries and Oceans, 1998). In the Scotia-Fundy region of Canada, elver fishing targets glass eels and elvers. Jessop (2000), estimated that 31 – 52 % of elvers ascending in the East River, Chester, Nova Scotia were caught by elver fishers. Between 2004 and 2007 in the Maritimes Region, elver landings increased by 18% relative to the average landings between 1997 and 2002 for the same river (Bradford et al., 2010). In 2005, the elver quota was reduced by 10% so that elvers could be used for stocking purposes in areas of low abundance (Bradford, 2010).

Stocking early stage eels may lead to the spread of a dangerous parasite in some locations. The nematode *Anguillicola crassus* (Kuwahara, Niimi & Itagaki, 1974) is a parasitic nematode that inhabits the swim bladder of several species of Anguillid eels and infects eels when they ingest an infected freshwater ostracod (Moravec, 1996). This parasite originates in East Asia where no pathological effects of the parasite have been found in its native host, the Japanese eel. The swim bladder parasite was first detected in 1982 in European eels in Germany (Han et al., 2008). Japanese eels were imported from Taiwan into Germany in 1980 to repopulate depleted local populations; however, infective parasite stages or infected hosts possibly spread the parasites to European eels. Another likely cause of introduction or spreading could be escapement from aquaculture sites or through truck water exchanges during eel transportation (Costa-Dias et al., 2010). Swim bladder nematodes have spread to American eel hosts in North America presumably through transferring infected European eels to an aquaculture facility in Texas prior to 1995 (Haro, 2000). The parasite was originally discovered in a single American eel caught in Winyah Bay, South Carolina (COSEWIC, 2006).

In contrast to the situation with Japanese eels, other eel populations including European and American eels are susceptible to this foreign parasite (Kirk, 2003). In European eels the swim bladder parasite causes a range of negative afflictions including internal bleeding (Mellergaard and Dalsgaard 1989), inflammation (Molnár, 1994), dilation of blood vessels, formation of granuloma, and thickening of the entire swim bladder wall (Würtz and Teraschewski, 2000). Quite often, swim bladders are discovered with irreversible damage from accumulation of dead parasites, digested blood, and debris, as well as becoming occupied with encapsulated adults and juveniles (Kirk, 2003). High pathogenicity of the parasite and its harmful effects may contribute to the decline in European eel populations (Han et al., 2008). Effects of swim bladder parasites on American eels are not well known in comparison with the effects on European and Japanese eels (Aieta and Oliveira, 2009). Sokolowski and Dove (2006) determined pathological effects of swim bladder parasites in American eels such as causing blood-filled swim bladders and damage to the various tissues lining the swim bladder wall. In Canada, Rockwell et al. (2009) discovered the swim bladder parasite in American eels in Cape Breton, but the parasite was not found to be widely distributed. The investigation of 174 localities throughout mainland Nova Scotia and New Brunswick determined the overall prevalence of *A. crassus* was 4 % with a mean intensity of of 3.8 ± 8 SD (1-63 parasites) (Campbell et al., 2012). The pathogenicity of the parasite can be lethal to European eels, and given the similarity in European and American eels, it is probable that widespread infestations could have a dramatic impact on American eel abundances (Haro et al., 2000).

Deforestation, farming practices, and urban development near watersheds and riparian zones have resulted in poor water quality directly and through erosion and sedimentation which decreases stream quality resulting in reduced habitat quality (Machut et al., 2007). Water levels and increased fluctuation of levels can also have a negative effect on eel movement and migration patterns and may cause overwintering habitat and shallow wetlands or riparian zones to be unsuitable habitat (Haxton and Findlay, 2009).

Bioaccumulation of pollution and contaminants such as polychlorinated biphenyls (PCBs) and heavy metals occur in American eels (Blake, 1982; Moreau and Barbeau, 1982), possibly having a negative impact on abundance. Sediments often accumulate contaminants, and increased contaminant levels have been suspected of decreasing reproductive success (MacGregor et al., 2010). Castonguay et al. (1994) looked at pollution in the Great Lakes and St. Lawrence River regions where lethal poisoning has occurred in American eels for the previous 25 to 30 years. Contamination levels in silver-phase eels were found to be much higher in the St. Lawrence River in comparison to a reference stock. Despite being significantly less contaminated than historical values in the 1960s and 1970s (Byer, 2013), a high prevalence of lesions and deformities occurred compared to the reference stock (Castonguay, 1994). However, eels were, on average, less contaminated with PCB (polychlorinated biphenyl) in 1990 than in 1982 (Castonguay, 1994). Effects of pollution can include spinal deformations, and changes in cholesterol, cortisol, glucose, lactate pyruvate and protein concentrations (Bengtsson and Larson, 1986). Reduced fecundity, slower growth rates, less viable offspring, and increased mortalities are also common (Haro, 2000). It is unclear whether pollution has had a direct impact on American eel abundances in the Great Lakes and St. Lawrence River regions because the area has been contaminated for a long time. It is probable that if contamination was a major contributing factor to eel decline the effect would have been documented sooner (Castonguay, 1994). Nonetheless, Byers (2013) presents evidence that increased contaminant levels may be a contributing factor to eel declines.

Barriers such as dams continue to be a serious problem for American eels in North America because they limit eel movement upstream and downstream. Dam construction in North American began during European colonization and peaked in the middle of the 20th century. Approximately 8 400 dams measuring at least 2.5 m in height (Verreault et al., 2004) occupy the St. Lawrence River watershed. In combination, these barriers prevent, delay or restrict over 12000 m^2 of freshwater eel habitat in the Great Lakes and St. Lawrence River regions (COSEWIC, 2012). Barriers such as these have led to extensive habitat loss in areas that produce large, and thus highly fecund, females (COSEWIC, 2012).

Barriers erected in freshwater negatively impact the upstream migration of juvenile eels if no fish passage is provided (Chaput et al., 2014). Dams with hydroelectric facilities pose further threats and substantial mortalities (Chaput et al., 2014) to downstream migrating eels because of blade interaction and pressure changes. Two Canadian hydroelectric dams that have been documented to contribute to the decline of eel abundance are the Moses-Saunders Dam and the Beauharnois Dam constructed in 1959 and 1961, respectively (Verreault and Dumont, 2003). Turbine specifications can produce different survival rates. For example, Francis turbines used at the Moses-Saunders and Beauharnois dams have estimated mean survival rates of 84% (CI = 77% – 92%), but fixed blade propeller turbines yielded survival rates of 76% (CI = 68% – 84%) and 75% (CI = 68% – 79%) (Desrochers, 1995; Normandeau Associates Inc. and Skalski, 1998). Upstream passage via eels ladders has only been present at the Moses-Saunders Dam since 1974 and the Beauharnois Dam from 1994 – 1995 and 1998 – present (COSEWIC, 2012), and these passageways may allow increased access to habitat. In another example, 25 silver eels were acoustically tagged on the Magaguadavic River, New Brunswick to determine passage success. Nineteen of the 25 tagged eels entered the turbine and none survived (Carr and Whoriskey, 2008).

Overall, there is limited evidence to substantiate swim bladder parasites, pollution, or barriers as fundamental or single causes of decline. However, there is sufficient evidence to suggest that a combination of factors centered around access to habitat and decreased habitat quality may be the leading threat to American eels. Long-term evidence suggests that declines in eel abundances are linked to progressive degradation of habitat due to industrial and coastal economic development beginning about 30 years ago (Kettle et al., 2010). And, long-term declines in fisheries catches suggest that spawning stock biomass may also be decreasing. Although there are limited empirical studies on eel abundance in Canada in general (COSEWIC, 2012), some studies have been completed indicating very low abundances with the possibility of reaching extirpation in all inland waters and rivers in Ontario (McGregor et al., 2010; Casselman and Marcogliese, 2010; COSEWIC, 2012). Other areas more directly connected to saline waters are faring no better. For example, Castonguay et al. (1994) reported an 81 – fold or 99% decline from 1985 to 1992 in juvenile American eels recruiting to Lake Ontario and a drastic decline in juvenile eel densities in tributaries connected to the Gulf of St. Lawrence. However, this decline appears to be unique to this area. While the overall picture in Canada is that American eels are in decline, some indices show abundance increases or variations (Cairns et al., 2014). For example, abundance indicators for fresh, estuarine and marine locations were found to be increasing in areas of the Southern Gulf of St. Lawrence. Variations in abundance with no statistically significant results included the elver recruitment index (East River Chester), standing stock index of the Southern Gulf of St. Lawrence for freshwater habitat and the silver eel abundance index from the St. Lawrence River Basin (Cairns et al., 2014).

Habitat Use

The American eel has been traditionally categorized as an obligate catadromous species, meaning it spends the majority of its growth phase (yellow-phase) in fresh water (rivers and lakes) and it spawns in saline water (Oliveira, 1999). However, analysis using otolith strontium:calcium ratios indicates that its movement patterns are more variable (Jessop et al., 2002; Daverat et al., 2006). These data demonstrate that American eels, as well as European and Japanese eels, are facultatively catadromous. As a facultatively catadromous species, American eels spend all or part of their yellow eel phase resident in fresh or saline waters, and may migrate periodically between habitats of different salinities (Jessop et al., 2002; Daverat et al., 2006; Jessop, 2010). Some yellow-phase eels continue their migration upstream into fresh water and remain there until sexually mature while a proportion of eels remain in the lower reaches of rivers and in brackish estuaries or sheltered coastal waters (Morrison et al., 2003; Cairns et al., 2004; Lamson et al., 2006). Evidence suggests that a variable but unknown proportion of yellow-phase eels remain in coastal, saline waters anywhere from one year to their entire juvenile life (Jessop et al., 2002). In the East River, Chester, Nova Scotia, Jessop et al. (2002) found that of the 25% of silver-phase eels that entered the river as juveniles and 69% showed interhabitat movement at some point during the yellow and silver phases.

Thibault et al. (2007) theorized that movement patterns between fresh and saline habitats may be regular and seasonal in nature as a response to low water temperatures in estuaries. Other studies suggest a link to food, growth, and maturation. Individuals which remain in saline water exhibit increased growth rate (Cairns et al., 2009), earlier maturation and begin their spawning migration sooner than those that utilize freshwater habitats (Helfman et al., 1987, Morrison et al., 2003; Lamson et al., 2009). These findings support Helfman et al. (1987) who suggest saline habitats are more productive for American eels than freshwater habitats. These saline habitats are believed to have greater food abundances, better quality food, and less thermal and osmotic stress (Morrison et al., 2003).

Little is known about American eel population dynamics within the various habitats they occupy. Because the prevailing evidence indicates that American eels are panmictic, it is probable that many eels entering a particular habitat are offspring of eels that developed in a much different habitat (Oliveira, 1999). This pattern is hypothesized to prevent local selection pressures in particular environments from producing long-term effects on life history strategies (Oliveira, 1999). High variability in their use of geographic locales and the temporary use of habitats by different life stages may be essential to maintaining panmixia (Jessop et al., 2002).

A home range is described as the spatial extent or outside boundary of an animal's movement during the course of its everyday activities (Burt, 1943). Food availability, competition, and predatory density are the three main factors that influence home ranges (Bozeman et al., 1985). A small-scale study completed on the South Shore of Nova Scotia to gain more insight into movement patterns and residency of the American eel found eels tended to have small home ranges mostly in pools in riverine habitats (Muise, 2012). Larger-scale studies found eels that were moved from their original pond of capture and moved to an adjacent pond returned to their home pond reinforcing small home ranges and indicating a homing ability (Lamothe et al., 2000). In the Penobscot Estuary, Maine, Parker (1995) found that more than half of the eels he captured and displaced returned to within 30 m of their capture site – three eels moved towards their capture site while some returned to within 50 m of their capture site and remained for several days. A study in the Great Sippewisset Marsh, Massachusetts, found that larger eels were generally found in larger creeks while smaller eels were primarily found in narrow creeks at the back of the marsh, and 93% of the eels traveled less than 100 m showing that home ranges are not large (Ford and Mercer, 1986). Morrison and Secor (2003) also found evidence that American eels occupy a home range. In that study, more than 70 % of PIT tagged eels in the Hudson River moved less than 1 km from their original tagging location in a 2 – 12 month period. The longest distance traveled by an eel was 4.2 km.

Yellow-stage American eels tend to be bottom dwellers and substrate oriented showing little movement during the day (Eales, 1968; Ogden, 1970; Tesch, 1977; LaBar and Facey, 1983; Helfman, 1986). Substrate preferences of American eels are not well documented. LaBar and Facey (1983) reported that American eels in Lake Champlain were found over weedy substrate while Ford and Mercer (1986) found small American eels in soft-bottomed creeks of landward marshes, and larger eels in soft mud to sandy-bottomed creeks of seaward marshes. In Chesapeake Bay, eels were found over detritus, hydroid, or shell bottoms (Geer, 2003). Thomas (2006) suggested that complex substrates were important to yellow-stage American eels, because eels were more likely to seek shelter in courser substrate in the morning and afternoon throughout the winter and spring months during periods of cooler temperatures. However, during more active periods through the evening and night and during warmer temperatures in the summer and fall eels are more likely to be found in areas with finer, less complex substrates (Thomas, 2006). Yellow-stage eels are known to hibernate during the winter months (Fahay, 1978) and when held at 5°C for more than five weeks eels stop feeding and reduced their oxygen consumption (Walsh et al., 1983). To, apparently, compensate for decreased temperatures and slower metabolic rates in winter, eels burrow into soft sediments (Chaput et al., 1997). Laboratory, excavation, and dye respiration experiments and field observations in the Maritime Provinces indicated that wintering eels burrow in the mud with their head close to the surface (Tomie, 2011). Daily movements between habitats or daily cycles are unlikely during cold winters; rather, yellow-stage eels found in Canadian waters burrow or hide in soft sediment for approximately 74% of their annual cycle (Tomie, 2011). Evidence for wintering behaviour is provided by traditional spear fishing through ice in Antigonish Harbour, Nova Scotia, and from local commercial eel fishers (Darren Porter, pers. comm.). Burrowing among yellow-stage eels is a common hiding technique to avoid predation.

Aside from temperature, vegetation also appears to play a key role in where American eels reside. Stevens (2010) found that American eels in a small Nova Scotian lake preferred areas with a higher percentage of vegetation. This was corroborated in a study detailing eel abundance in relation to vegetation changes over time (Cottreau, 2013). Thomas (2006) suggested that riparian vegetation was also important to yellow-stage American eels. However, when 27 brackish and salt water estuaries were examined in the Gulf of St. Lawrence using a glass bottom boat, American eel density showed no significant relation to percent vegetation cover by site (Hallett, 2013). The ability to move between different habitats is partly accomplished because of their facultative catadromous behaviour. However, this ability may not be beneficial to the species wellbeing as changing environmental conditions may lower species fitness (Cairns et al., 2009). Therefore, determining and protecting habitat that is conducive to higher fitness among all life stages of the American eel and across broadly different habitats is important to conservation of the species.

Similar to other habitat characteristics, depth patterns are also highly variable and probably linked to the many habitats eels occupy (Cairns et al., 2012, 2014; Poirier, 2013). Stevens (2010) found the majority of yellow-stage eels trapped in Oakland Lake, Nova Scotia, were caught at shallow depths (0.7 – 1.8 m) indicating that eels in this lake are occupying shoreline surface waters during night (assuming eels are caught during dusk till dawn). Westerberg et al. (2007) used data storage tags and found that silver stage European eels spend the majority of the night within 0.5 m of the surface in shallow depths while resting on the substrate at depths between 2 – 32 m during the day. Similarly, Facey and Labar (1981) and Thomas (2006) found yellow-phase American eels occupy depths between 0.4 – 1 m. However, in the latter study, available depths ranged from 0 to 2.9 m. Thomas (2006) also found eels to be 0.2 – 0.3 m deeper during the evening and night in comparison with the morning and afternoon, in contrast to Westerberg (2007) and Facey and Labar (1981). Silver stage American eels occupy a wide range of depths during their outmigration to the Sargasso Sea. Depths between 6.6 – 10 m were occupied most frequently by silver stage American eels on the Connecticut River, Massachusetts in a hydroelectric forebay, but were found swimming near the surface at night (Haro et al., 2000). Bradford et al. (2009) tagged 20 silver stage American eels using hydroacoustic telemetry tags to track their vertical and horizontal movements in a macrotidal estuary and bay. The majority of eels migrated downstream at night and were indifferent to ebb or flood tides. Eels did not show bias for incoming or outgoing tidal currents and had little preference for depth. Eels in saline waters are commonly found close to shore and in estuaries, less commonly at depths of 21 – 165 m, and rarely at extreme depths ranging from 221 – 495 m (Poirier, 2013).

In summary, American eels use a wide variety of habitats during different times of the day and year based on food availability, water temperature, predation, competition, migration, and life cycle stage. It is important to characterize specific habitat use of eels in order to formulate pathways to conservation. Characterizing habitat use in a simple system such as a single, small lake with one inlet/outlet stream over an extended period may provide valuable information about habitat use and local population dynamics that can then be applied to larger systems.

Capture – Mark – Recapture

Capture-mark-recapture (CMR) is an experimental methodology in which individual animals are captured, marked, released and recaptured by repeated sampling. Because CMR can estimate abundances (population size), the data can be used to determine if local populations are declining, remaining stable or increasing and, therefore, over time, this technique can be used as a tool for conservation monitoring. Furthermore, if animals are uniquely marked, CMR provides capture histories of individual animals caught within a local population and can provide information on probability of survival, probability of capture, and recruitment (Pradel, 1996). When covariates are added such as habitat type, eel size, etc., a multistate CMR (MCMR) model can be developed which can further characterize survival and abundances (local population estimates), as constrained by these factors. More simply and specific to this thesis, uniquely marked eels can be tracked within or between specific trap sites to identify individual capture and recapture histories, length-mass data, habitat characteristics and abundance estimates.

The simplest population size estimate is calculated by the Lincoln-Peterson method and requires only two capture occasions (Lincoln, 1930). On occasion one, individual animals from a population are captured, given a generic mark, and released. The population is resampled on a later occasion and the ratio of marked to unmarked animals is used to estimate population size. Although simple, Lincoln-Peterson estimates often require pooling data from multiple capture occasions which can mask biases that may be found in each occasion (Donkers et al., 2011). A variation of the Lincoln-Peterson estimate known as the Schnabel method can be used to calculate population size and account for potential biases of Lincoln-Peterson estimates by taking into account sequential occasions (repeat sampling) (Schnabel, 1938; Gazey and Staley, 1986).

Schnabel estimates work well when large samples are obtained relative to the population size, but pose problems when samples are small. Small sample sizes can lead to negative bias and large confidence intervals if the total combination of animals marked and examined is low in comparison to the actual population size (Gazey and Staley, 1986). When sample sizes are small, Bayesian methods can be used to provide a more accurate characterization of error structure. Bayesian statistics consider quantities in two parts: those known to the person making the inference and those unknown to the person (Gazey and Staley, 1986). The unknown quantity can be described by formulating a set of prior distributions (prior) of unknown parameters. Multiplying the prior with the likelihood function and then normalizing results creates a posterior probability distribution. The posterior distribution is the distribution of the uncertain quantity from which inferences can be made. There is little difference between Schnabel and Bayesian estimates when sample sizes are large (Gazey and Staley, 1986).

Building upon the methods of Lincoln-Peterson and Schnabel, Cormack (1964), Jolly (1965), and Seber (1965) introduced maximum likelihood estimation for estimating population size, survival and capture probabilities using CMR data. CMR data generally consist of capture histories of individuals rather than ratios of marked to unmarked animals. In the simplest case, both models assume all animals are randomly sampled from the population of interest and that captures of marked and unmarked animals are equally probable (Steven et al., 2005). In other words, original models by Cormack, Jolly, and Seber (CJS models) assumed that animals in a population were homogenous, meaning each individual has equal probability of being captured (equal catchability), and equal probability of surviving between sample times (equal survivability). However, such homogeneity is unrealistic in many systems and with animals with complex life cycles.

To overcome the assumption of homogeneous probabilities or, conversely, to embrace heterogeneous probabilities, covariates can be introduced that will allow different capture and survival probabilities among animals within different environments by placing animals in “strata” or “states”. For example, stratification exists when there is spatial separation of animals or animals are separated based on size categories. Further complexities arise when individuals in a population are not fixed, but randomly move between groups (spatial areas) over time (Lebreton et al., 1992). Accounting for heterogeneous movement within a population is beneficial to producing accurate models. Changes in strata can be divided into two categories. First, changes may be predictable (e.g. progression from one age class to the next), and second, changes may be random (e.g. movement among geographical areas during feeding) (Steven et al., 2005). Accounting for random movement was the motivating factor behind the development of multistate CMR, or MCMR, models (Lebreton et al., 1992; Lebreton and Pradel, 2002). These, and other, more sophisticated models are also possible, but are beyond the scope of this thesis.

Overlaying estimation methods are two main categories of populations: closed and open populations. Study periods for closed population estimates are typically completed over short time intervals to ensure the population remains approximately constant (i.e. no births, deaths, immigration or emigration). It follows that the definition of a closed population is one where these characteristics exist. On the other hand, open population estimates are intended to estimate survival over a long period of time and account for births, deaths, immigration and emigration (Pradel, 1996). Three more assumptions for both closed and open population estimates are also made:

1. All animals have an equal probability of being captured (thus factors that may influence capture probability are outlined in the analysis);
2. Marks are not lost; and
3. All marks are reported on recovery.

Open populations have an additional assumption that sampling time is negligible in relation to intervals between samples (Krebs, 1999). Two main advantages of estimates under open populations include the ability to estimate survivability and recruitment.

Estimating population sizes under the assumption of a closed population has been empirically researched for over a century leading to the discovery of some advantages and disadvantages. One advantage of closed models include very accurate estimates when all four assumptions are met and a robust experimental design is in place. Closed models are very useful when the study area is geographically defined and individuals in the population have restricted ranges. Finding study locales which are geographically defined and have populations with restricted ranges can be difficult because natural environments tend to have “open borders” with transient individuals, but, because the study locale used for this thesis meets the assumptions well, closed population models were used.

Statistical inference and visualizations will be used to characterize abundance and habitat use of American eels to gain a better understanding of a local eel population in a small watershed with minimal human influences. In Chapter II: General Demographics and Habitat Use by the American Eel in a Small, Protected Watershed, the focus will be on comparing habitat use of American eel in Oakland Lake, Nova Scotia. Habitat characteristics will be related to eel abundances using catch-per-unit-effort (CPUE). Acoustically tagged eels provide further, and potentially non-biased, movement information and can be compared with habitat use by passively tagged and trapped eels. In Chapter III: Local Population Estimates and Trap Efficiency, Schnabel abundance estimates will be calculated, and compared with monitoring protocols. Bayesian and open models are probably obtainable given the dataset, but are also probably not necessary given the underlying assumptions of closed models for this geographically enclosed system. Testing trap efficiency (the ability and consistency of eel traps to catch eels) will provide information on trap monitoring such as how often traps should be fished and checked. CMR analysis allows for population estimates for closed populations and it provides an excellent starting point, especially coupled with habitat use information, before exploring survival and movement patterns using more advanced analyses such as MCMR.

The general hypotheses are:

1. Population size estimates using closed models will be consistent among years.
2. Catches will vary among different strata of habitat type because preliminary evidence suggests that eels are caught more often in areas with vegetation and softer substrates.
3. Trap efficiency is constant.

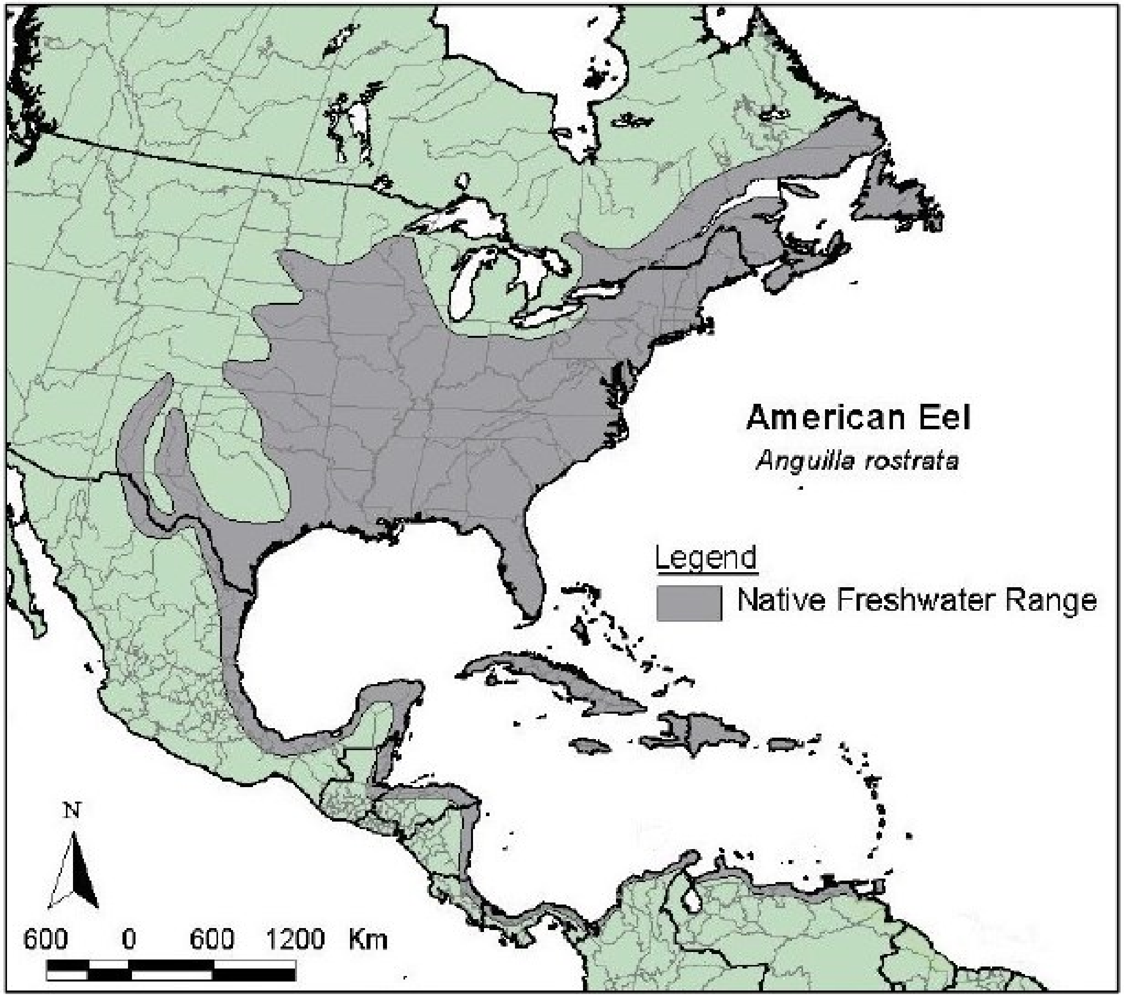

Figure 1. Geographic distribution of American eel in continental waters (from Shepard, 2015).

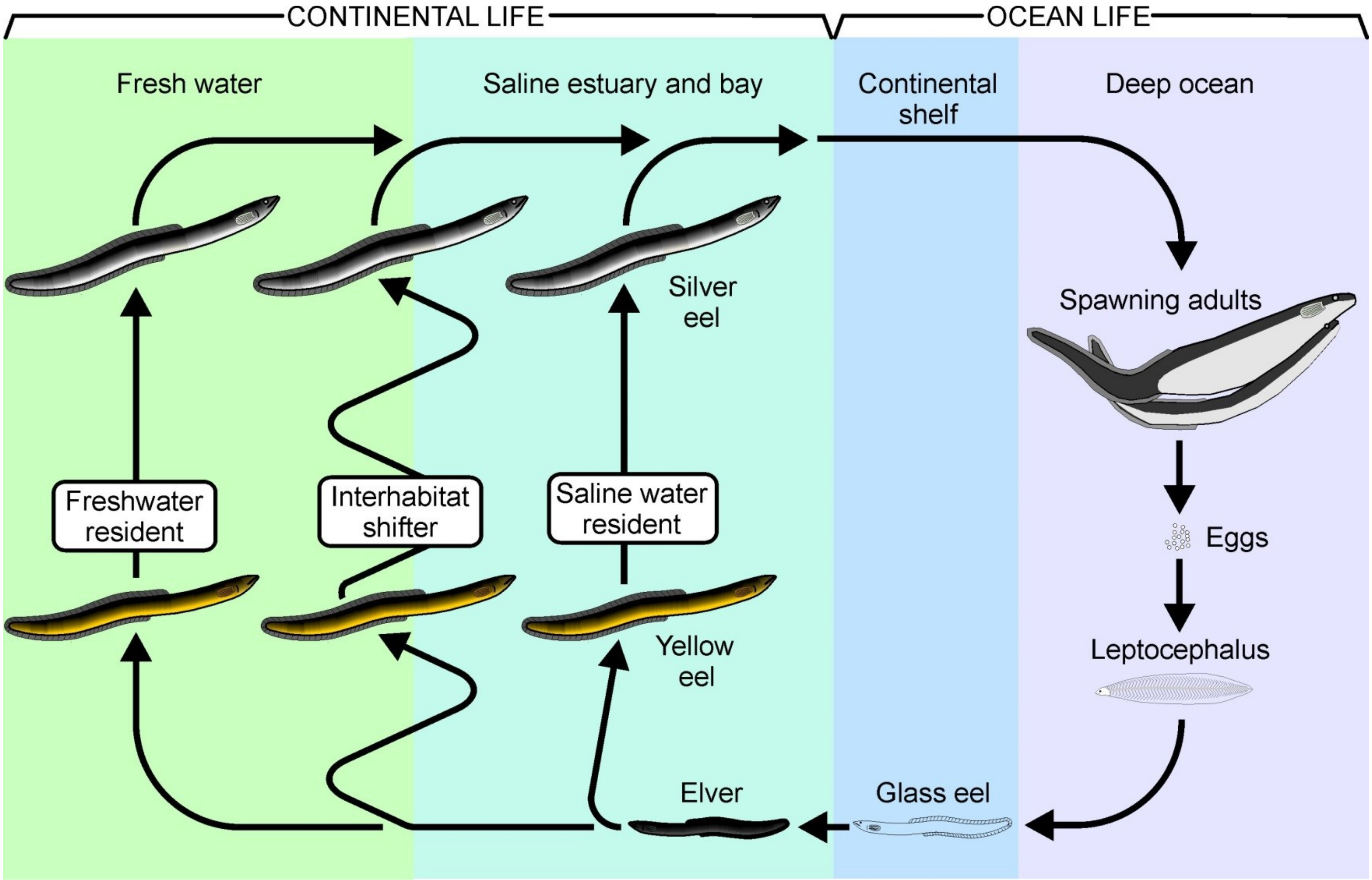

Figure 2. Life cycle of the American eel, *Anguilla rostrata* (from Cairns et al., 2014).

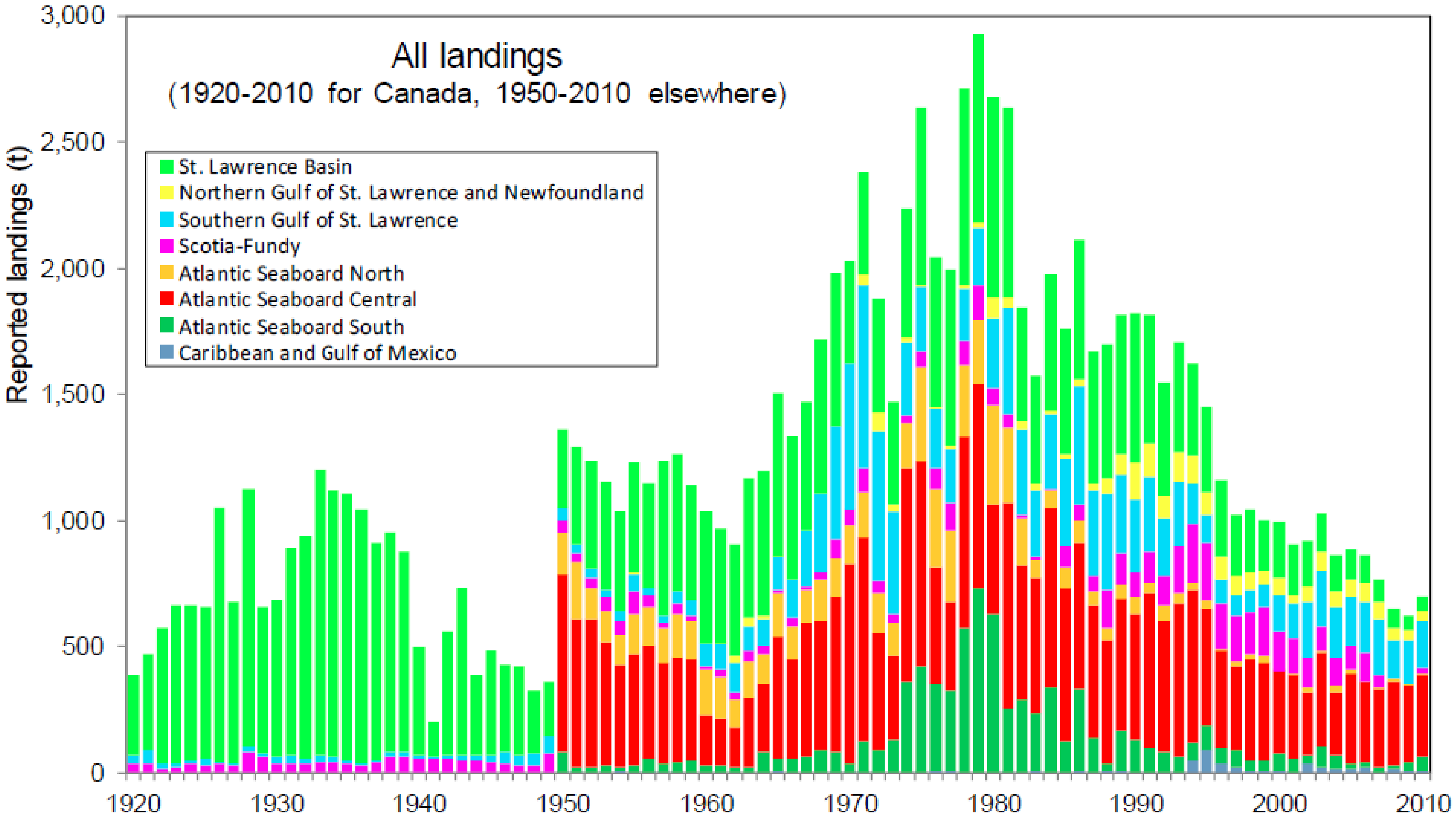

Figure 3. Reported landings of American eels, 1920 – 2010 (from Cairns et al., 2014).

Chapter II

General Demographics and Habitat Use by the American Eel in a Small, Protected Watershed

Introduction

In Lake Ontario between 1983 and 2000, large declines in juvenile American eels were reported contributing to their national designation as Threatened (COSEWIC, 2012). Factors considered to contribute to local population declines include habitat alteration and habitat loss (COSEWIC, 2012; Chaput et al., 2014). The habitat range of American eels in Canada includes all saline (marine bays and estuaries) and freshwater areas that are accessible and linked to the Atlantic Ocean (COSEWIC, 2012); therefore, broad statements pertaining to habitat change and loss as they affect local populations are incomparable.

American eels are particularly influenced by their habitat because of its influence on both growth and sex determination (Cairns et al., 2009; Pratt et al., 2014), both of which are important in describing population dynamics. In north-eastern North America, eels have shown higher growth rates in saline water compared to freshwater habitats (Cairns et al., 2009). Overall, sex ratios are similar between freshwater and saline environments (Cairns et al. 2014), but changes in habitats and habitat locations (e.g. distance from sea) can affect eel densities that may, in turn, affect sex ratios. High eel densities have shown to favour male production and low densities have shown to favour female production (Davey and Jellyman, 2005).

Habitat type differentially influences an eel's ability to forage, feed, rest, and hide. In general yellow-phase eels are nocturnal benthic omnivores (COSEWIC, 2006).

Generally they forage at night and use olfaction to identify prey (Barbin, 1998). Wunder (1936) noted that yellow-phase eels stay in dimly lit or dark places during daytime because they possess a retina, which is very sensitive to “half-light”. Wunder (1936) showed that eel retinas contain extremely small cones indicating reduced visual capabilities in daylight. Other fishes generally live in well-lit areas during daytime apparently because they are less sensitive to daylight. In the day, yellow-phase eels are found associated with substrate, burrowing in soft sediments such as mud and sand, or hiding in spaces among rocks, vegetation and debris such as submerged wood that is used for protection and cover (Glova, 2002; Tesch, 2003). However, Tomie (2011) found eels rarely burrowed in sand when compared to mud and gravel. Overall, aside from nocturnal foraging habits, yellow-phase eels exhibit sedentary rather than migratory behavior (Aoyama et al., 2002). However, in cold or temperate climates, eels may move between rivers and estuaries for summer feeding before returning to freshwater to overwinter (Thibault et al., 2007).

Habitat temperature ranges for American eels are broad. Eels were captured in Chesapeake Bay in temperatures ranging from 3 – 31°C (Geer, 2003). However, Haro (1991) found 17 – 20°C to be the preferred temperature of American eels in a study site with a horizontal thermal gradient. Walsh et al. (1983) held American eels at 5°C for over five weeks and showed eels stopped feeding, displayed a dramatic decrease in oxygen consumption and remained inactive for months.

Wiley et al. (2004) consider eels to be habitat generalists suggesting no consistent preferences for habitat type, cover, substrate or temperature. Lloyst et al. (2015) argued that, although American eels fit the description for habitat generalists, individual eels establish a home range and use specific habitat types depending on eel length. For example, smaller eels in New York were found in cobble and gravel (Machut et al., 2007). Similarly, in Ontario, Lloyst (2012) observed smaller eels more often in gravel and layered bedrock. Larger eels in both New York and Ontario were found associated with larger cobble, boulders and sand (Machut et al., 2007; Lloyst, 2012). Yellow-phase eels may also show evidence of homing to specific areas (Parker, 1995), fidelity to specific habitats (Jellyman & Sykes, 2003), or demonstrate occupancy of distinct locations according to diel period (Helfman et al., 1983; Thibault et al., 2007).

Home ranges of American eels have been found to vary with eel size (Thibault et al. 2007), food availability, competition and predator density (Bozeman et al., 1985). Home ranges up to 0.02 km^2 have been estimated in estuarine habitats (Ford and Mercer, 1986) and tidal streams (Bozeman et al., 1985; Dutil et al., 1988), but home ranges up to 0.65 km^2 have been reported in Lake Champlain (LaBar and Facey, 1983). Ford and Mercer (1986) found evidence of home ranges and territorial behavior in the Great Sippewisset Marsh, Massachusetts where larger eels occupied larger creeks and smaller eels occupied narrow creeks. Over the five week study individual eel movement was usually less than 100 m. Helfman et al. (1983) used ultrasonic telemetry to study eight immature eels in a Georgian estuarine stream. Limited movement and regions with concentrated activity also suggests home ranges exist within creeks. Parker (1995) estimated 64% of displaced yellow-phase eels in the Penobscot River, Maine, returned to their point of capture within 36 days.

Muise (2012) found eels tended to use lower reaches of a watershed when compared with upper reaches in a tributary with an intermediate lake as indicated by catch per unit effort (a surrogate measure for density). Remaining in the lower reaches of a watershed could be a result of greater resources and suitable habitat within a freshwater/saline interface as well as the ability to easily migrate to saline waters if resources deteriorated within freshwater areas. Lobon-Cervia et al. (1995) showed that temperature, distance from the river mouth, and size and numbers of eels at sites along multiple tributaries were important drivers for eel density, and that eel density decreased while eel size increased with distance from river mouth. Jessop et al. (2002, 2008) studied strontium-calcium ratios in otoliths and found American eels are capable of using fresh and saline habitats during all continental life phases. As a result, American eels are now considered facultatively catadromous. For yellow-phase eels, saline habitat use is generally considered to be largely limited to shallow protected areas (COSEWIC, 2006; Poirier, 2013). However, MacGregor et al. (2010) observed yellow-phase eels occupying a wider depth range in lotic (flowing water) and lentic (still water) habitats from the surface to 15 m.

Little information is known about the habitat of yellow-phase eel in the neritic environment; however, eel captures in the Gulf of Maine Scotian Shelf area by DFO groundfish research vessel surveys from May – July since 1978 captured eels over a wide depth range including some sites >100 m deep (Bradford, 2013). In Chesapeake Bay, Geer (2003) captured eels at trawl depths of 1 – 33 m at various freshwater and saline sites. A compilation of depth-abundance relationships in American and European eels indicates eel abundance is strongly associated with depth, but the nature of depth abundance relations varies markedly among sites (Cairns et al., 2014). In contrast, Poirier (2013) compared trawl, longline and beach seine eel by-catch using broad habitat descriptions provided by Cairns et al. (2012) and found depth was not a useful component of abundance models across the coastal Atlantic area. Still, in some localized cases, eel abundances increase in waters deeper than 20 m in depth (Cairns et al., 2014).

The distribution of American eels covers a large geographical area and a wide range of depths. Both fresh and saline waters are suitable habitats, so habitat based on salinity level is not likely limited. Yellow phase eels are found in exposed ocean waters, but more so in near shore areas that have greater protection and shallower areas appear to have greater abundances of eels (Poirier, 2013; Cairns et al., 2014). Eel habitat range is large and diverse, and there is only a general understanding of eel habitat use especially at smaller scales. For example, surveys conducted at night using a lit glass bottom boat in southern Gulf of St. Lawrence bays, estuaries and freshwater ponds found eels are most often associated with substrate or sometimes associated with vegetation floating in the water column (Hallett, 2013). Specific habitat information pertaining to local American eel populations is not well known, and thus has yet to be linked to local eel abundances. In the Maritimes Region (northern tip of Cape Breton to the New Brunswick-Maine border), only a few time series abundance estimates have been collected. The main studies have included electrofishing surveys on the St. Marys River (since 2002), LaHave River (since 2003), a short time series from New Brunswick, and a recruitment index based on elver abundance from the East River (Chester) (since 1996) (Department of Fisheries and Oceans, 2010).

In general, population demographics can be defined as particular characteristics that describe quantifiable aspects of a population. Growth rate, age structure and size distribution are a few examples included in population demographics. These three measures are obviously linked, but much less is known about eel age specifically because age can only be determined through examining otoliths, and obtaining otoliths is lethal to the animal. In eels, the relationship of age to length is highly variable, although growth rates are generally determined using ages. The American eel can be long-lived having a continental growth phase ranging from 3 – 40 years (Helfman et al., 1987, Jessop, 1987). Yellow phase eels may stay in the Upper St. Lawrence River and Lake Ontario up to 25 years before they start maturing into the silver phase eels and descend the St. Lawrence River on their way to the Sargasso Sea (COSEWIC 2006; MacGregor et al. 2008).

Little is known about eel habitat use in relation to age but recent evidence suggests American eels have ecotypes. They are genetically distinct geographically and able to adapt to specific environmental conditions. For example, saline or freshwater habitats are linked to maturity schedules and, therefore, age (Cairns et al., 2009; Pavey et al., 2015). Freshwater individuals tend to have longer rearing times than eels that remain in saline habitats. Moreover, eels in Lake Ontario and the Upper St. Lawrence River produce individuals that are 99.9 % female, sometimes exceeding 1 m in length and are sexually maturing at about 20 years (Pavey et al., 2015). Eel abundance in Lake Ontario and the Upper St. Lawrence River has declined by as much as 99 % in the last 40 years (although increases are noted within the past decade) which raises concern for conservation (Pavey et al., 2015). Characterizing the relationships between eel demographics and habitat use is relatively unknown.

The aim of this chapter is to gain a better understanding of the demographics and habitat use of American eel in a local population because links of specific habitat information to demographics are not well described. Specific habitat characteristics can easily be examined in a single, small lake, and trapping is a time-tested method to obtain demographics information. Common demographic information such as age and size, as well as CPUE, were related to habitat use.

Materials and Methods

Study Area

Oakland Lake (44°27'42"N 64°21'51"W), Nova Scotia, is a protected lake with restricted access and no recreational activity including the use of gasoline-powered motors, recreational and commercial fishing, bathing, swimming, disposal of wastes, storage and accumulation farm wastes near the lake, vegetation removal, and watercourse and wetland alterncations (Government of Nova Scotia, 2007). The lake provides the water supply for the town of Mahone Bay with an approximate surface area of 0.66 km^2 surrounded by a drainage basin of approximately 4.056 km^2 (D. Mackenzie, pers. comm.) (Figure 4). A long peninsula divides the lake into two sections; the north-northeastern section is shallow with the majority of vegetation, while the south-southwestern section is deeper with little vegetation. A small stream connects the lake to the Mahone Bay estuary providing a location for estimating elver recruitment and adult out-migration. The stream is approximately 2 km long with two culverts. The lake characteristics make it an ideal study site for long-term monitoring of eels and to study population dynamics of this species.

Traps and Trap Sites

Trapping occurred over several months in each of four consecutive years (2009 – 2012). Traditional style eel traps were cylindrical with a 30.5 cm diameter. Length was either 61 cm or 91.4 cm and all traps had a mesh size of 10 x 24 mm. The entrance hole was 7.3 cm. Traps were attached to a line and buoy. Trap sites were recorded using UTMs and selected to cover a wide variety of local habitats. Generally, traps were placed close to shore and trap distance from shore was measured except for two traps in 2011 that were placed far from shore and set in water 10 m or deeper. Traps were replaced within 10 m of their original trap site, but thrown in a “random” direction upon replacement. This haphazard replacement procedure was adopted to ensure that the broader site area was being sampled rather than a narrowly defined location. This method successively spatially sampled each site. Because of how traps were placed, trap distance from shore varied over sampling periods.

Number of traps used each year varied. In 2011, trap sites were close to those used in 2009 and 2010, but an additional 15 traps were set in new sites. In 2012, only 12 traps were set close to sites used in previous years, but an additional 23 traps were set in new sites (Table 1). Sometimes traps were lost or stolen which contributed to inconsistent site sampling. To analyze data across all four years, standardization of trap sites and trap site numbers was necessary. Trap sites over all four years were plotted by their original coordinates (UTMs). If trap sites fell within 10 m of one another they were considered to be the same trap site because UTMs are accurate to approximately 3 m, which is about the distance of the trap lines. If traps fell more than 10 m apart that trap site was considered a new site. In total, there were 67 different trap sites, which varied among years (Figure 5). This trap site numbering scheme was used in all analyses and any reference to trap sites (also sometimes referred to as “location”) provided in any cited report or thesis is replaced by these standardized site numbers.

Eight minnow traps were set in 2012 from 6 July – 6 September to increase the probability of capturing small eels capable of passing through the larger mesh of traditional eel traps. Minnow traps were moved around Oakland Lake on four occasions (Figure 6). Minnow traps were cylindrical and tapered on either end with a diameter of 22.5 cm at their midpoint and 17.5 cm at their ends. Traps had a total length of 42 cm and a mesh size of 10 mm x 6 mm. Each end had a conical entrance with an entrance hole of 2.5 cm. One entrance was pinched shut to create a single entrance/exit similar to the larger, cylindrical traditional eel traps. Minnow traps were placed at sites, and sampled using the same materials and methods as traditional eel traps.

Depending on weather and number of eels captured, traps were checked at approximately two day intervals. Traps were set, checked, and retrieved using a 3.7 m aluminum boat powered with a 55 lb thrust MinnKota electric motor. High wind and lightning were the main weather conditions that prevented traps from being checked. If many eels were captured and sampled on a single day fewer traps could be checked due to time constraints. Every time a trap was checked, the number of days it had spent in the water since being baited was recorded and defined as fishing time.

Trap Bait

From 2009 – 2011 traps were baited with one or two pieces frozen Atlantic herring (*Clupea harengus*). If herring were small (~15 cm total length [TL]) typically two pieces of bait were used. If herring was > 15 cm TL, only one piece was added. In 2012, traps were baited with five small full-bodied herring of approximately the same size (Ross, 2013). Minnow traps were baited with 1 – 2 small herring cut into pieces (Ross, 2013). Bait was supplied by local fishers in Fox Point or Lunenburg, Nova Scotia.

Powdered latex gloves were used when handling bait to protect hands and minimize contamination of bait with human oils. Traps were not always baited directly after being checked in 2012, but this was the standard protocol used in 2009 – 2011.

Biological Sampling and Tagging

Eels captured in either trap type were placed individually into mesh holding bags that were tied to the side of the boat. Each bag had a different colour "pool noodle" secured around the top for flotation and identification. Multiple traps were often checked before biological sampling if traps were in close proximity. Eels were taken to designated shore sites where they were sampled. Eels were first scanned for a PIT (Passive Integrated Transponder) tag prior to clove oil exposure to determine if measuring and weighing was required. Yearly variations to this protocol were minor. In 2010, length and mass were only measured and recorded if eels had not been anesthetised for one month or more. If eels had been captured within the previous month, sampling consisted of only recording the PIT tag identification number. In 2009, 2011 and 2012 eels were anesthetised and measured regardless of capture history to increase length and mass information of individual eels captured at different periods.

Clove oil is a relatively inexpensive anesthetic. The active ingredient is Euogenol and has anesthetic properties (Anderson, 1997) in addition to having anti-bacterial activity, (Karapmar and Aktug 1987; Briozzo, et al., 1989), antifungal activity (Bullerman et al., 1977). To conduct anesthetisation, each eel was transferred from its holding bag into a 16 L bucket pierced with numerous small holes. A larger 20 L bucket without holes was filled halfway with water and approximately 5 mL of clove oil in 2 L of water used as an anaesthetic was added to this bucket. The 16 L bucket was then placed inside the 20 L bucket submerging the eel in a clove oil suspension. The 16 L bucket could be readily removed from the clove oil solution. Eels exposed to clove oil for approximately 20 – 90 s decreased movement and eventually becoming listless. Small eels required less time to become anesthetized than larger eels. Once anesthetised, eels were removed from the clove oil and length and mass recorded. If the anaesthesia exposure period was inadequate, the eel was placed back in the clove oil for an additional few seconds. After biological sampling and tagging, eels were placed in fresh water and moved back and forth to pass oxygenated water over their gills. Within 2 – 10 minutes, eels recovered, regained their equilibrium and were released.

While anesthetized, lengths were measured to the nearest 0.5 cm by placing eels on a measuring board. Mass was measured using a portable digital scale. If no PIT tag was present and the eel was greater than 25 cm in length, either a Biomark HPT8 8.4 mm 134.2 kHz FDXB or Biomark HPT12 12.5 mm 234.2 kHz ISO FDXB PIT tag was inserted with either a Biomark MK165 (N165 needles) or Biomark MK10 (N125 needles) implanter, respectively. To insert tags, one technician inserted a needle containing a tag while the other held the eel. Tags were injected approximately 2 cm anterior to the dorsal fin to one of either side of the spine. Once successfully tagged, eels were scanned using a handheld weatherproof Biomark 165 reader and their ID numbers were recorded for future identification. From 2009 – 2010 only 12.5 mm tags were used, but in 2011 and 2012, 12.5 mm and 8.4 mm tags were used interchangeably. When 12.5 mm tags were used, ID numbers consisted of 15 digits, which began with the same 9 digits (985 121 020). When 8.4 mm tags were used ID numbers consisted of 12 digits, which began with the same 9 digits (982 196 024). Data were recorded on a waterproof notepad using pencil.

In 2011, 34 eels were sacrificed to determine an age-length curve for this local population. Several eels were selected within length ranges of 5 cm from 30 – 70 cm. This was done to determine the variability between eel age and length. Because few eels less than 30 cm were captured and extracting otoliths from small eels is difficult, only eels ≥30 cm were collected. Eels were lethally anesthetized with a clove oil overdose, transported back to a holding facility, and placed in a freezer. Otoliths were extracted from eels using methods found in Manual for the Ageing of Atlantic Eel (2009) and sent to Guy Verreault (Quebec Ministry of Natural Resources and Wildlife) for aging.

Eels produce a layer of slime as a defence mechanism and therefore it is important to handle them with care. Prior to anaesthetizing and during recovery, cotton gloves were always used overtop of latex gloves for better control while handling eels and to reduce interaction with eel skin. Latex gloves were also used because clove oil may cause a numbing and/or burning sensation when in contact with human skin.

Acoustic Tagging

In 2012, in addition to receiving PIT tags, eight American eels, with weight >300 g, were acoustically tagged; three each on 4 July 2012 and 30 July 2012, and two on 14 August 2012. Anesthetisation was conducted using the same protocol as Biological Sampling and Tagging to facilitate tag implantation. Once anesthetised, ttransmitters (V9P-6L, Vemco Ltd., Nova Scotia) with a depth sensor calibrated to the finest scale under 50 m were surgically implanted into the abdominal cavity and length and mass were recorded. To insert the acoustic tag, anaesthetised eels were placed ventral side up, and a 3 – 4 cm incision was made on either side of the linea alba approximately 2 – 4 cm anterior to the anal fin. Once inserted, transmitters were pushed approximately 2 – 4 cm anteriorly using a blunt probe. Two horizontal mattress sutures using sterile absorbable 1/0 Ethilon monofilament nylon sutures with a reverse cutting edge (Johnson & Johnson, Ontario) were used to close the incision. All equipment, including transmitters, was disinfected prior to surgery using a 10% Betadine solution, followed by a saline rinse. Surgeries took between 4 – 6 minutes excluding anaesthesia and recovery time. Recovery time and procedure following surgery and anesthesia followed the same protocol as Biological Sampling and Tagging.

Four VEMCO hydroacoustic receivers (model VR2W) were placed around the lake to gather movement and depth data on the tagged eels from 3 July – 15 October 2012 (Figure 7). Receivers were placed approximately 45 cm above the bottom with small buoys and moored with two cinderblocks per unit. Excess line at the surface was removed and a large buoy was attached to keep receivers in place.

Habitat Characterization

Initially the lake was surveyed using a habitat assessment specifically designed for this study, and these habitat characteristics were applied in 2009 and 2010 to establish trap sites. These initial habitats were described using a block approach where characteristics such as depth, shoreline slope, underwater slope, and scoring of substrate composition (boulder, cobble, sand) were measured and described. Depth was recorded at each trap site in 2009 using a fish finder and coordinates taken by GPS. To complement the site-specific depths of 2009, and provide depth contours for acoustic telemetry analysis, a comprehensive bathymetry was completed in 2011 from georeferenced depths acquired using a fish finder and mapped using QGIS (version 2.10) (Figure 7). Where site-specific depths were not available, site depths were estimated from bathymetry. Shoreline slope and underwater slope were approximated and categorized on a scale of 1 – 4, where 1 was a slope near zero and 4 was a steep slope. Shoreline and substrate composition was recorded based on percentage of sand, cobble and boulder, adding to 100. Substrate composition that could not be determined with the naked eye was determined using an Aquavue underwater viewer.

In 2011, additional habitat characteristics were added including pH, temperature, DO, vegetation cover and vegetation type, and substrate composition (Cottreau, 2013). Habitat surveys were completed three times: P1=24 May – 2 June, P2=29 June – 7 July, and P3=13 – 14 August using a glass-bottom boat to characterize seasonal changes. Cottreau (2013) determined habitat transition points around the perimeter of Oakland Lake as locations where a marked change in habitat occurred based on vegetation or substrate changes. These points were recorded using UTM coordinates. The center between two habitat transition points was calculated by calculating the midpoint using UTM coordinates. The resulting midpoints were assigned as habitat zones. Traps were then assigned to habitat zones based on their closest proximity to a zone.

Transition points between vegetative habitats occurred if a new taxon of vegetation was observed or if a vegetation taxon was no longer present. Plant taxa included pickerelweed (*Pontederia cordata*), lily pads (*Nunphar microphyllum, Nunphar variegatum, and Nymphoides cordata* were pooled as one taxon), eelgrass (*Vallisneria*), and smartweed (*Polygonum lapathifolium*). Various types of green algae (Chlorophyta) were observed and pooled as one taxon. Each taxon was scored as present (1) or absent

(0). Transition points between substrate habitats occurred if any substrate component changed by more than 20 %. Substrate type was recorded based on percent coverage of detritus, sand, gravel, cobble, boulder, adding to 100. Temperature and dissolved oxygen were measured at the surface and just above the substrate in each habitat zone using a Hanna Oxy Check probe (Hanna Instruments, model HI 9147). Periodically, pH measurements were conducted at the surface during the daytime.

These additional habitat characteristics were merged where appropriate with initial (2009) habitat characteristics to enhance habitat characterization in Oakland Lake. Temperature, pH, DO, and vegetation were assigned to the three survey periods P1, P2, P3 of Cottreau (2013) roughly equivalent to late spring (before 17 June), summer (17 June – 25 July), and late summer/early fall (after 25 July), respectively. Temperature, pH, and DO were merged with 2011 habitat characteristics only because these physical measures would probably change yearly. Pooled means of substrate type across the three survey periods were used for substrate condition because it was deemed that substrate would change little over the sampling periods. Substrate characteristics were considered stable across all four years so 2011 data were used for all years. Vegetation characteristics were probably variable in timing among years (e.g. onset of lily pads), but because periods were coarsely defined, it was deemed appropriate to use vegetation characteristics from 2011 across all four years. Full details regarding additional habitat characteristics of Oakland Lake can be found in Cottreau (2013).

Visualizations and Statistical Analysis

Trap CPUE was the number of eels captured divided by the number of trap checks per individual trap. Trapping events varied by fishing time (i.e. set time to check time varied). This means that during each trapping event some traps may have fished for longer periods (days) than others. This variability was not considered in calculating trap CPUE because eels in Oakland were capable of escaping from traditional eel traps regardless of how long a trap fished for (Cox, 2012).

Eel length data are presented as TL, a straight-line measure from the tip of the snout to the end of the caudal fin. Mean length(s) and mass were calculated using the first measurements for each eel to avoid bias from multiple recaptures. ANOVA with a 95 % confidence interval was used to determine if any significant difference in length or mass existed among years. Tukey HSD (honest significant difference) tests were used for pairwise comparisons when the omnibus ANOVA was significant. An independent T-Test using a 95 % confidence interval was conducted to determine if a significant difference existed between traditional eel traps and minnow traps for eel length and mass. Histograms were used to check for normality of residuals, and where non-normality was detected, non-parametric Kruskal-Wallis tests using a 95 % confidence interval were used instead of ANOVA. Following Kruskal-Wallis tests, Wilcoxon signed-rank tests were used for pairwise comparisons. Where comparison groups were unequal in size (unbalanced), the glm procedure was used instead of aov in R. All analyses and visualizations were conducted using the R programming language (R Core Development Team, 2014; version 3.2.1).

Length-mass relationships are generally non-linear in fishes. Most length-mass relationships in fishes follow a two-parameter power function with a multiplicative error term:

$$W_i = \alpha L_i^{\beta} 10^{\epsilon_i} \tag{1.0}$$

where α and β are parameters (empirical constants) and 10^{ϵ_i} is the multiplicative error term for the *i*th fish. Equation (1.0) was transformed to a $\log_{10}$-$\log_{10}$ (linear) model and plotted by applying common logarithms to both sides and simplifying:

$$log_{10}(W_i) = \ log_{10}(\alpha) + \ \beta log_{10}(L_i) + \ \epsilon_i \qquad (1.1)$$

In addition to being linear, equation (1.1) has errors that are additive and will show a constant variability around the line for all lengths. Thus, linear regression methods are used to fit a linear model to $\log_{10}(W)$- $\log_{10}(L)$ data, where the slope is an estimate of β and the intercept is an estimate of log10(α). The fit of Equation (1.1) may be used to predict $\log_{10}(W)$ given a $\log_{10}(L)$, which will then be back-transformed (i.e., anti-logged) to the more useful W. Values that are back-transformed from the log scale are often biased and can be corrected by multiplying the back-transformed value by (Sprugel, 1983):

$$e^{\frac{(log_e(base)^S X|Y)}{2}} \qquad (1.2)$$

where $^{s}Y\,|X$ is the residual standard error and $\log_e$(base) is used to adjust for the base of the logarithm used.

Mean temperature and DO were calculated for each sampling month in 2011. Regression analyses were used to compare trap CPUE with temperature and DO for 2011 only. The {glht} function was used to compare trap CPUE with substrate type and violin plots and boxplots were used simultaneously for visualization. A 2-way ANOVA with a 95 % confidence interval compared sampling months to trap CPUE, and both vegetation and vegetation type. Boxplots with data points were used for visualization where each dot represents a trap. Violin plots show the density of points and aid in identifying trends. Boxplots provide statistics (median, interquartile range, etc.) that are useful for comparisons.

Depth patterns and movement trajectories of acoustically tagged eels were plotted to visualize depth with eel activity during the night and day. Daytime was set as the earliest sunrise and sunset for each month. An independent T-test with 95% confidence intervals was used to determine differences. Details regarding acoustic tagging and Vemco Position System (VPS) arrays can in found in McLean (2013). These, and all other plots were created using ggplot2 – a package for visualization in R. Values are presented as mean ± SD unless otherwise stated.

Recapture distances by individual eels were calculated and plotted to describe movement patterns (from original trap sites to recapture trap sites) and home range size and/or presence. Recapture distance was calculated as the distance between an original trap site and subsequent recapture locations. Maximum recapture distance was calculated as the greatest distance between an original trap site and any recapture location. However, this distance is linear which may underestimate the true distance eels travelled particularly in relation to movement around the peninsula. Maximum recapture distance travelled may be underestimated in some instances, but still provides valuable information on how far eels travel within Oakland Lake.

Animal handling and tagging protocols and procedures were approved by the Acadia University Animal Care Committee under Protocol 16-11 and revisions.

Results

Tags, Captures and Recaptures

A total of 368 PIT tags were implanted across all four years into eels captured in traditional eel traps (Table 1). Traditional eel traps produced a total of 842 eel captures or recaptures. New trap sites were added in 2011 and 2012, with most trap sites repeated from 2009 in 2010 and 2011, but only 12 trap sites repeated in 2012 (Table 1). Multiple recaptures of individuals occurred within each study year, but the majority of eels were captured once (unique captures). Fewer trapping events in 2009 produced fewer captures, whereas more trapping events in 2011 produced more captures. However, trap CPUE was higher in 2009, with the fewest captures, than in 2011 with the most captures (Table 1). In 2010 and 2012 a similar number of trapping events occurred, but trap CPUE was highest in 2010 compared with the lowest in 2012 (Table 1). Trap CPUE was lowest in 2012, with a difference from 2009 owing mainly to an increase in trapping events.

New tag implants increased successively each year until 2012, but in 2012 new tags decreased to the level of 2009 (Table 2). From 2009 – 2011, the number of eels recaptured increased successively with a quadrupling from 2009 to 2010 and a further 25% increase in 2011. In 2012, eel recaptures within that year decreased and were similar to 2009. From 2009 – 2011, the number of unique eels recaptured within each year increased successively with a tripling from 2009 to 2010, stable from 2010 to 2011, and a decrease in 2012 (Table 2). From 2009 – 2011, total and unique cumulative tag recaptures increased successively with a large increase from 2009 to 2010, moderate increase in 2011, and a severe drop in 2012. In general, 2012 shows several differences than other years despite a similar number of traps, trapping events and mean eels captured per trap.

In 2011 and 2012, 71 and 23 eels, respectively, were captured in traditional eel traps, but these eels did not have PIT tags or PIT tag data recorded. In 06 July – 31 August 2011, 34 eels without PIT tags were killed for length-age analysis. Of these eels, 31 had complete mass-length data. On 20 and 27 June 2011, four and 33 eels, respectively, were captured that did not have PIT tags, PIT tag data, or associated length-mass data recorded. From 15 June – 29 June 2012, 23 eels were captured in traditional eel traps without PIT tags or PIT tag data, but all 23 had associated length-mass data recorded. Lack of PIT tags or PIT tag data resulted from running out of tags and a failure of the tag reader. Poor weather conditions required traps to be emptied to prevent eels from remaining in traps over a long period, but sometimes prevented length-mass data from being obtained. Capture frequency decreased as total recaptures increased in traditional eel traps (Figure 8). Across all four study years, 201 eels were captured only once and 167 eels were captured more than once. It is possible, that eels captured only once may have previously been captured at a time when tags were unavailable. No eel was recaptured more than 12 times. As unique traditional eel traps increased, the frequency of eels captured decreased (Figure 9). On 232 occasions, eels were captured in one unique traditional eel trap, dropping to only 68 occasions where eels were captured in two different traditional eel traps, further declining with increasing, and different, traditional eel traps. The majority of time, eels were captured only once in only one trap. Yet, the most extreme case was eel (985 121 020 147 195), which was recaptured in traditional eel traps 12 times in eight different traps from 2010 –2011 (Figure 10). This eel was primarily captured southwest of the peninsula in the deeper areas of the lake with the exception of one capture in 2010 on the northeast side. No discernable movement pattern was detected, likely because of the temporal coarseness of recaptures. The greatest number of eels captured in one traditional eel trap within one year was 41 eels in 2011 in trap 6, located in the northern cove (Figure 11). Each year, more eels were captured in the northern cove relative to total eels captured, but eels were captured essentially along the shore in all areas. Minnow traps captured 18 eels; 17 captures of single eels with only one recapture. Only three eels captured in minnow traps had previously been captured in traditional eel traps indicating traditional eel traps may be size selective towards larger eels.

Eel Size and Age

Length ranged from 15 – 82 cm, and mass ranged from 40 – 1,373 g across all four study years for eels captured in traditional eel traps (Table 3; Figure 12). Mean length and mass were highest in 2009 and lowest in 2012. Wilcoxon signed-rank tests confirmed all years were significantly different from one another ($p = < 0.001$) in length and mass except for 2009 and 2010 (length $p = 0.300$; mass $p = 0.321$), and 2011 and 2012 (length $p = 0.321$; mass $p = 0.314$) (Table 4; Figure 12). Length of eels captured in minnow traps ranged from 28 – 48 cm and mass ranged from 40 – 220 g (Table 3; Figure 13). Eels captured in minnow traps were not significantly smaller in length and mass than eels captured in traditional eel traps (length $p = 0.489$; mass $p = 0.089$) (Table 3; Figure 13). However, both eel length and mass varied less in minnow traps than eels captured in traditional eel traps and the statistical non-significance is probably due to the increased variance around traditional eel traps and low sample size ($n=17$) for minnow traps compared with traditional eel traps, rather than a biological effect. Overall, eels of length 37 – 42 cm were captured most often (Figure 14).

Data from both trap types were pooled to calculate a length-mass relationship. A strong positive relationship exists between Log_{10}length and Log_{10}mass ($p = <0.001$; R^2 adj = 0.919) (Figure 15). Of the 34 eels extracted for aging, 23 were successfully aged. Some otoliths could not be found resulting in only one otolith for aging, and one otolith was insufficient for aging so no ages were obtained for some eels. In other cases, incorrect labeling of samples prevented using that data. Age ranged from 13 – 28 years with a mean of 18.2 ± 3.9 years. Length for these eels ranged from 30 – 66.5 cm with a mean 47.4 ± 11.5 cm. A biologically weak, but statistically significant relationship exists between age and length ($p = 0.005$; R^2 adj = 0.281) (Figure 16). Age at length is highly variable.

Habitat Characteristics

Daytime surface and bottom temperatures ranged from 17.9 – 27.7 °C and 17.5 – 27.6 °C, respectively where temperatures were lowest in June and highest in July and relatively stable through August and September of the sampling period. Surface temperature was warmer than bottom temperature in July; otherwise surface temperature was slightly higher than bottom temperature for most other paired measurements. As bottom temperature increased, surface temperature increased (Figure 17). Monthly mean surface and bottom temperature ranged from 21.5 ± 3.2 – 22.3 ± 2.6 °C and 21.0 ± 2.8 – 22.1 ± 2.7 °C, respectively (Table 5).

Surface DO and bottom DO ranged from 6.2 – 13.8 ppm and 6.6 – 13.9 ppm respectively, with lowest values in July and highest values in June. Bottom DO was generally higher than surface DO, particularly in July. As bottom DO increased relative surface DO decreased (Figure 18). Monthly mean surface and bottom DO ranged from

9.1 ± 1.6 – 9.2 ± 0.8 ppm and 9.3 ± 1.0 – 9.5 ± 1.6 ppm, respectively. Monthly mean surface DO remained relatively stable with the exception of July. Monthly mean bottom DO remained relatively stable from June – July and decreased successively thereafter (Table 6). The pH ranged from 7.6 – 9.0 and was highest in June and lowest in July. Mean pH was the same in May and June but was slightly lower in July (Table 7).

Substrate was variable between trap sites (Appendix 1). Of the 67 traditional eel trap sites, 16 had only one type of substrate. One trap site contained 100% boulders, one trap site contained 100% sand, five trap sites contained 100% cobble and nine trap sites contained 100% detritus. Gravel was found at only four trap sites and made up 50% or less of the substrate. Of the 67 traditional eel trap sites, 43 trap sites contained 0% boulder, 32 contained 0% cobble, 63 contained 0% gravel, 30 contained 0% sand and 42 contained 0% detritus.

The presence and absence of vegetation was variable between trap sites and survey periods (P1, P2, P3) (Appendix 2). Algae were the most common vegetation type and were found at all but four trap sites during at least one sampling period. Lily pads were the second most common vegetation type followed by eelgrass, pickerelweed and smartweed (Table 8).

Habitat and trap CPUE

In 2011, there was a significant negative relationship between trap CPUE and both surface temperature ($p = 0.011$; Figure 19) and bottom temperature ($p = 0.004$; Figure 19); more eels were captured when water temperatures were cooler. However, both of these relationships explained very little (1.1 % and 1.5 %, respectively) of this change. In 2011, there were non-significant positive relationships between trap CPUE and surface DO ($p = 0.325$) and bottom DO ($p = 0.282$) (Figure 20).

Trap CPUE appeared higher when trap sites only contained 20 – 30 % boulder substrate or when trap sites contained 80 % boulder substrate. Trap CPUE appeared lowest when trap sites contained 10 % boulder substrate, but no significant difference was found between trap CPUE and percent boulder (Figure 21). Trap CPUE appeared higher when trap sites contained 40 % or 90 % cobble substrate and lowest when trap sites contained 60 % cobble substrate, but no significant difference was found between trap CPUE and percent cobble (Figure 22). Eels were captured when trap sites did contain gravel substrate. Trap CPUE appeared higher when trap sites contained 0 % gravel and lowest when a trap site contained 10 % gravel, but no significant difference was found between trap CPUE and percent gravel (Figure 23). Trap CPUE appeared highest when trap sites contained 70 % sand and lowest when a trap site contained 100 % sand, but no significant difference was found between trap CPUE and percent sand (Figure 24). Trap CPUE appeared highest when a trap site contained 40 % detritus and lowest when a trap site contained 30 % detritus, but no significant difference was found between trap CPUE and percent detritus (Figure 25).

Overall, for any single substrate type, or combination of, eels were captured but no discernible pattern was detected. The shortest and longest eels were captured in a trap sites containing 80:20 % boulder:sand substrate, and 50:50 % cobble:gravel substrate, respectively. Trap CPUE appeared higher when underwater slope was steeper but no significant difference was found between trap CPUE and individual underwater slopes. Trap CPUE appeared higher when shoreline slope was steeper but no significant difference was found between trap CPUE and individual shoreline slopes (Figure 26). It seems eels of varying sizes in Oakland Lake use a combination of substrate types and underwater and shoreline slopes not using one type or incline over another.

When vegetation was present, 790 eels were captured compared with 52 eels when vegetation was absent. Trap CPUE was higher when vegetation was absent but no significant difference in trap CPUE and vegetation was found ($p = 0.535$) (Figure 33a). Regardless of the presence or absence of vegetation, trap CPUE was significantly higher in May decreasing successively and significantly until July. Trap CPUE continued to decrease from July to September but the decrease was only significant between July and September (Figure 27).

Trap CPUE was significantly lower when algae were present ($p = < 0.001$) (Figure 33b). Of the 67 trap sites, 65 contained algae at some point during the sampling period. Regardless of the presence or absence of algae, trap CPUE was significantly higher in May decreasing successively and significantly until July. Trap CPUE continued to decrease non-significantly from July to September (Figure 28).

Trap CPUE was not significantly different when eelgrass was present or absent ($p = 0.422$) (Figure 33c). In total, 15 trap sites contained eelgrass at some point during the sampling period. Regardless of the presence or absence of eelgrass, trap CPUE was significantly higher in May decreasing successively and significantly until July. Trap CPUE continued to decrease from July to September but the decrease was only significant between July and September (Figure 29).

When lily pads were present at trap sites trap CPUE appeared lower than when lily pads were absent but no significant difference was found ($p = 0.551$) (Figure 33d). In total, 34 trap sites contained lily pads at some point during the sampling period. Regardless of the presence or absence of lily pads, trap CPUE was significantly higher in May decreasing successively and significantly until July. Trap CPUE continued to decrease non-significantly from July to September (Figure 30).

When smartweed was present at trap sites trap CPUE appeared slightly higher than when smartweed was absent but no significant difference was found (p = 0.499) (Figure 33d). In total, nine trap sites contained smartweed at some point during the sampling period. Regardless of the presence or absence of smartweed, trap CPUE was significantly higher in May decreasing successively and significantly until July. Trap CPUE continued to decrease non-significantly from July to September (Figure 31).

When pickerelweed was present at trap sites trap CPUE appeared higher than when pickerelweed was absent but no significant difference was found (p = 0.145). In total, 10 trap sites contained pickerelweed at some point during the sampling period. Regardless of the presence or absence of pickerelweed, trap CPUE was significantly higher in May decreasing successively and significantly until July. Trap CPUE continued to decrease non-significantly from July to September (Figure 32).

Overall, for any vegetation, single vegetation type, or combination of, eels were captured but no discernible pattern was detected with the exception of eels preferring no algae despite it being present at nearly all trap sites at some point during the sampling period. Regardless of vegetation or single vegetation type, a significantly higher number of eels were captured in May and June and successively decreased thereafter suggesting, eels tended to be more active and feed immediately after over-wintering (Figure 33). Additionally, as the study period progressed and natural food abundance, vegetation, and temperature increased, eels likely found other natural food sources and hiding places and became less active, not having to move far to feed.

Trap depths ranged from 0.46 – 3.05 m with the exception of the two traps set in water 10 m or deeper in 2011. No eels were captured in the two deep traps. From 2009 – 2012 mean eel count was variable, but high counts were seen in each year at different depths with the exception of 2010 and 2012 (Figure 34). All acoustically tagged eels were detected at depths ≤ 15 m, but were primarily detected at depths < 5 m and frequently moved from one depth to another (Figure 35). There appears to be no relationship with number of eel detections based on day and night and depth ($p = 0.824$; Figure 36).

Home Range

The maximum recapture distance eels travelled from their original trap site varied. Eels captured two or three times were recaptured within 10 m of their original trap site on 26 and 5 occasions, respectively. Eels captured more than three times travelled a maximum recapture distance of at least 260 m (Figure 37). Eels travel within all areas of Oakland Lake so the peninsula and habitat differences including substrate composition, vegetation type and shoreline and underwater slope do not appear to be barriers. Eel length did not appear to affect the maximum recapture distance travelled by eels (Figure 38).

The recapture distance eels travelled from their original trap site was variable. Of the 842 recaptures, 30 individual eels were recaptured at their original trap site. Of those 30 eels, one eel was recaptured three times and three individual eels were recaptured twice. Eel 985 121 020 147 195, was captured less than 200 m from its original trap site

50 % of the time and on its eighth recapture was captured at its original trap site (Figure 39).

The number of detections varied between individually acoustically tagged eels and ranged from 112,670 – 1,396,541. In total, there were 4,856,665 detections from all acoustically tagged eels (Table 9). The three eels (1418, 1419, 1420) acoustically tagged 3 July 2012 were originally captured in the south-eastern part of the lake and were detected primarily on the westerly side (receivers 3 + 4) of Oakland Lake for nearly one month. Eel 1418 went undetected for a period of time near the end of July and early August (Figure 41). It was later detected near the outgoing stream (receiver 1) until September thereafter remaining undetected. Eel 1419 was detected in the northern cove (receiver 2) from late July to early September, but was detected briefly on the westerly side (receivers 3 + 4) of the lake in mid-August. Eel 1420 was detected frequently at all receiver stations from early August to mid-September, thereafter remaining undetected. The second batch of three eels (1408, 1409, 1421) acoustically tagged 30 July 2012 were originally captured on the north and south-eastern part of the lake and were detected at all receiver stations with the exception of 1421. In total, Eel 1408 was detected 744,508 times. It was frequently and primarily detected at receivers on the westerly side (receivers 3 + 4) and near the outgoing stream, but only periodically detected in the northern cove and not detected after early October (Figure 40). Eel 1409 was frequently detected at all receiver stations just prior to their removal on 15 October 2012. Eel 1421 was briefly detected on the westerly side of Oakland Lake (receiver 4) and only periodically in the northern cove, which may indicate an error in the receiver, the tag, or the receiver data, or that this eel remained undetected for periods. The last two eels (1267, 1273) acoustically tagged 14 August 2012 were originally captured on the north and south-eastern part of the lake and were both detected at all four receiver stations. Eel 1267 was detected at all receiver stations in mid-August, but went undetected until late August when it was detected again on the westerly side of Oakland Lake and also near the outgoing stream (receiver 1). This eel was detected until the receiver stations were removed, but only on the westerly side of Oakland Lake (receiver 3) and near the outgoing stream (receiver 1). Eel 1273 was primarily detected near the outgoing stream, but was also detected at all other receiver stations until early October. An increase in detections at receiver stations 3 and 4 immediately after surgery was probably because acoustically tagged eels were brought to a shore site near those receiver stations for surgical implantation. Overall, eels are sometimes detected in one area, sometimes detected in two areas on the same side of the peninsula and sometimes detected everywhere. When two or more receiver stations simultaneously detected the same eel it could mean the eel travelled between receiver stations or the stations detected the eel in unison (Figure 41). This depth of inquiry is not required to present the overall case that eels travelled throughout the lake, often being detected at all receivers, and using shallow water depths with no indication of diurnal depth differences.

Discussion

The 2009 season had the fewest number of eels were captured and the fewest trapping events. The 2011 season had the greatest number of eels captured and the most trapping events. Trapping events are not a comparable measure across years because of variable numbers of traps. Instead, trap CPUE is a reasonable measure to compare eel captures across years and under various other conditions (e.g. trap CPUE presence/absence vegetation). Because individual trap sites in Oakland Lake were checked inconsistently, trap CPUE provides the average number of eels captured at each trap site based on effort (number of trap checks) therefore, making it a comparable measurement to other traps sites.

Across all four study years, more than half of eels captured had PIT tags. Assuming capture probability (catchability) is constant, this suggests the majority of eels >30 cm in Oakland Lake have been tagged which could underestimate the true population because a higher number of recaptures would exist. However, size appears to affect catchability. In 2011 and 2012, trap CPUE was lowest despite adding 12 trap sites. The 34 eels extracted in 2011 may have contributed to a lower trap CPUE in 2012 because the removed eels were larger, significantly decreasing mean eel length in 2011 and 2012. As well, eight larger eels were acoustically tagged in 2012. Studies looking at acoustically tagged species assume surgical implantation of tags does not affect the behavior of tagged individuals. Hondorp et al. (2015) found the activity of acoustically tagged lake sturgeon did not differ between newly tagged individuals and conspecifics tagged in prior years. It was concluded that their findings should be applicable to most tag sizes given that they used some of the largest tags available, but sturgeon are also very large fish. Catchability is influenced by fishing time, bait quality, environmental variables (e.g. temperature, salinity, and current velocity), gear saturation and escapement, inter and intra-specific interactions, gender- and age-specific behaviors, and behaviors related to tidal or seasonal cycles (Miller, 1990). The main factor herein contributing to variable annual catches was likely trapping events because bait quality and environmental factors described by Miller (1990) were consistent across all four years, and fishing time remained haphazard in all four years. It was impossible to gauge gear escapement, know inter/intra-specific interactions or gender/age-specific behaviours affected catchability. Because the study herein was conducted across four years and seasonally, similar tidal cycles would have been experienced. This is important because eel activity has been linked to lunar cycles. For instance, increased eel activity during new moon periods was found for yellow and silver-phase eels in Prince Edward Island, and Rhode Island Estuaries (Cairns and Hooley, 2003; Winn et al., 1975).

Collected eels in 2011 were probably already established in Oakland Lake. After being removed, recruits may have been smaller and therefore, removing any eels would result in an overall local population size decrease. In 2012, minnow traps were set with the intent to capture smaller eels but did not catch significantly smaller eels than traditional eel traps, although no larger eels were captured in minnow traps probably because the minnow trap opening was small. The small sample size, and maximum size of eels captured in minnow traps may explain why both eel length and mass varied less in minnow traps than eels captured in traditional eel traps. Minnow traps also captured far fewer individual eels than traditional eel traps. Cox (2012) filmed smaller eels traveling through traditional eel trap mesh without issue, suggesting that smaller eels feed in eel traps, but are able to leave easily, and, therefore, have no need to enter smaller minnow traps for food. Winn et al. (1975) used a length threshold of 40 cm to identify females. Mean eel length across all four study years suggests traditional eels traps used in Oakland Lake were size selective towards larger eels and these eels were mostly females. However, eels that remain in saline water have shown increased growth rate (Cairns et al., 2009) compared to yellow eels residing in freshwater that have shown slower growth rates (Morrison et al., 2003). Therefore, it is possible that the threshold Winn et al. (1975) proposed may be biased towards eels residing in either saline or freshwater.

A low trap CPUE in 2011 and 2012 also could be indicative of learned behavior over time. Steven et al. (2005) describes the catchability of individuals as variable and that some eels may be “trap-happy” or “trap-shy” skewing trapping results. Most eels were only captured once suggesting eels may become trap-shy after their first capture. Conversely, baiting traps may lead to trap-happy eels explaining why some eels were recaptured multiple times. Underwater camera surveys conducted in Oakland Lake showed that baiting traps led to eels using the traps repeatedly, and also showed many eels learned to escape and at least remembered the escape location for a short period (Cox, 2012). Cox (2012) showed eels entering traps, eating bait and leaving, but also that eels would return to traps multiple times over short periods (minutes) to feed again. Eels that tend to get captured in only one trap or a few traps close together may learn these traps provide a consistent and constant food source. However, only a small proportion of eels were recaptured at their original trap site suggesting that even if there is a home range, close proximity to a trap site for a period of time or learned behavior towards a specific trap site may be more indicative of learned behavior for consistent food source. Eels are not considered trap happy unless they are captured multiple times. Most eels were captured only once, and thus considered trap shy, just may be quick learners and better at escaping.

Mean age of eels captured in 2011 suggests eels in Oakland Lake spend many years in the growth phase before becoming sexually mature. Late-age maturity coincides with Morrison et al. (2003) who found that yellow eels residing in freshwater had slower growth rates than those that spent their entire lives in brackish. Similarly, Facey and Lebar (1981) proposed American eels in the northern part of their range exhibit slower growth and remain in freshwater and estuarine systems longer before beginning their migration back to sea. Other studies have shown that after about 12 – 13 years and a mean size of 69 cm American eels from Newfoundland, Lake Champlain and Lake Ontario migrate back to the Sargasso Sea (Gray and Andrews, 1971; Hurley, 1972; Facey and LaBar, 1981; McGrath et al., 2003). More recently, Cairns et al. (2014) generally found the length of silver-phase eels sampled south of the Cabot Strait varied little with latitude and distance from the spawning ground. Female silver-phase eel length was greatest beyond the Cabot Strait at the maximum distance from the spawning ground (St. Lawrence Basin). American eels in the southern part of their range begin migration earlier than their northern counterparts (Hansen and Eversole, 1984; Helfman et al., 1984; Owens and Geer, 2003). In Cooper River, South Carolina, American eels older than 7 years and greater than 65 cm in length were sparse suggesting adults migrate at a younger age and smaller size (Hansen and Eversole, 1984).

American eels are known to be highly tolerant of a wide range of temperatures as seen by Geer (2003) in the Chesapeake Bay where eels were captured at temperatures ranging from 3 – 31°C. Haro (1991) identified a temperature preference range 17.8 – 19.8°C for yellow-phase American eels residing in freshwater. Interestingly, trap CPUE was highest in Oakland Lake when surface and bottom temperature were cooler. Despite a statistically significant negative relationship between trap CPUE and temperature, temperature only accounted for a very small proportion (1.1 % and 1.5 %) of trap CPUE variability. If temperature was the main factor influencing trap CPUE, it would be expected that as temperature increased fewer eels would have been captured given the temperature preference described by Haro (1991). However, Oakland Lake is small and does not have varied temperatures from which eels can choose. Instead, there seems to be more factors influencing trap CPUE such as increased activity and feeding post over-wintering when temperatures in Oakland Lake were cool in relation to the remainder of the study period. Early spring, late fall and over-wintering sampling was not conducted so the coolest temperatures were not measured and recorded. Hawkins (1995) and Smogor et al. (1995) found eels in freshwater streams generally do not demonstrate consistent preferences for habitat type, cover, and substrate or water temperature. Similarly, in Oakland Lake eels did not demonstrate consistent preferences for habitat characteristics including temperature, DO, pH, substrate type, substrate percent, shoreline and underwater slope, vegetation, vegetation type and depth. Perhaps rather than one habitat type or characteristic it is a combination of factors driving habitat use and consequently influencing trap CPUE in Oakland Lake.

Temperature influences the degree of seasonal movement and eels become less active when the temperature drops below 11°C (Department of Fisheries and Oceans Canada, 2006). Similarly, Wenner and Musick (1975) found the number of eels captured during each month (January – December) over three study years varied greatly, but some trends were found, including more eels were captured during the spring and fewer eels were captured during the winter. When trap CPUE was highest in late spring and early summer, Oakland Lake's surface and bottom temperature were coolest. However, these temperatures would be warm compared with winter months. Therefore, a high trap CPUE may be influenced more by high initial activity post over-wintering rather than cool temperatures. Because Oakland Lake is relatively small it is capable of warming quickly and appeared to have little variation in temperature after the initial spring increase. Because temperature and DO are related (as temperature increases DO decreases), DO also showed little variation over the period it was measured.

DO is a key factor in determining overall water quality. The effect of low oxygen is species specific, but when concentration falls below 4 mg/L (4 ppm) most fish become stressed (Francis-Floyd, 2003). Low DO levels may limit American eel distribution (Rulifson et al., 2004). During the study period in Oakland Lake, DO never dropped below the critical 4 mg/L (4 ppm). Similarly, abundant catches of American eel in North Carolina were nearly always in waters with DO levels above 4 mg/L (Rulifson et al., 2004). Trap CPUE in Oakland Lake was highest in late spring and early summer when DO levels peaked.

Wiley et al. (2004) describes American eel as habitat generalists with little consistent preference for habitat type, cover, substrate, or water temperature, which may explain why eels in Oakland Lake did not appear to use one bottom substrate type over another. Instead, it appears eels used trap sites containing a combination of different substrate types. Similarly, Hawkins (1995) and Smogor et al. (1995) determined no consistent preference for habitat type, cover, and substrate or water temperature. Tomie (2012) found eels held in captivity rarely burrowed in sand and gravel bottoms. In Oakland Lake, eels appeared to use a moderate amount of sand substrate but trap CPUE was highest in trap sites that did not contain gravel. Conversely, in Ontario, smaller stocked eels were associated with gravel and layered bedrock (Loyst, 2012). Loyst (2012) argued that while American eel fit the definition of habitat generalists, individuals use specific substrate features that change with increasing length. In Ontario, Loyst (2012) found larger eels at sites with boulder substrate. Contrastively, the smallest eel captured in Oakland Lake was captured in a trap site containing boulder substrate. The majority of trap sites were located around the perimeter of the lake possibly creating trap bias toward eels in living in shallow water. It is possible, however, most eels reside around the perimeter in Oakland Lake because eels use substrate (rock, sand, mud), wood debris and submerged vegetation for protection (Hallatt, 2013; Pratt et al., 2014). The majority of trap sites in Oakland Lake were set in water less than 10 m. The two experimental trap sites set 10 m or deeper did not capture eels, which coincides with Pratt et al. (2014) who found yellow eels in freshwater are found at variable depths but the majority are found between 1 – 10 m. Traps in Oakland Lake set in deeper water were covered in mud upon retrieval suggesting there was little habitat structure. This was confirmed with underwater camera surveys taken in the central portion of the lake which showed substrate type as fine sand/silt with no structure (Avery, pers. comm.). This may explain why no eels were captured in traditional eels traps in deeper portions of the lake. As well, acoustically tagged eels were primarily detected in < 5 m suggesting eels did move through the deeper areas of the lake, but were not resident there for long periods. Additionally, it appeared eels did not enter and escape these deep traps because bait remained in them upon retrieval suggesting well developed habitat structure is more important than substrate type.

Many areas in Oakland Lake are shallow and host an abundance of vegetation (Cottreau, 2013), which is linked to fish recruitment because vegetation provides suitable habitat for macroinvertebrates and increasing food sources (Diehl, 1988). Ichthyological surveys in freshwater eelgrass habitat were conducted from June – September in Forillon National Park, Quebec and frequently captured eels (Daniel Sigouin, Parks Canada, pers. comm., 2011). A higher number of eels were captured when eelgrass was absent, but overall eelgrass did not affect trap CPUE in Oakland Lake. A higher absolute number of eels were captured when vegetation was present possibly because the majority of the study period contained vegetation. Contrastively, Hallett (2013) surveyed American eels and found they were always close to the substrate or associated with vegetation. Those surveys were done at night from a light equipped glass-bottom boat, which likely would not influence an eel's feeding behavior. Herein, baited traps may influence catches. Hallett (2013) also found eel abundance did not vary with vegetation density, within the range of vegetation cover, which allowed eels to be seen. In late spring and early summer in Oakland Lake, vegetation was absent, but trap CPUE was actually highest. During this period, temperature started to rise and DO levels were highest. Perhaps vegetation is a more important factor to eels residing in areas where substrate type (gravel) is not conducive to hiding or protection. Because little or no vegetation in Oakland Lake exists for long periods, eels may seek areas based on other advantageous hiding factors including substrate type, wood and debris or simply increased structure.

Little information exists on how American eels use underwater and shoreline slope in relation to their habitat. However, regardless of size, eels have been observed climbing slopes with surface irregularities or vegetation and traversing damp substrates such as moss, grass, rocks and cement outside of the water (MacGregor et al., 2010; COSEWIC, 2012). Despite eels never being observed outside of the water in Oakland

Lake, no difference was found at trap sites on various inclines containing different habitat characteristics.

Original trap sites in Oakland Lake are an arbitrary starting point for home range analysis of eels, but subsequent trap captures are useful indicators of recapture distances, and provide some indication of home range. In rivers and streams, home ranges of American eel are typically <10 km (Oliveira, 1997; 1999; Morrison and Secor, 2003). Recapture data conducted in a similar fashion to this study, found movement between adjacent trap sites in freshwater, but only over relatively short distances (≤ 250 m) (Muise, 2012). Displaced American eels seem to return to their home range with great accuracy over distances of several kilometers (Parker, 1995) to ≤ 80 km (Vladykov, 1971). Green et al. (2009) reported home ranges in freshwater habitats appear larger than those reported in brackish or saltwater. Conversely, Morrison and Secor (2003) found evidence that American eels occupy a home range of less than 1,000 m along a river section. More than 70 % of their PIT tagged American eels moved less than 1 km from the original tagging area in a 2 to 12 month time period. The longest distance travelled was 4.2 km from the tagging site. However, based on otolith microchemistry, Morrison and Secor (2003) did suggest American eels might have dispersed in the estuary over longer time periods. Lamson et al. (2006) also used microchemistry to trace American eel movement in Prince Edward Island. It was determined that 69 % of established continental individuals moved between freshwater and saltwater. Eels in Oakland Lake were often recaptured hundreds of meters away from their original trap site, but because the lake is relatively small (< 1,000 m in any direction), it is possible their home range is the entire lake. Given the short distance between Oakland Lake and the Mahone Bay estuary (~ 2 km), individuals may travel between the lake and estuary via Oakland stream. Acoustically tagged eels last detected near the outgoing stream (receiver 1) may have left Oakland Lake on their spawning migration or to over-winter in the estuary. Eel 1418 was periodically detected near the outgoing stream and may have travelled between the stream and lake periodically. In the fall of 2009, traditional eel traps set in the Mahone Bay estuary captured five eels. It is unknown whether these eels were previously tagged from Oakland Lake, re-entered Oakland Lake, or remained in the estuary. A custom-built trap placed within Oakland Stream during the fall of 2009, 2011 and 2012 captured 221, 283 and 405 eels, respectively, of which all were assumed to be leaving Oakland Lake as spawners. Of these eels two were tagged in 2009, one in 2010, and 13 in 2011 (Crnec, 2012). Eels captured were captured within a narrow period in September shortly after the trap was deployed. Thibault et al. (2007) indicated eel movement between freshwater and brackish habitats might be regular and seasonal in nature as a response to low winter temperatures in estuaries. As well, home range size can be influenced by competition, predator density and food availability (Bozeman et al., 1985). Many eels, regardless of size, may travel across the lake to avoid predators (find better hiding places) or to find food.

The results of this study show eels of all sizes are capable of using a combination of habitat characteristics. Eels tended to use all areas of Oakland Lake regardless of temperature, DO, substrate type, vegetation type and underwater and shoreline slope. Depth appears to be the only habitat characteristic that may have affected how eels use habitat in Oakland Lake. Based on temperature, DO and vegetation type, temporal factors seemed more influential on trap CPUE than the specific habitat characteristics themselves. When trap CPUE was highest for temperature, DO and vegetation type, eels were likely starting to become more active and feed after over-wintering.

In the future, temperature and DO should be taken regularly and consistently throughout the entire study period. Length and mass data should be recorded consistently at each capture during the entire study period. Instances such as missing and stolen traps were unfortunate unforeseeable events that occurred. Mitigating problems such as these are difficult but may be made less likely if signs or trail cameras are used. Ensuring all gear is functional such as batteries charged, working and on hand is important for consistent data collection.

This study contributes to the understanding of habitat use by American eels in freshwater providing information on potential habitat conservation. Because eels appeared to use most areas of Oakland Lake for long periods of time it is important to protect all aspects of freshwater systems.

Table 1. Number of traditional eel trap sites within each year (2009 – 2012) showing duplicated traps from previous years, new traditional eel trap sites that same year and total eels captured during the target year in Oakland Lake, Mahone Bay, Nova Scotia. Trap CPUE was the number of eels captured divided by the number of trap checks per individual trap.

Year	**Trapping Events (Days)**	**Number of Trap Sites**	**Trap sites from previous years**	**New Trap Sites**	**Total Eels Captured**	**Mean eels per trap site**	**Trap CPUE**
2009	15	29	0	29	91	3.1	0.38
2010	35	29	29	0	240	8.2	0.47
2011	48	44	29	15	372	8.5	0.31
2012	38	35	12	23	167	4.8	0.15

Table 2. Total eels captured each year in traditional eel traps based on days fished with new tag implants from 2009 to 2012. Number of eels recaptured and unique eels captured (tagged eels captured once) based on new tag implants within each year from 2009 – 2012. Number of eels recaptured and unique eels captured based on cumulative tags from 2009 – 2012. Eels captured without tag data in 2011 and 2012 were a result of not having any PIT tags or failure of the PIT tag reader. It is possible that eels captured when the PIT tag reader was malfunctioning that those eels may have had a tag.

Year	**Date Range**	**Total eels captured**	**Eels captured without tag data**	**New tags Applied**	**Eels recaptured**	**Unique eels recaptured**	**Cumulative tags**	**Eels recaptured (cumulative years)**	**Unique eels captured (cumulative years)**
2009	28 Jul – 21 Aug	91	0	66	25	20	66	25	20
2010	31 May – 24 Aug	240	0	110	108	57	176	130	64
2011	06 Jun – 29 Sep	372	71	127	137	66	303	174	81
2012	15 Jun – 06 Sep	167	23	65	29	24	368	51	39

Table 3. Mean ± SD (range) total length (TL) and mass of unique eels captured in traditional eel traps from 2009 – 2012 and minnow traps in 2012 in Oakland Lake, Mahone Bay, Nova Scotia. Same letter indicate no significant difference between TL or mass across years.

Trap Type	**Year**	**n**	**TL (cm)**		**Mass (g)**	
Eel						
	2009	66	54.9 ±10.3	a	354 ± 202	a
	2010	110	53.3 ± 9.90	a	329 ± 221	a
	2011	127	44.6 ± 9.80	b	188 ± 163	b
	2012	65	40.7 ± 8.70	c	148 ± 124	c
	Overall		48.4 ± 11.0 (15.0 – 82.0)		250 ± 200 (40.0 – 1,373)	
Minnow						
	2012	17	38.5 ± 5.00 (28.0 – 48.0)		107 ± 53.0 (40.0 – 220)	

Table 4. Yearly significance (p-value) of total length and mass of unique eels captured in traditional eel traps and minnow traps in Oakland Lake, Mahone Bay, Nova Scotia.

	Year	2010	2011	2012
Length (cm)	2009	0.300	<0.001	<0.001
	2010		<0.001	<0.001
	2011			0.009
Mass (g)	2009	0.321	<0.001	<0.001
	2010		<0.001	<0.001
	2011			0.314

Table 5. Mean ± SD of surface and bottom temperatures (°C) from June – September in 2011 in Oakland Lake, Mahone Bay, Nova Scotia.

Month	**Surface**	**Bottom**
June	21.5 ± 3.2	21.0 ± 2.8
July	22.4 ± 3.0	21.8 ± 2.7
August	21.9 ± 2.6	21.7 ± 2.6
September	22.3 ± 2.6	22.1 ± 2.7

Table 6. Mean ± SD of surface and bottom DO levels (ppm) from June – September in 2011 in Oakland Lake, Mahone Bay, Nova Scotia.

Month	**Surface DO (ppm)**	**Bottom DO** (°C)
June	9.2 ± 1.5	9.5 ± 1.5
July	9.1 ± 1.6	9.5 ± 1.6
August	9.2 ± 0.8	9.4 ± 1.0
September	9.2 ± 0.8	9.3 ± 1.0

Table 7. Mean ± SD of monthly pH levels from May – July 2011 in Oakland Lake, Mahone Bay, Nova Scotia.

Month	**pH**
May	8.3 ± 0.4
June	8.3 ± 0.5
July	7.8 ± 0.2

Table 8. The number of occasions each vegetation type (algae, lily pads, eelgrass, pickeralweed and smartweed) was present and the number of trap sites each vegetation type was found at in 2011 in Oakland Lake, Mahone Bay, Nova Scotia.

Vegetation Type	**Number of Occasions Present**	**Number of Trap Sites**
Algae	72	63
Lily pads	36	34
Eelgrass	16	15
Pickeralweed	10	10
Smartweed	9	9

Table 9. The number of detections from acoustically tagged eels in 2012 in Oakland Lake, Mahone Bay, Nova Scotia.

	Acoustic Eel ID	**Number of Detections**
	1421	127222
	1420	820704
	1419	127613
	1418	112670
	1409	1396541
	1408	744508
	1273	525336
	1267	1002071
Total		4856665

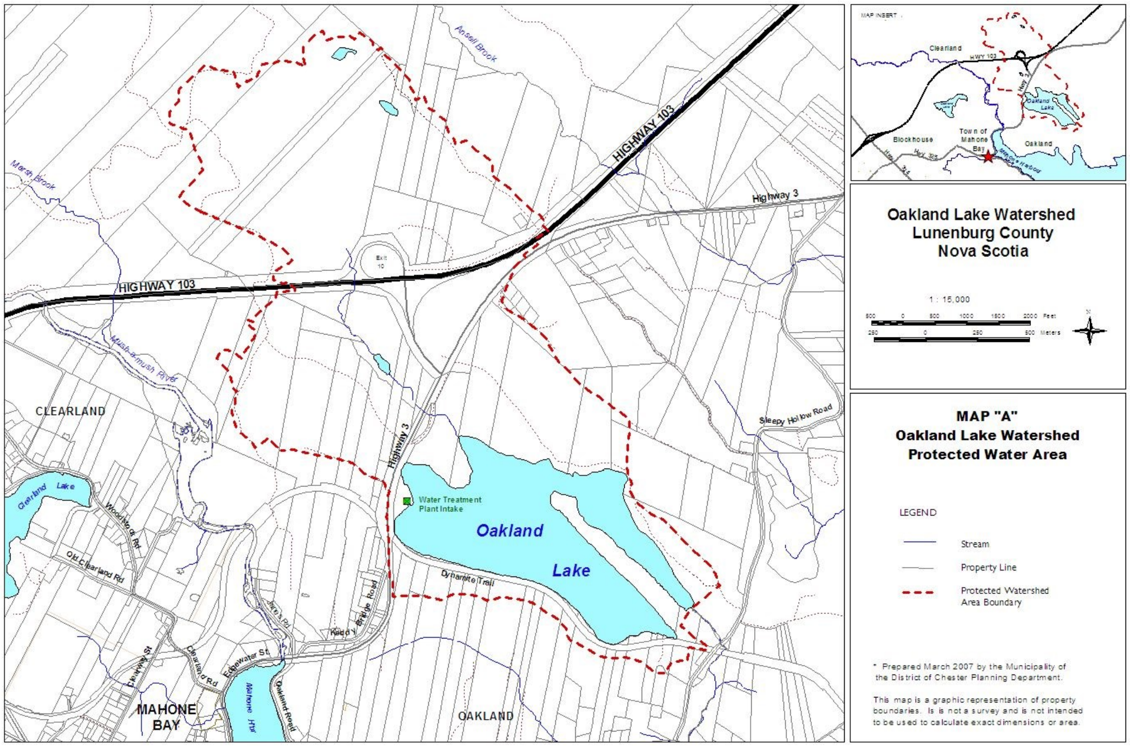

Figure 4. Oakland Lake, Mahone Bay, Nova Scotia located at approximately 44°27'42"N 64°21'51"W. Blue lines are streams. Oakland Stream drains from the south-eastern part of Oakland Lake. Solid black lines indicate property lines. Dashed red line indicates protected watershed areas boundary.

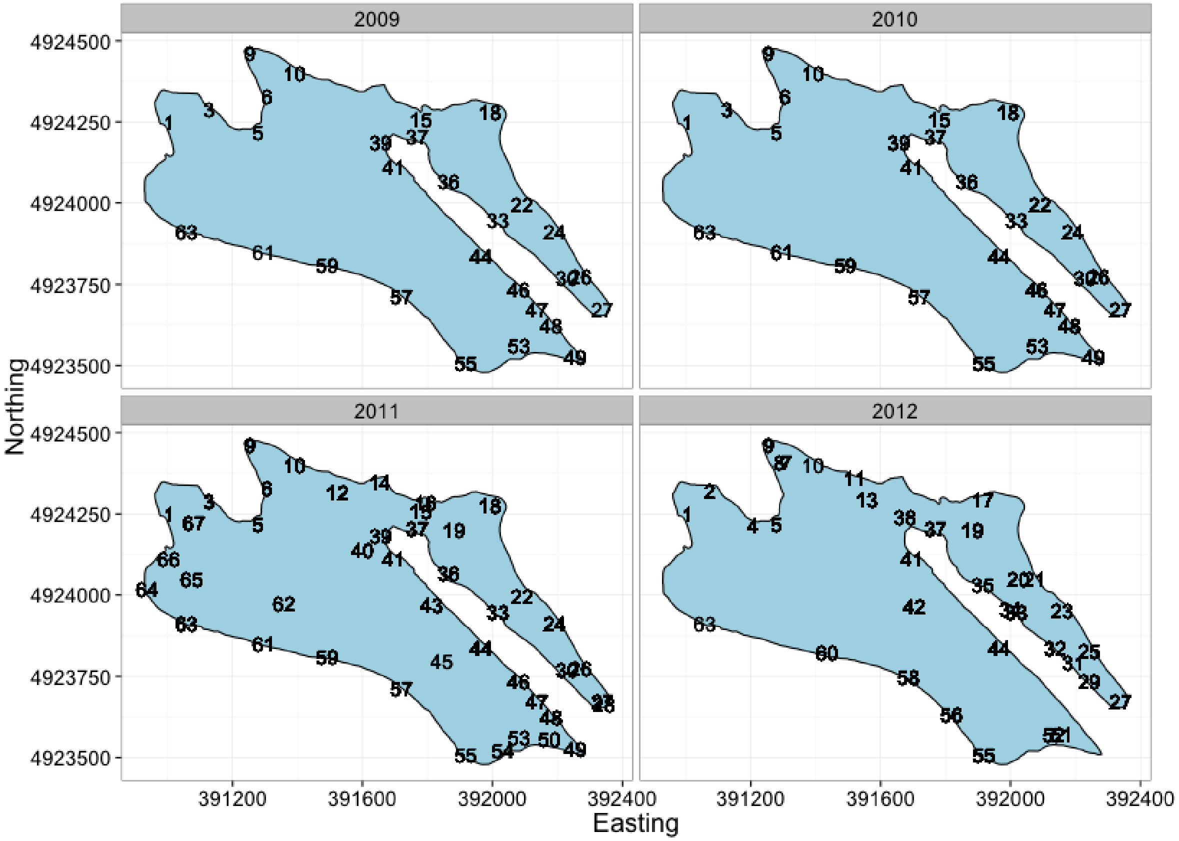

Figure 5. Standardized traditional eel trap sites across all four years (2009 - 2012) in Oakland Lake, Mahone Bay, Nova Scotia.

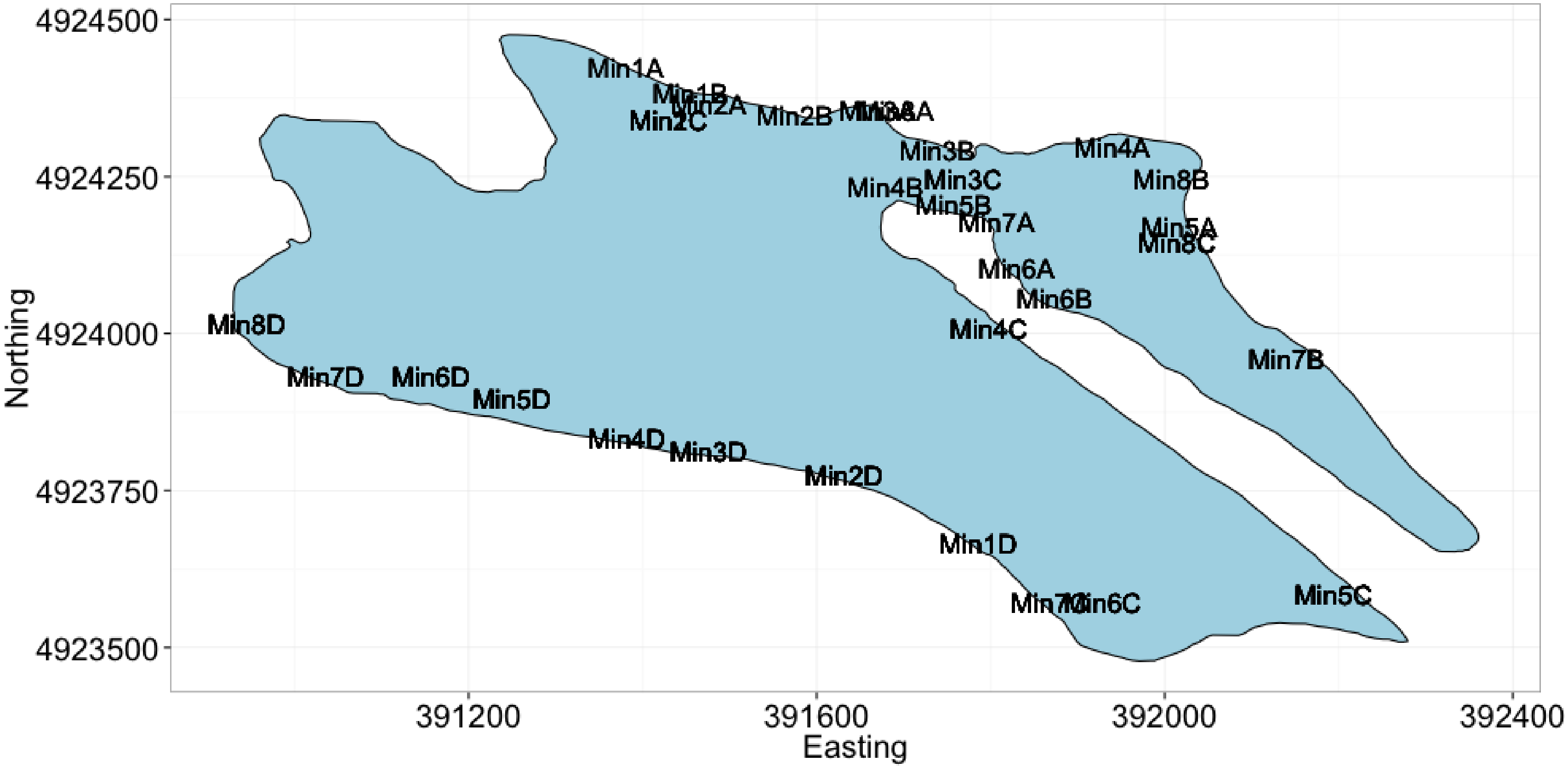

Figure 6. The four trap sites of eight minnow traps set in 2012 in Oakland Lake, Mahone Bay, Nova Scotia.

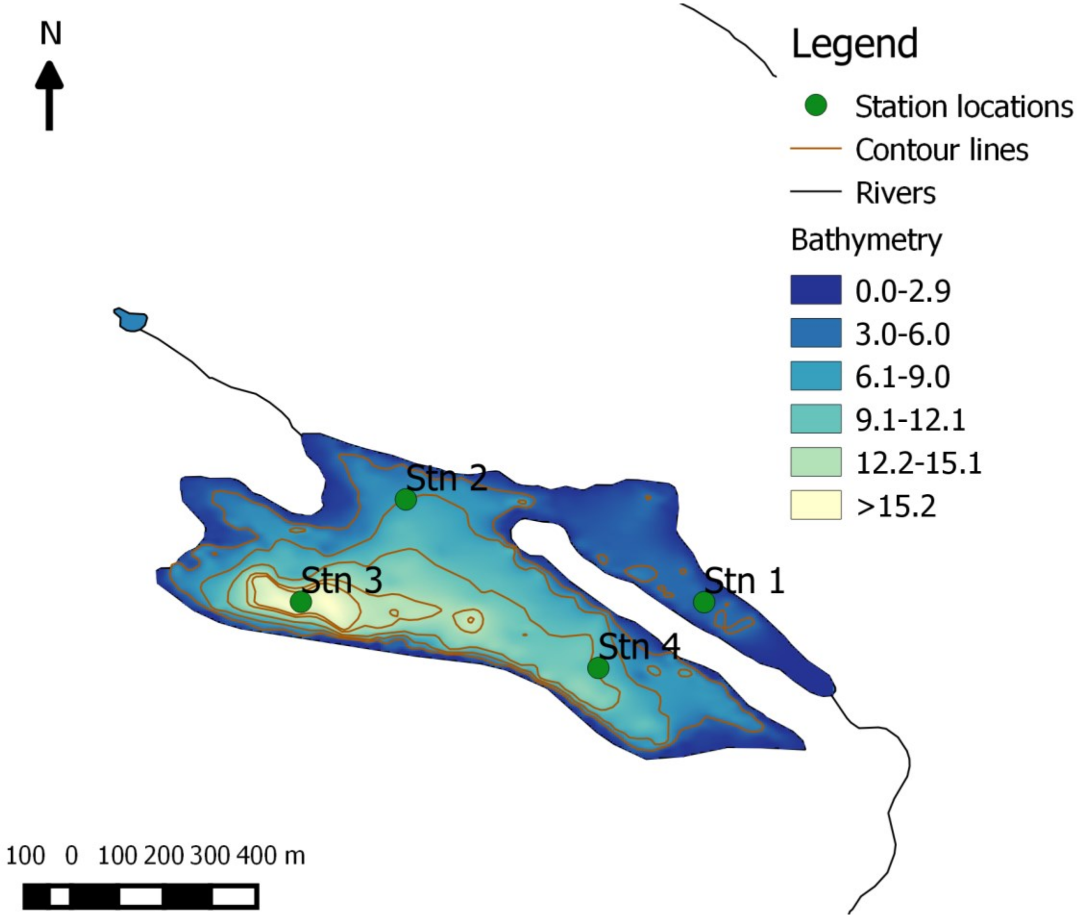

Figure 7. Bathymetry and location of four hydroacoustic receivers deployed in 2012 in Oakland Lake, Mahone Bay, Nova Scotia. Depths are in m. Oakland Stream drains from the south east of Oakland Lake.

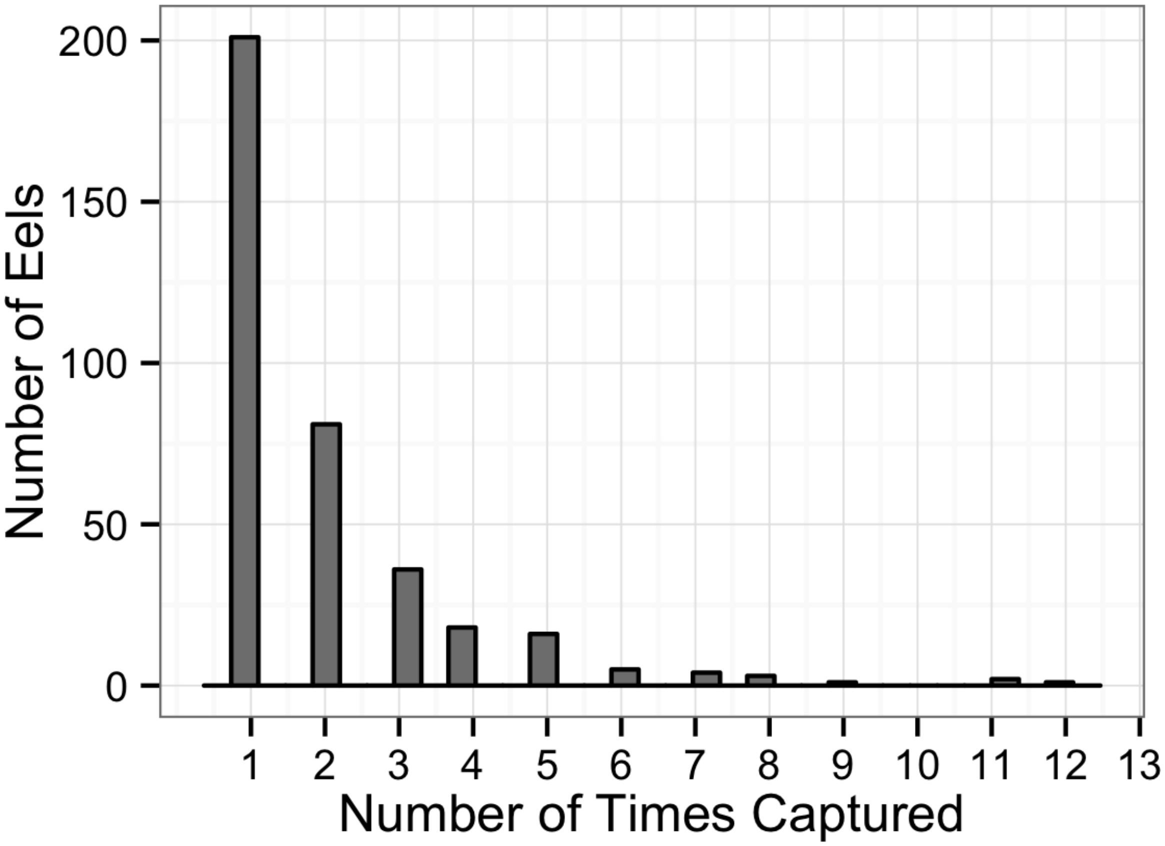

Figure 8**.** Number of American eels captured in traditional eel traps across all four years (2009 – 2012) in Oakland Lake, Mahone Bay, Nova Scotia.

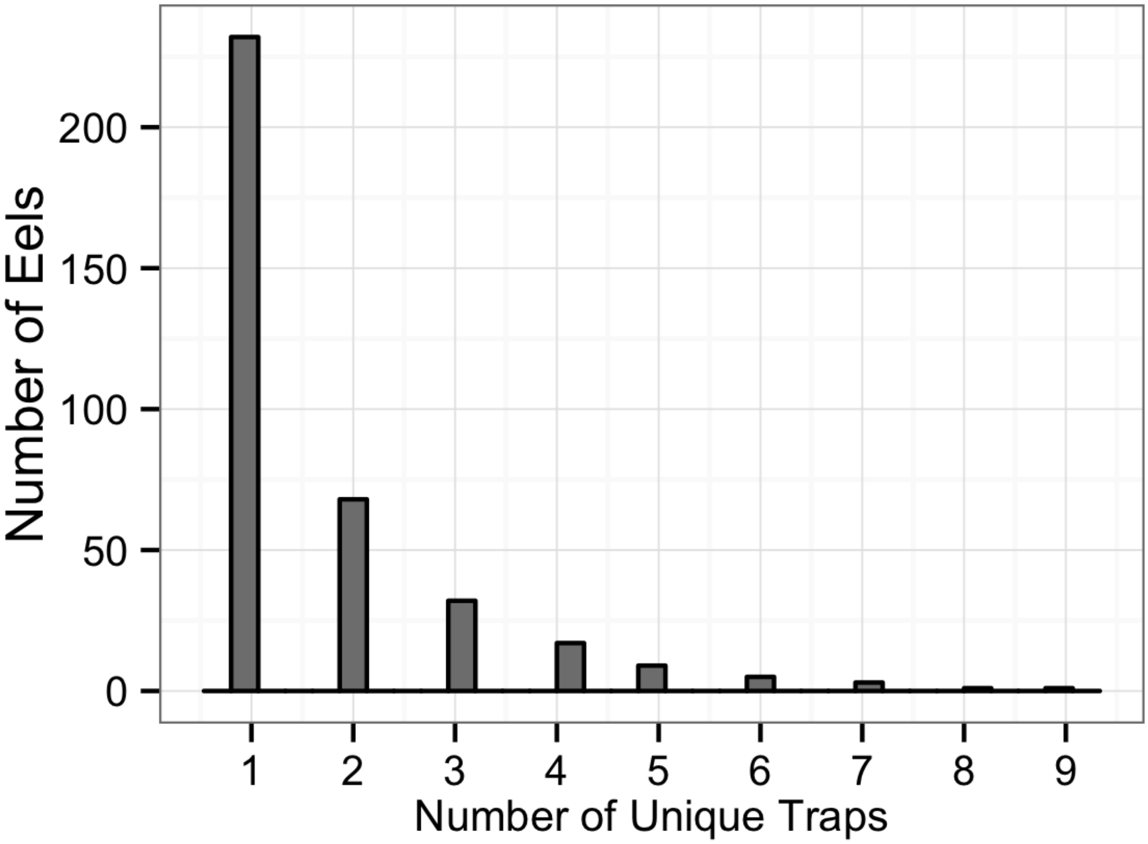

Figure 9. Frequency of unique traditional eel trap captures across all four years (2009 – 2012) in Oakland Lake, Mahone, Nova Scotia.

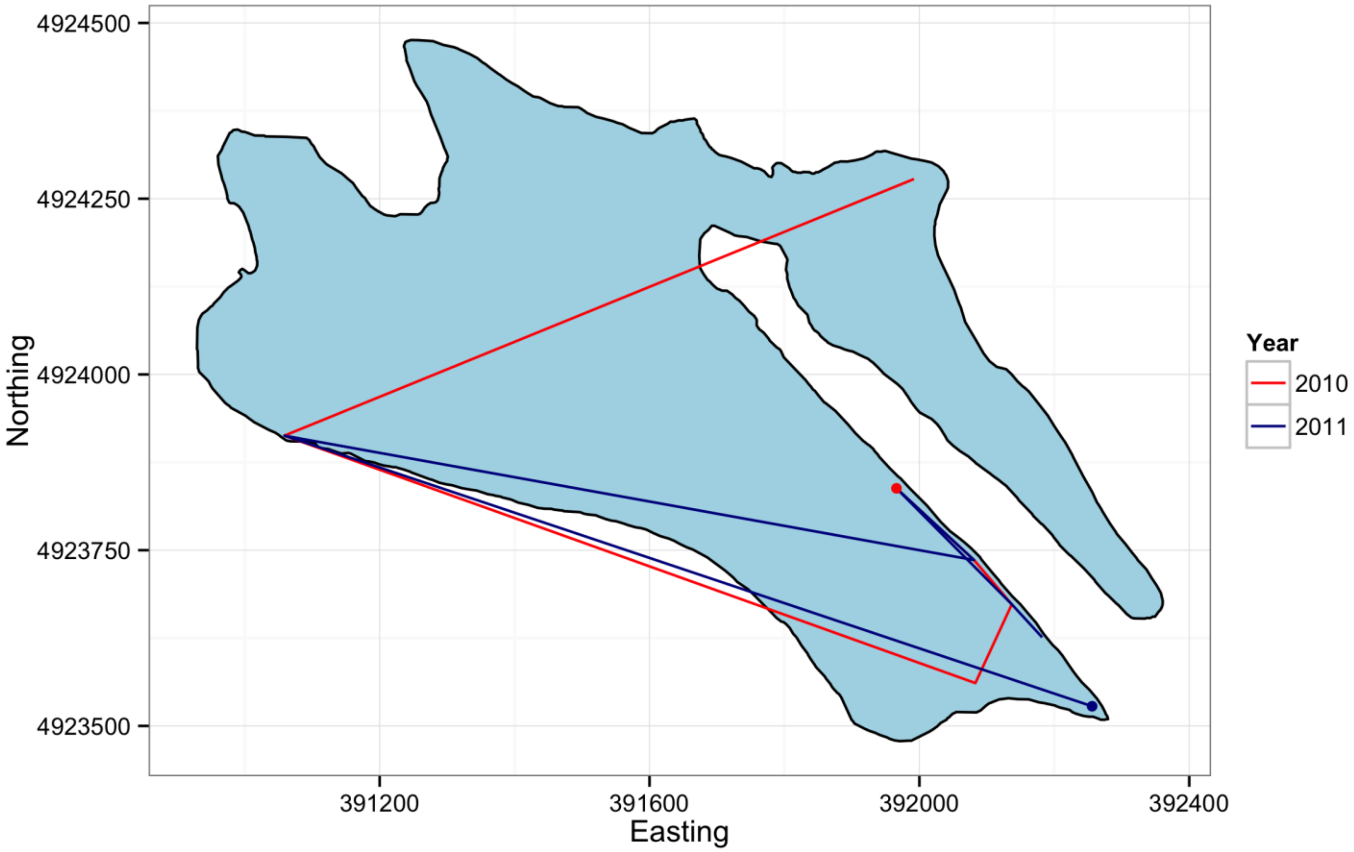

Figure 10. Eel, 985 121 020 147 195, captured a total of 12 times in eight unique traps in traditional eel traps from 2010 – 2011 and its movement around Oakland Lake, Mahone Bay, Nova Scotia.

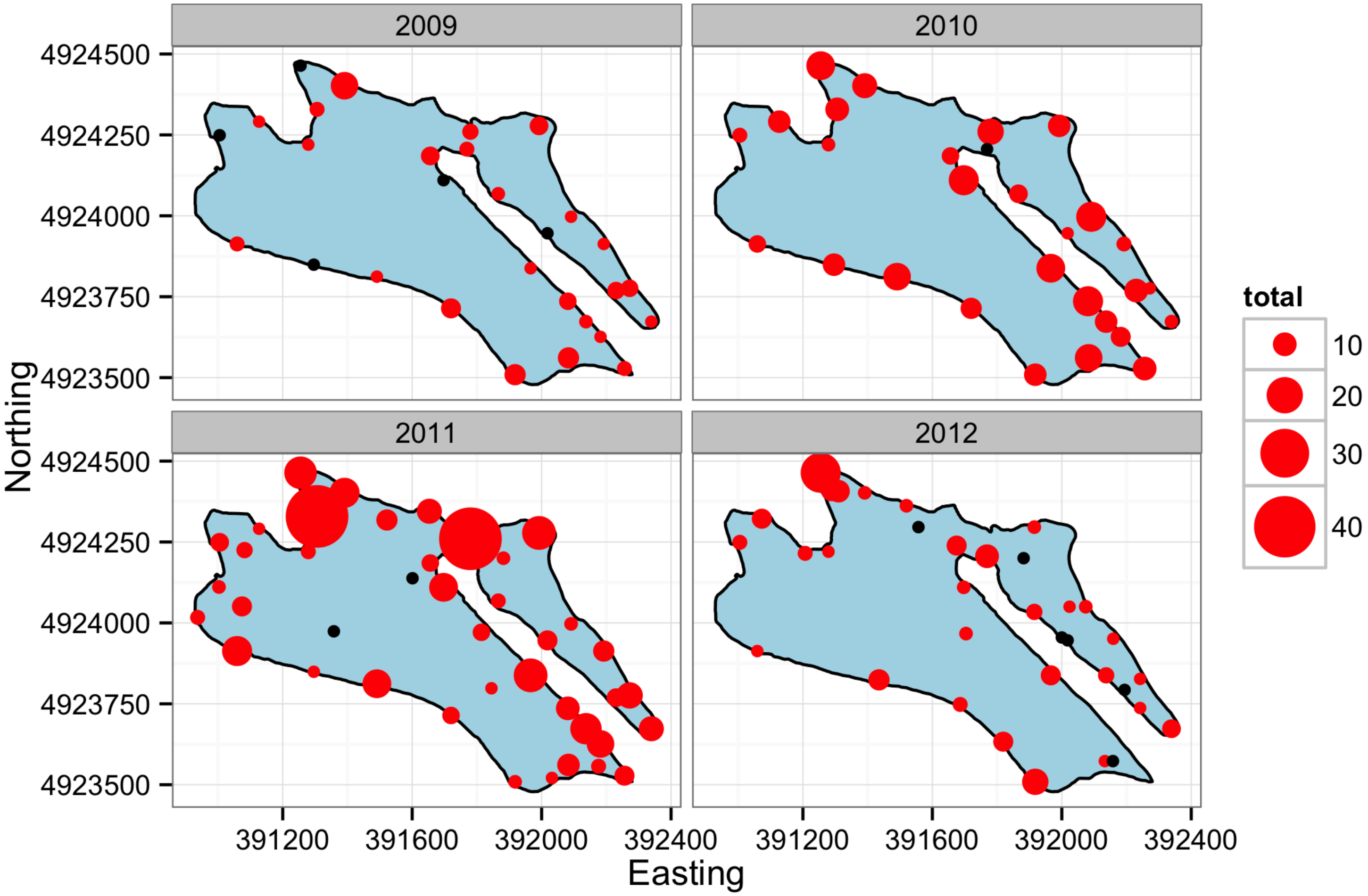

Figure 11. Total number of American eels captured per eel trap across all four years (2009 – 2012) including recaptures, using traditional style eel traps Oakland Lake, Mahone Bay, Nova Scotia. Bubbles were standardized across years. Black bubbles indicate a trap site where no eels were captured.

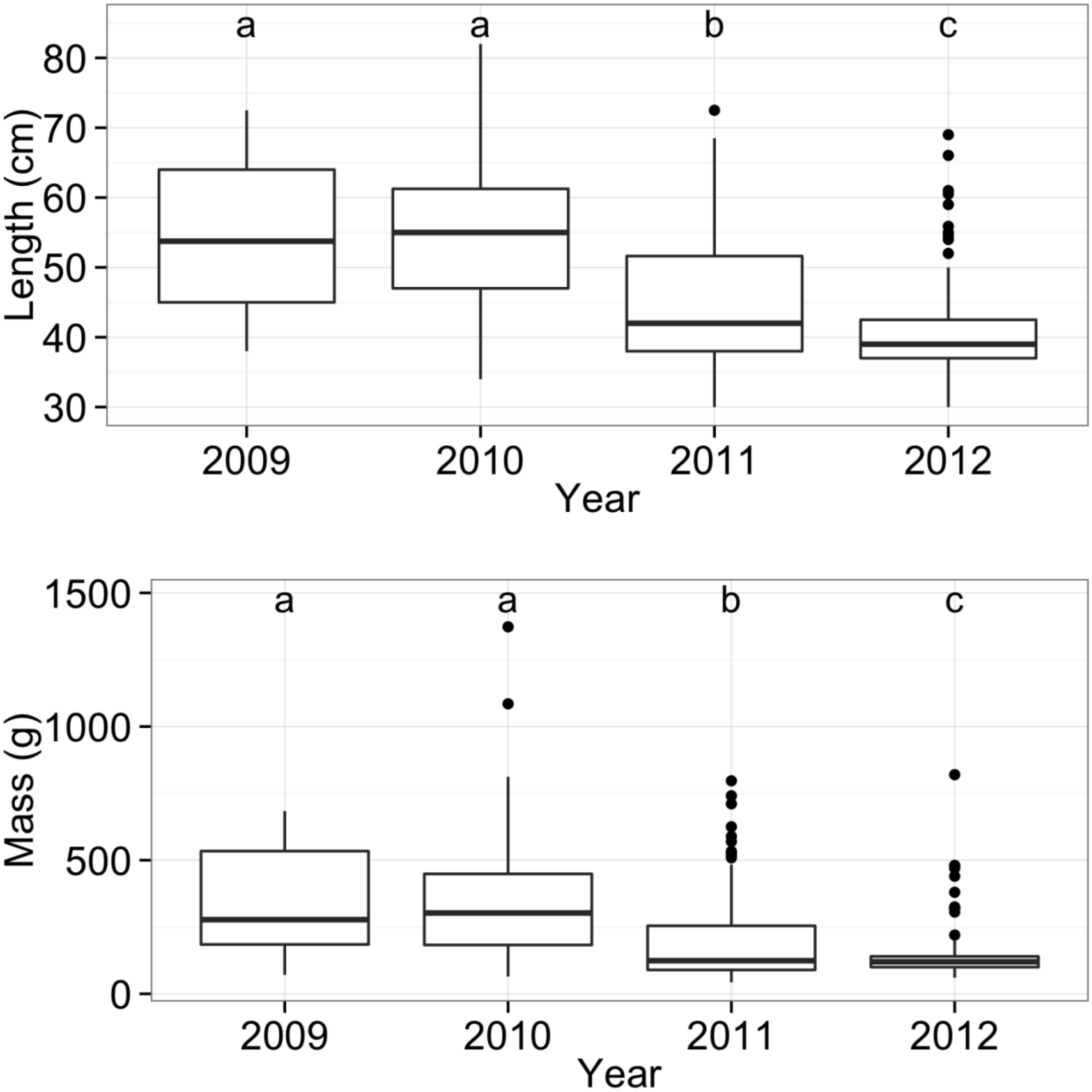

Figure 12. Unique (non-repeated eel captures) total length (cm) (top) and mass (g) (bottom) of American eels captured in traditional eel traps in Oakland Lake, Mahone Bay, Nova Scotia. Same letters indicate no significant difference between length or mass at alpha = 0.05.

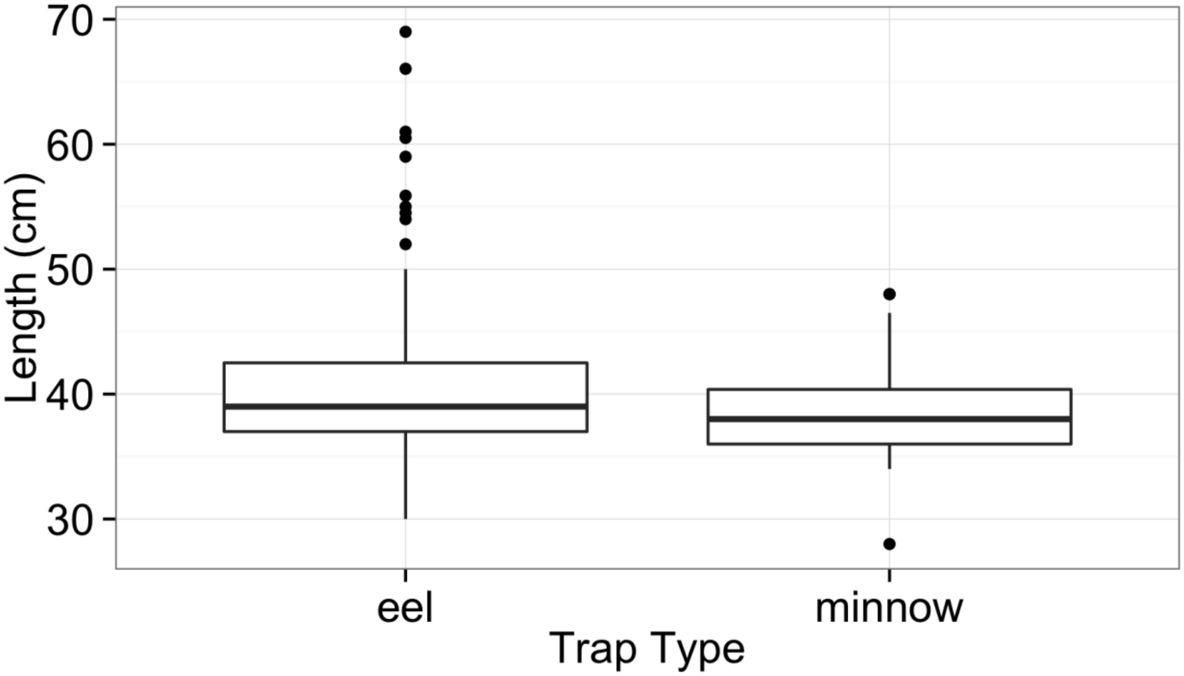

Figure 13. Unique total length (cm) of American eels captured in traditional eel traps (mean 40.76 ± 7.35 cm; n=65) and minnow traps (39.08 ± 5.24 cm; n=16) in Oakland Lake, Mahone Bay, Nova Scotia in 2012. No significant difference was found between eel length and trap type (p = 0.300).

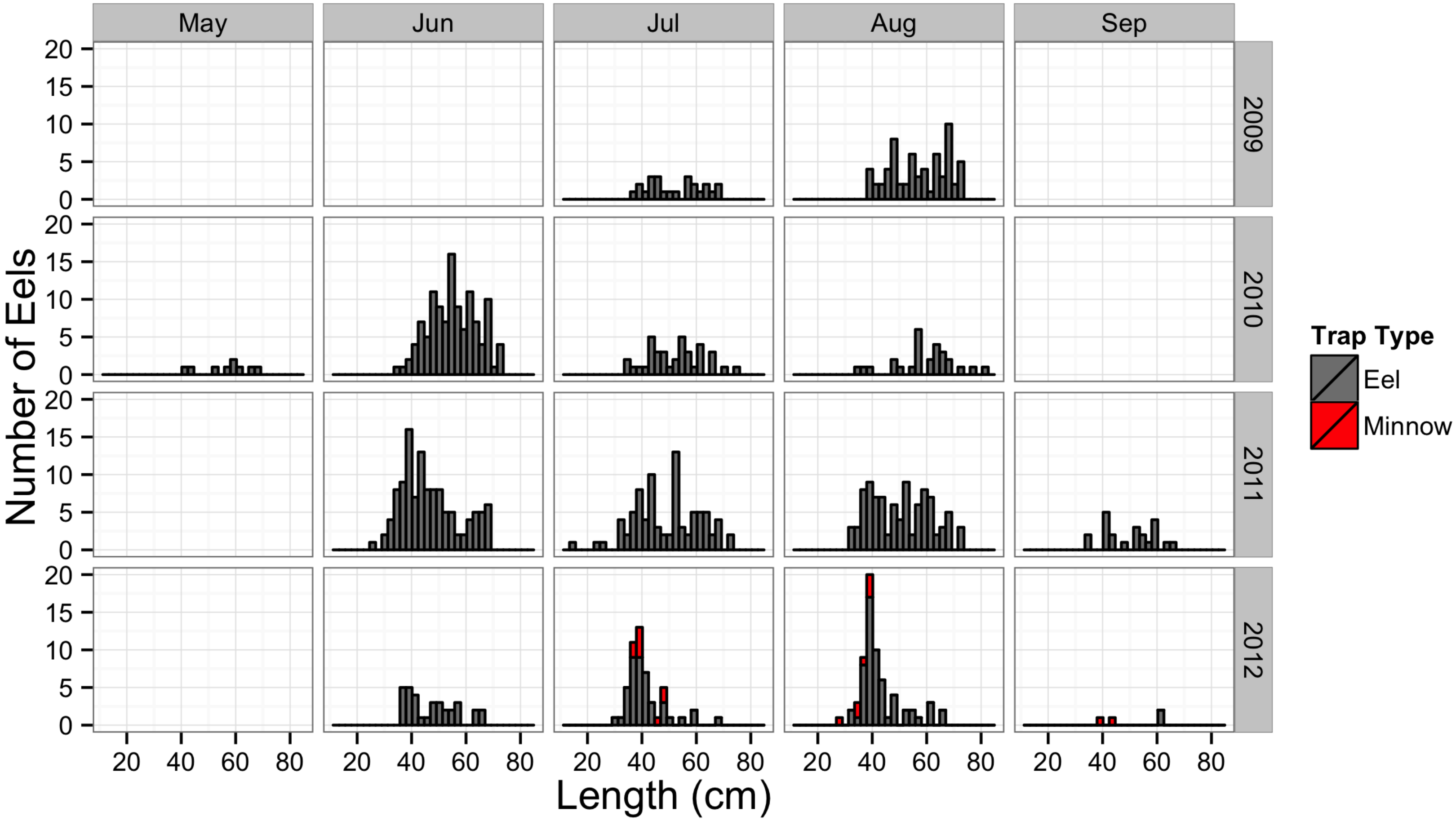

Figure 14. The number of American eels captured by length (cm) and trap type across all four years (2009 – 2012) in Oakland Lake, Mahone Bay, Nova Scotia.

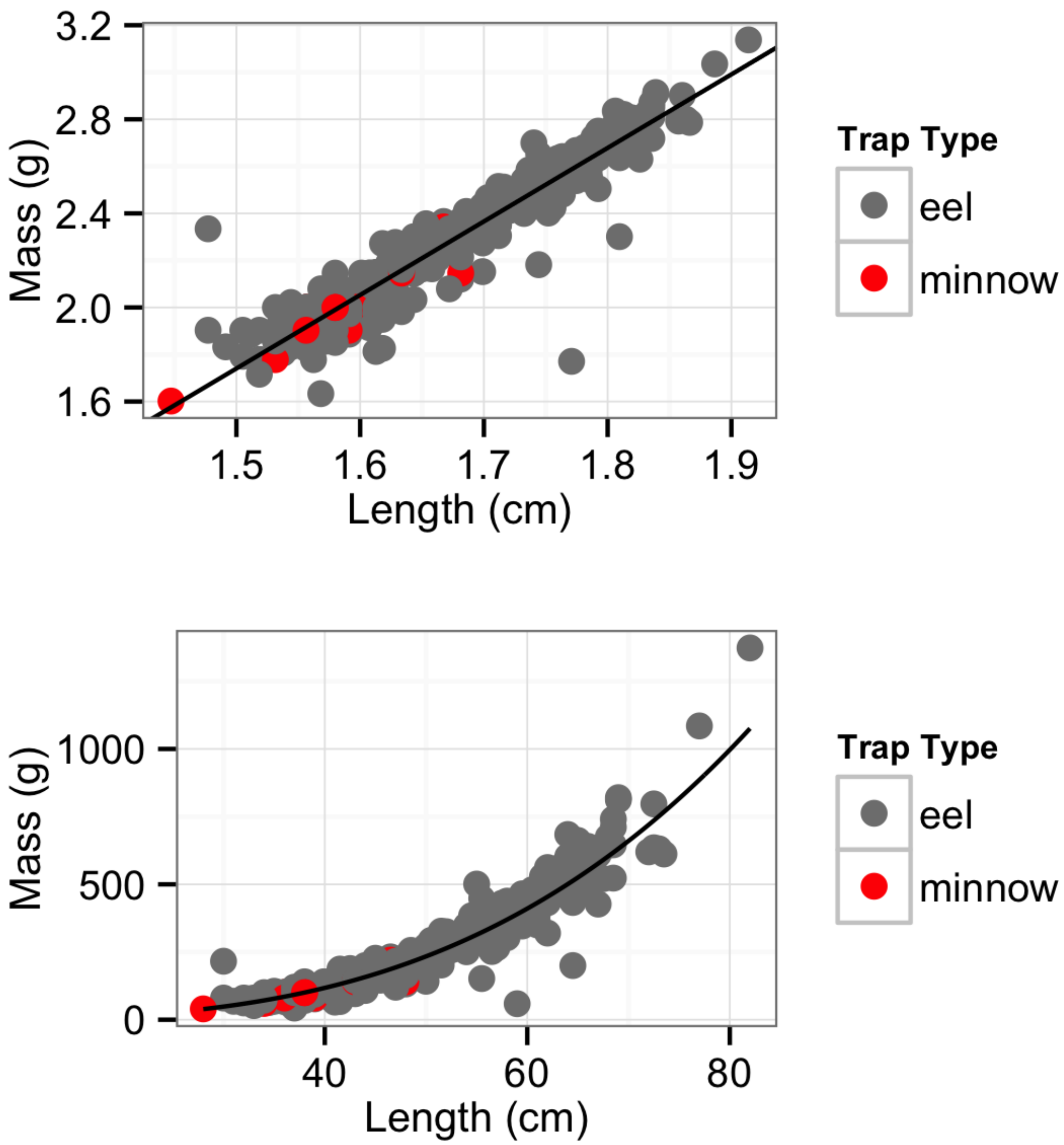

Figure 15. Log_{10}-log_{10} transformed (R^2 adj= 0.918; $p < 0.001$) (top) and untransformed (R^2 adj = 0.928; $p < 0.001$) (bottom) mass-total length relationship of unique American eels captured in traditional eel traps (2009 – 2012) and minnow traps (2012) in Oakland Lake, Mahone Bay, Nova Scotia ($y=3.127x – 2.950$).

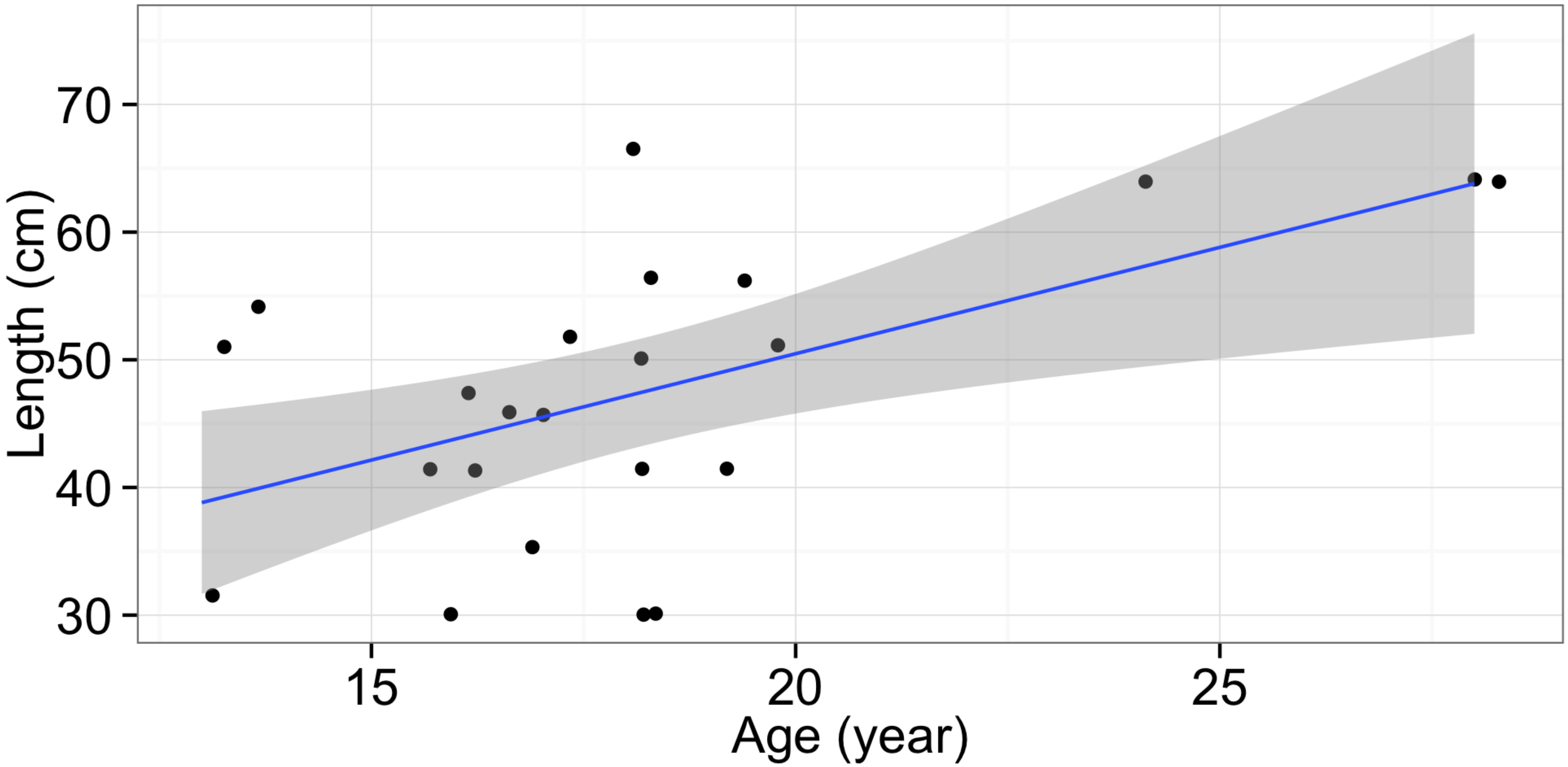

Figure 16. American eel total length (cm) by age (years) of eels (N = 23) extracted in 2011 from traditional eel traps from Oakland Lake, Mahone Bay, Nova Scotia. (R^2 adj = 0.281; p = 0.005; y = 9.234x + 0.188). Blue line is regression line and grey area is confidence region.

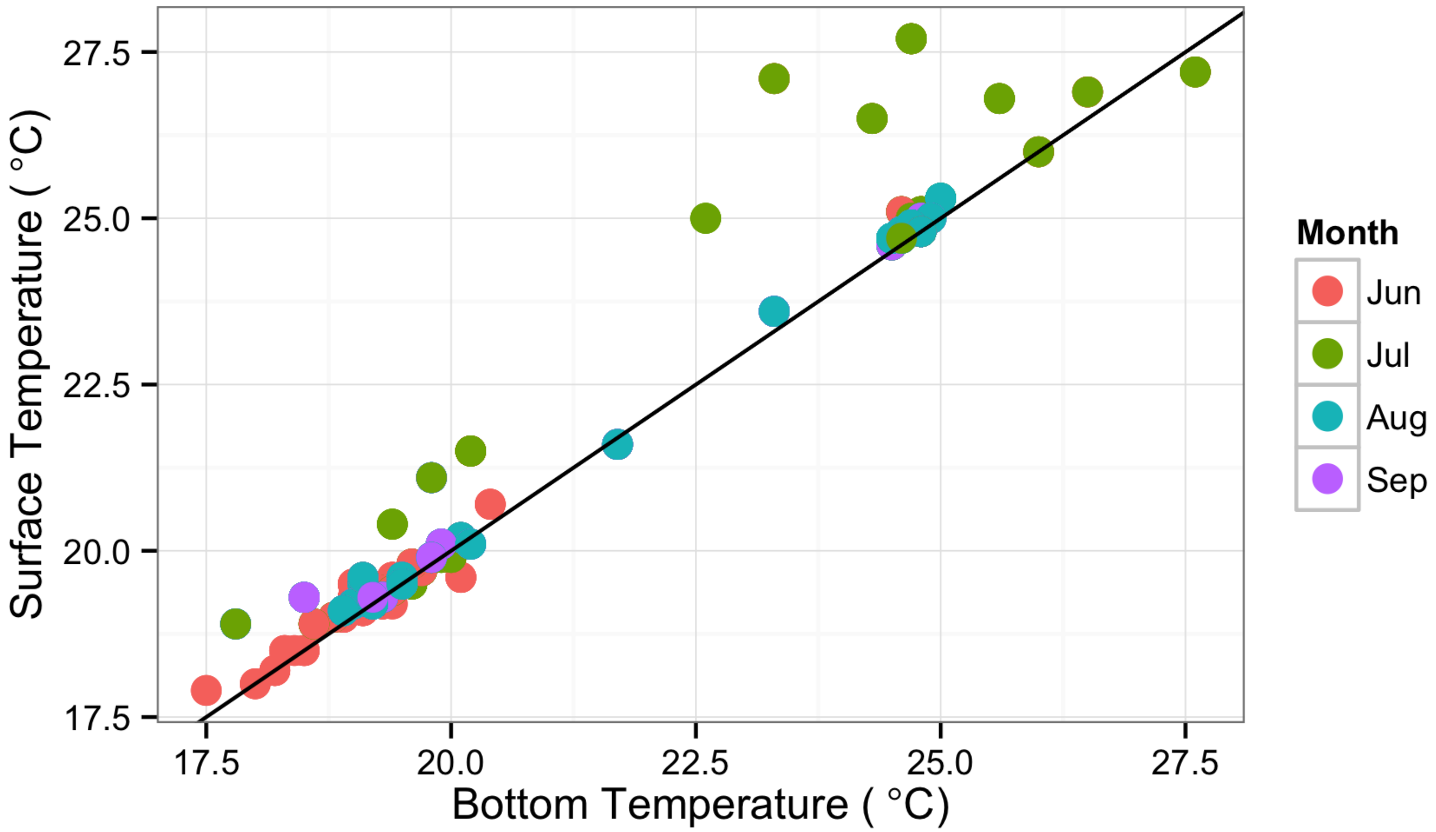

Figure 17. Surface and bottom temperatures (°C) by month (June – September) in 2011 in Oakland Lake, Mahone Bay, Nova Scotia. Black line is the 1:1 relationship of temperature. Points along the line indicate homogeneous temperature.

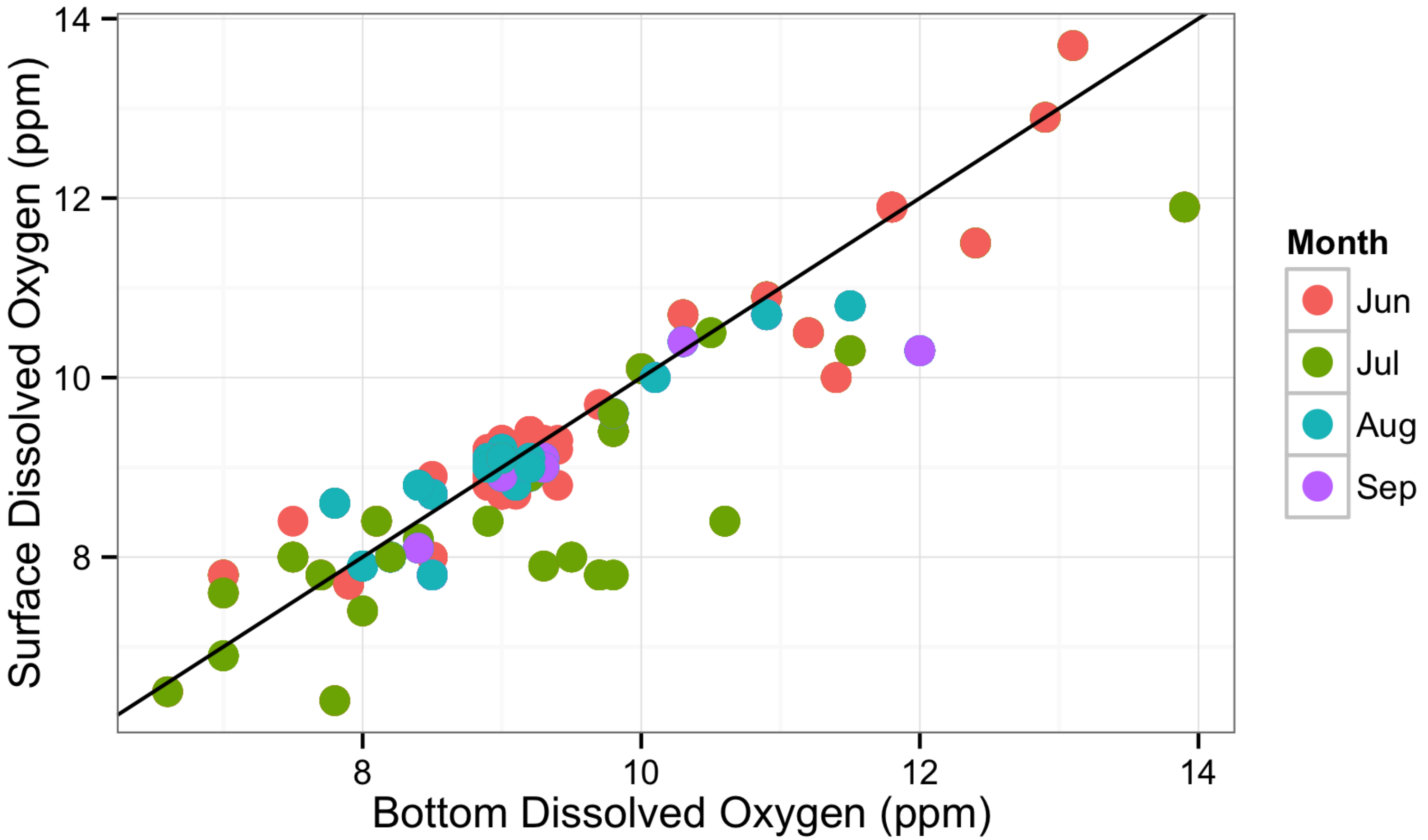

Figure 18. Surface and bottom DO (ppm) by month (June – September) in 2011 in Oakland Lake, Mahone Bay, Nova Scotia.

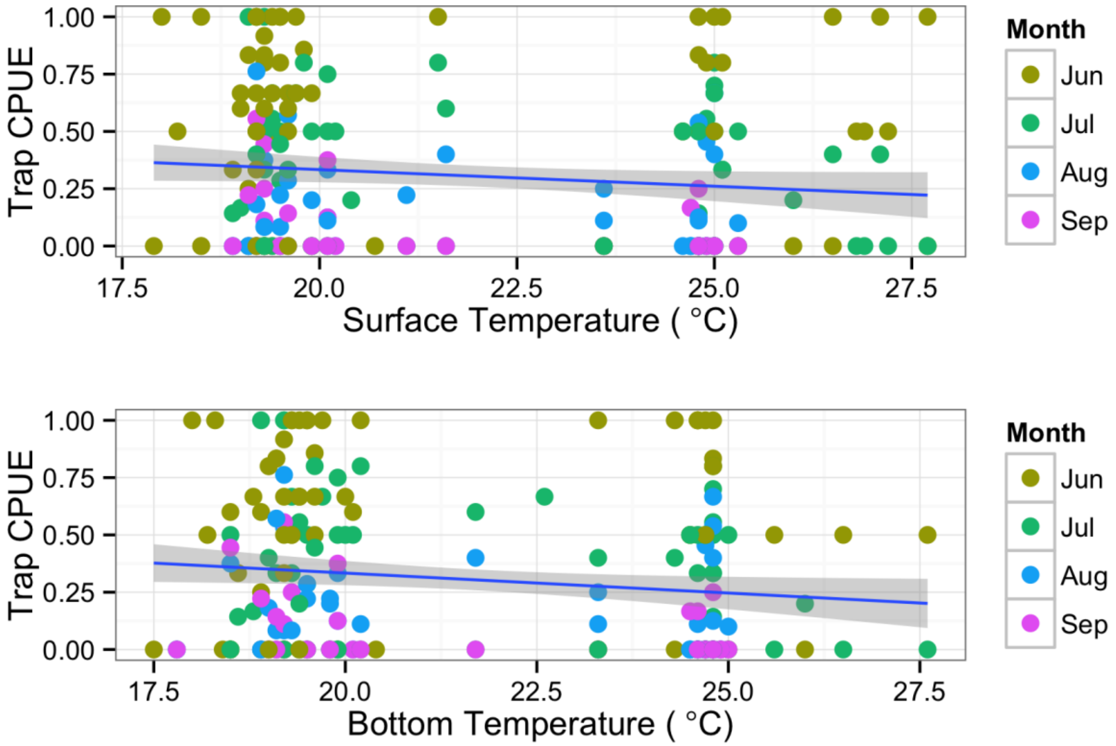

Figure 19. Trap CPUE of American eel by surface temperature (°C) (R^2 adj= 0.01051; p = <0.001; y = -0.021227x + 0.735615) and bottom temperature (°C) (R^2 adj= 0.0153; p = <0.001; y = -0.021400x + 0.731766) in traditional eel traps and minnow traps in Oakland Lake, Mahone Bay, Nova Scotia. Each dot represents a trap.

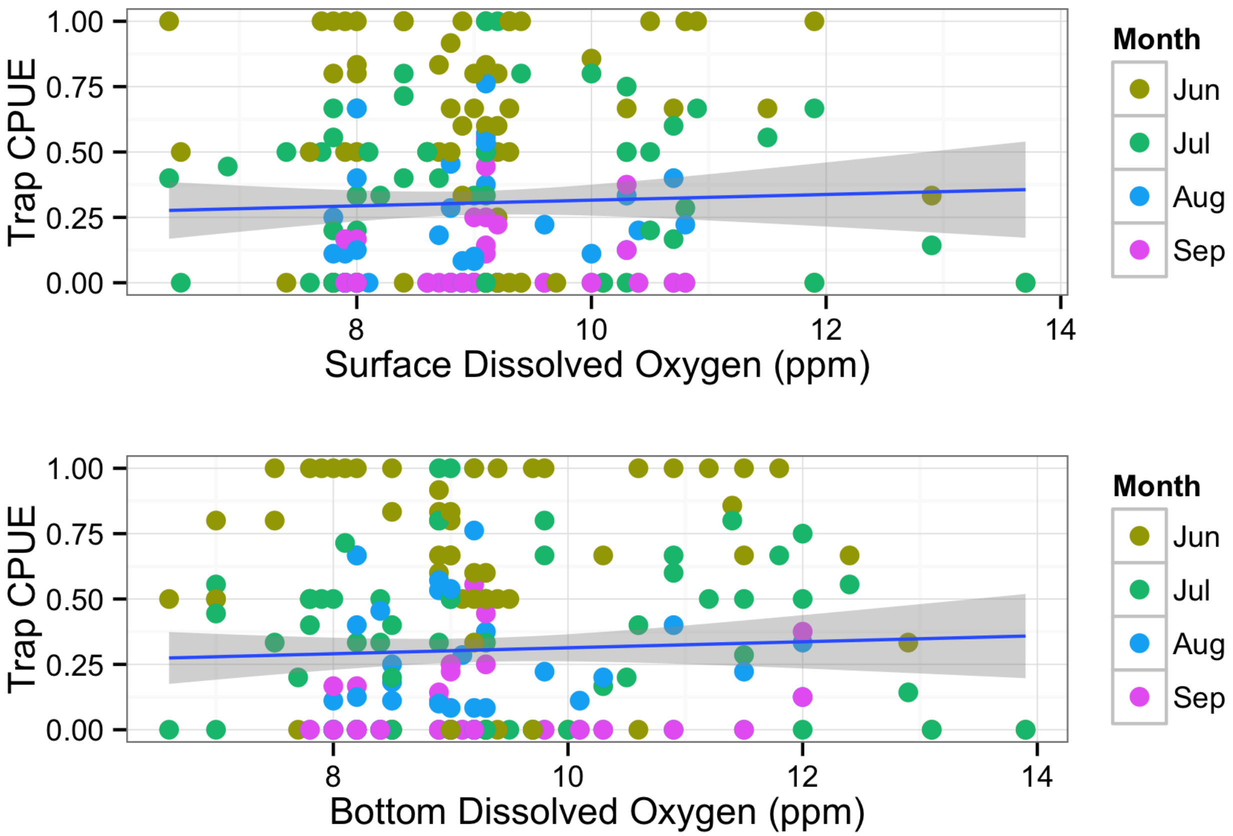

Figure 20. Trap CPUE of American eel by surface DO (ppm) (R^2 adj= 0.0001214; p = 0.308; y = 0.01325 + 0.14935) and bottom DO (ppm) (R^2 adj= 0.002988; p = 0.964; y = -0.0005597x + 0.2746379) in traditional eel traps and minnow traps in Oakland Lake, Mahone Bay, Nova Scotia. Each dot represents a trap.

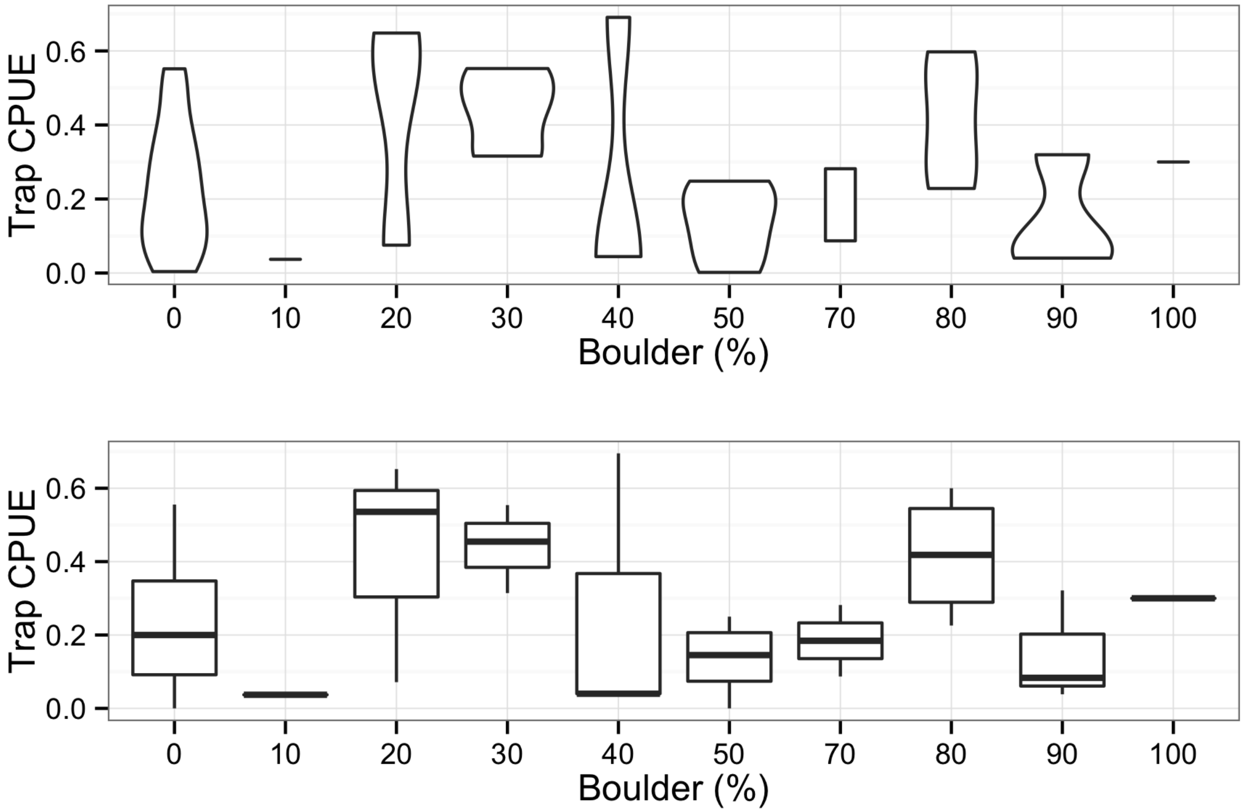

Figure 21. Trap CPUE of American eel by boulder substrate (%) in traditional eel traps in Oakland Lake, Mahone Bay, Nova Scotia. No significant differences were found between trap CPUE and percent boulder substrate. Violin plots (top) show the density of points where boxplots (bottom) show statistics.

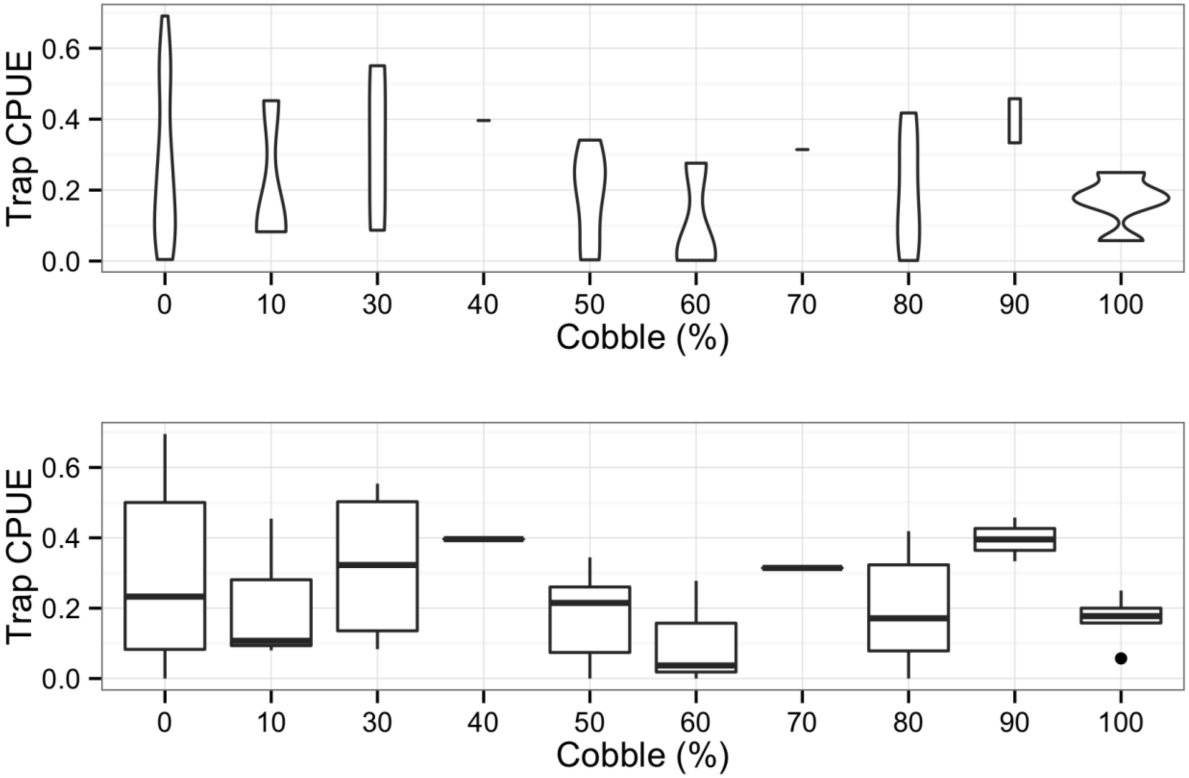

Figure 22. Trap CPUE of American eel by cobble substrate (%) in traditional eel traps in Oakland Lake, Mahone Bay, Nova Scotia. No significant differences were found between trap CPUE and percent cobble substrate. Violin plots (top) show the density of points where boxplots (bottom) show statistics.

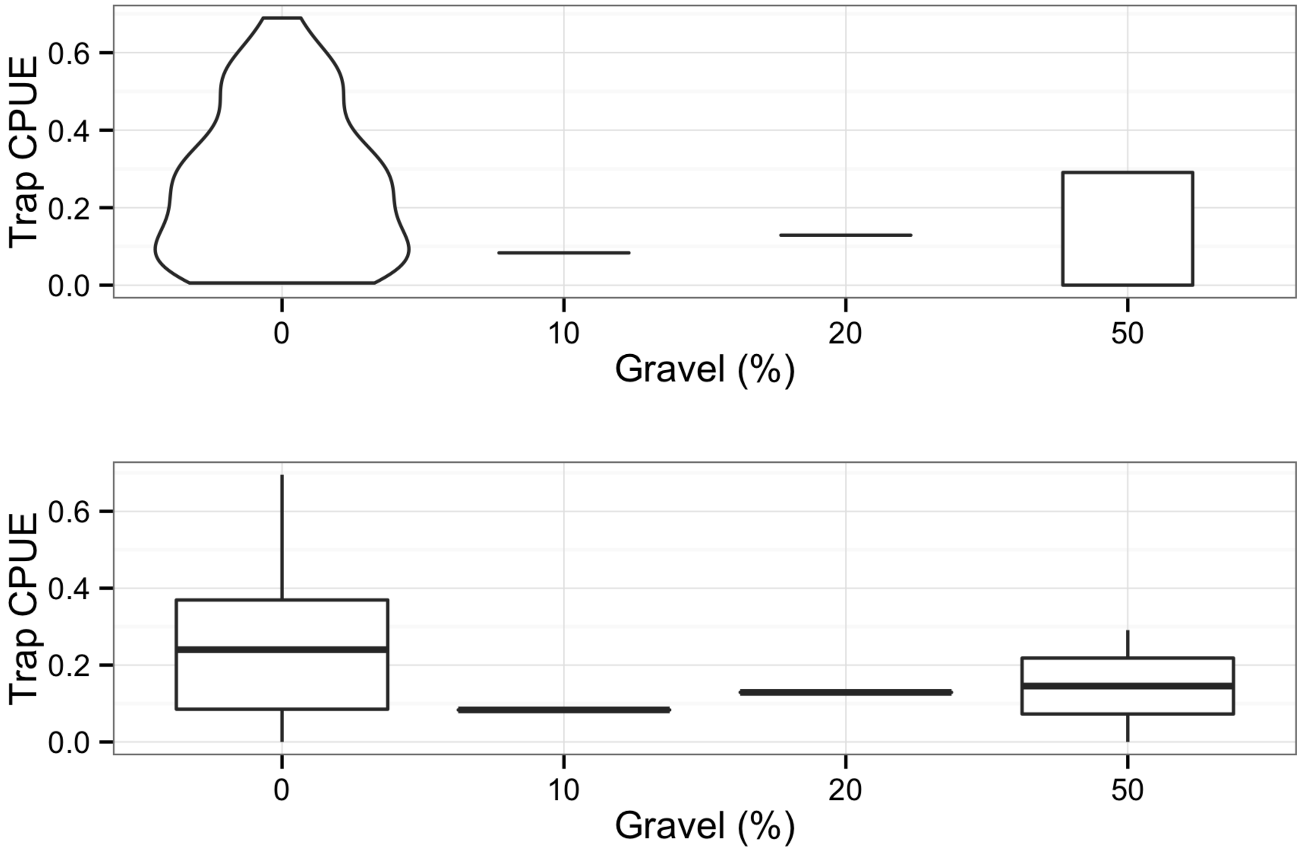

Figure 23. Trap CPUE of American eel by gravel substrate (%) in traditional eel traps in Oakland Lake, Mahone Bay, Nova Scotia. No significant differences were found between trap CPUE and percent gravel substrate. Violin plots (top) show the density of points where boxplots (bottom) show statistics.

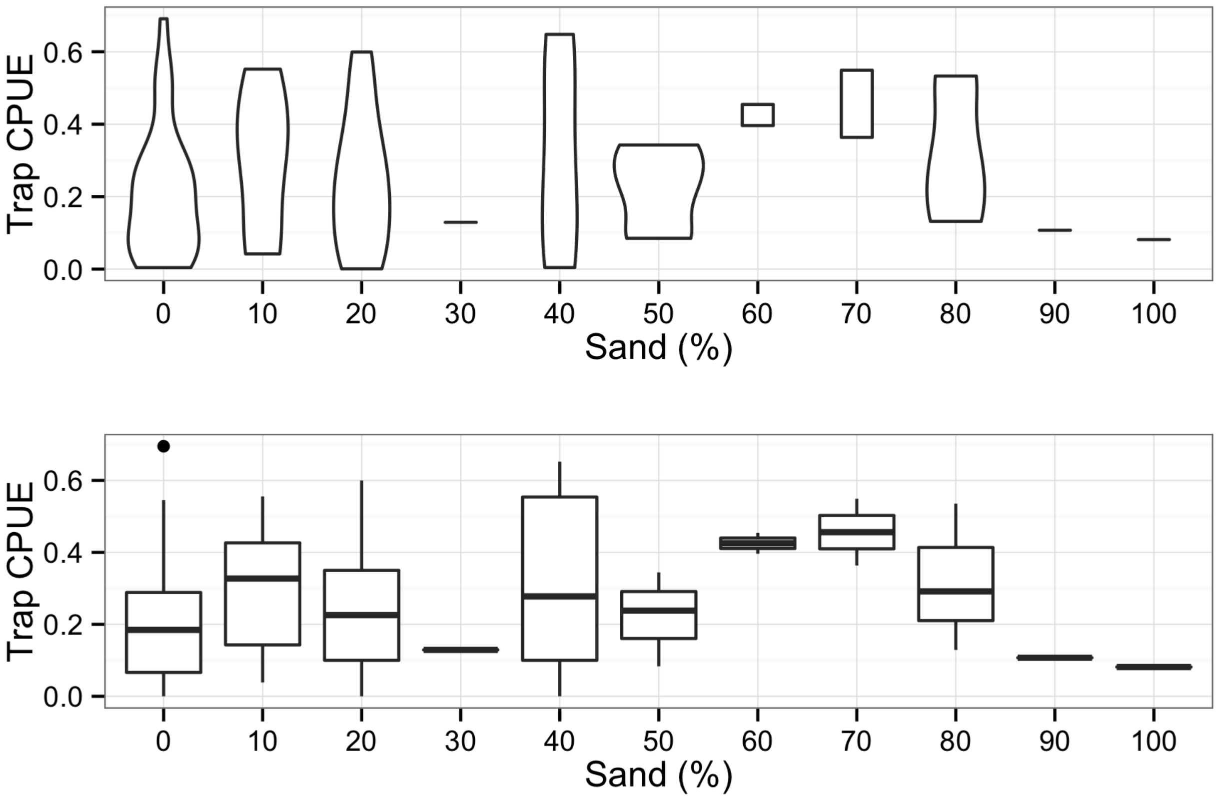

Figure 24. Trap CPUE of American eel by sand substrate (%) in traditional eel traps in Oakland Lake, Mahone Bay, Nova Scotia. No significant differences were found between trap CPUE and percent sand substrate. Violin plots (top) show the density of points where boxplots (bottom) show statistics.

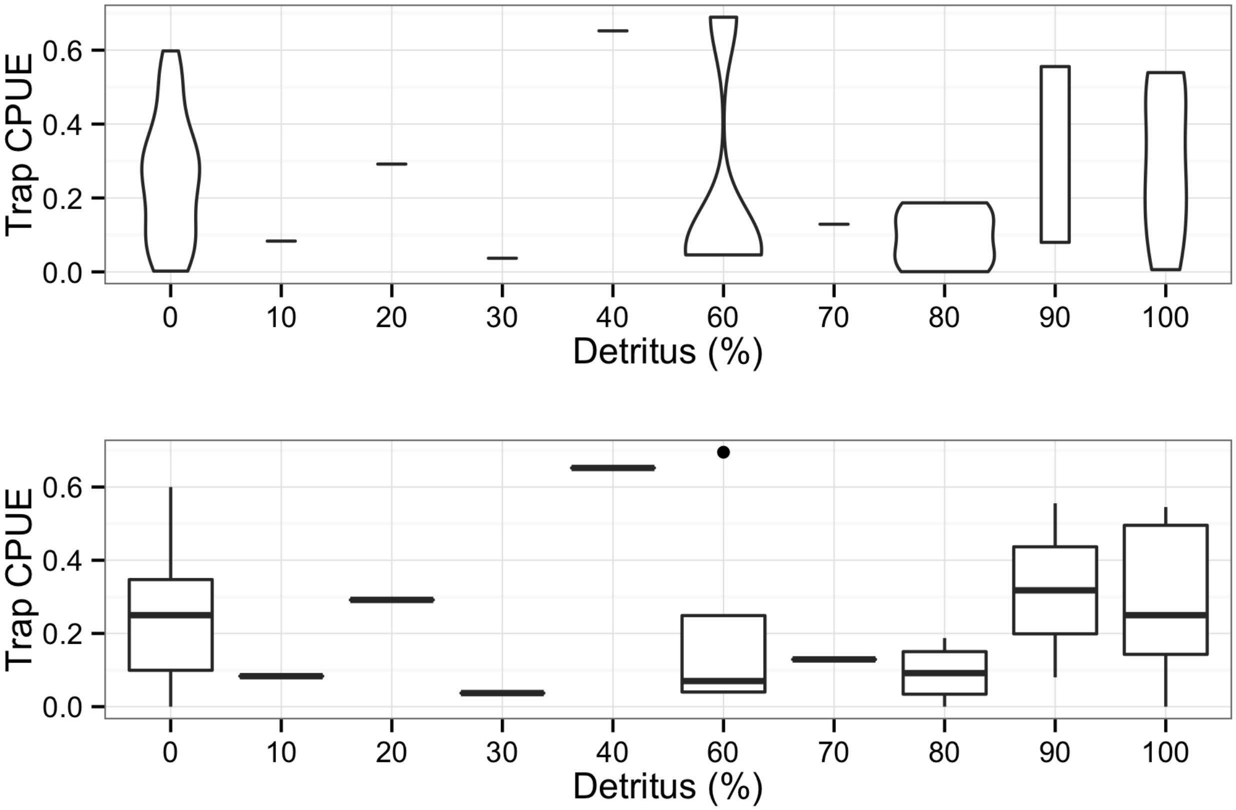

Figure 25. Trap CPUE of American eel by detritus substrate (%) in traditional eel traps in Oakland Lake, Mahone Bay, Nova Scotia. No significant differences were found between trap CPUE and percent detritus substrate. Violin plots (top) show the density of points where boxplots (bottom) show statistics.

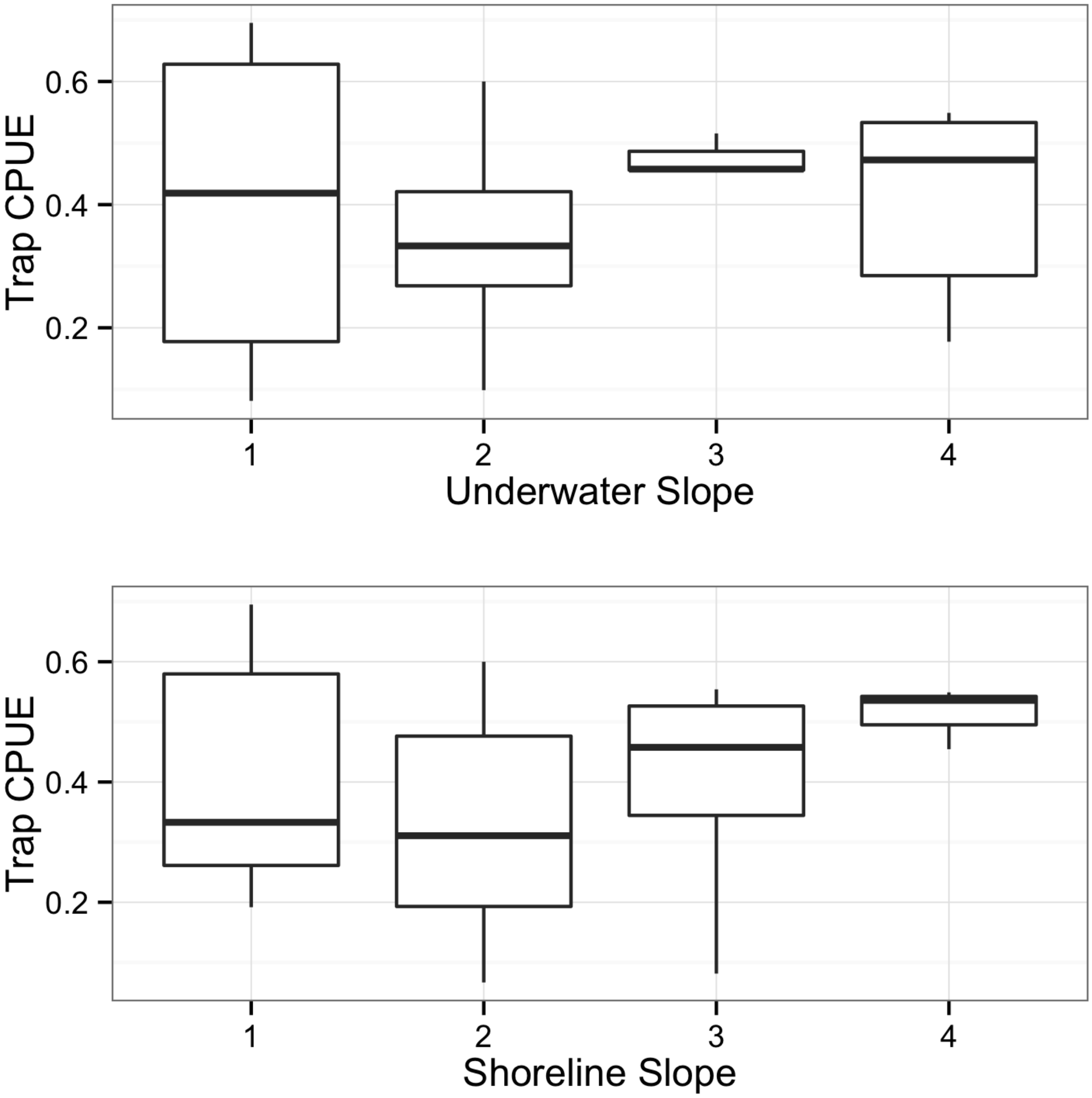

Figure 26. Trap CPUE of American eel by underwater slope and shorelines slope (1 = slope near 0, 4 = steepest slope) in Oakland Lake, Mahone Bay, Nova Scotia. No significant differences were found between trap CPUE and individual underwater and shoreline slopes.

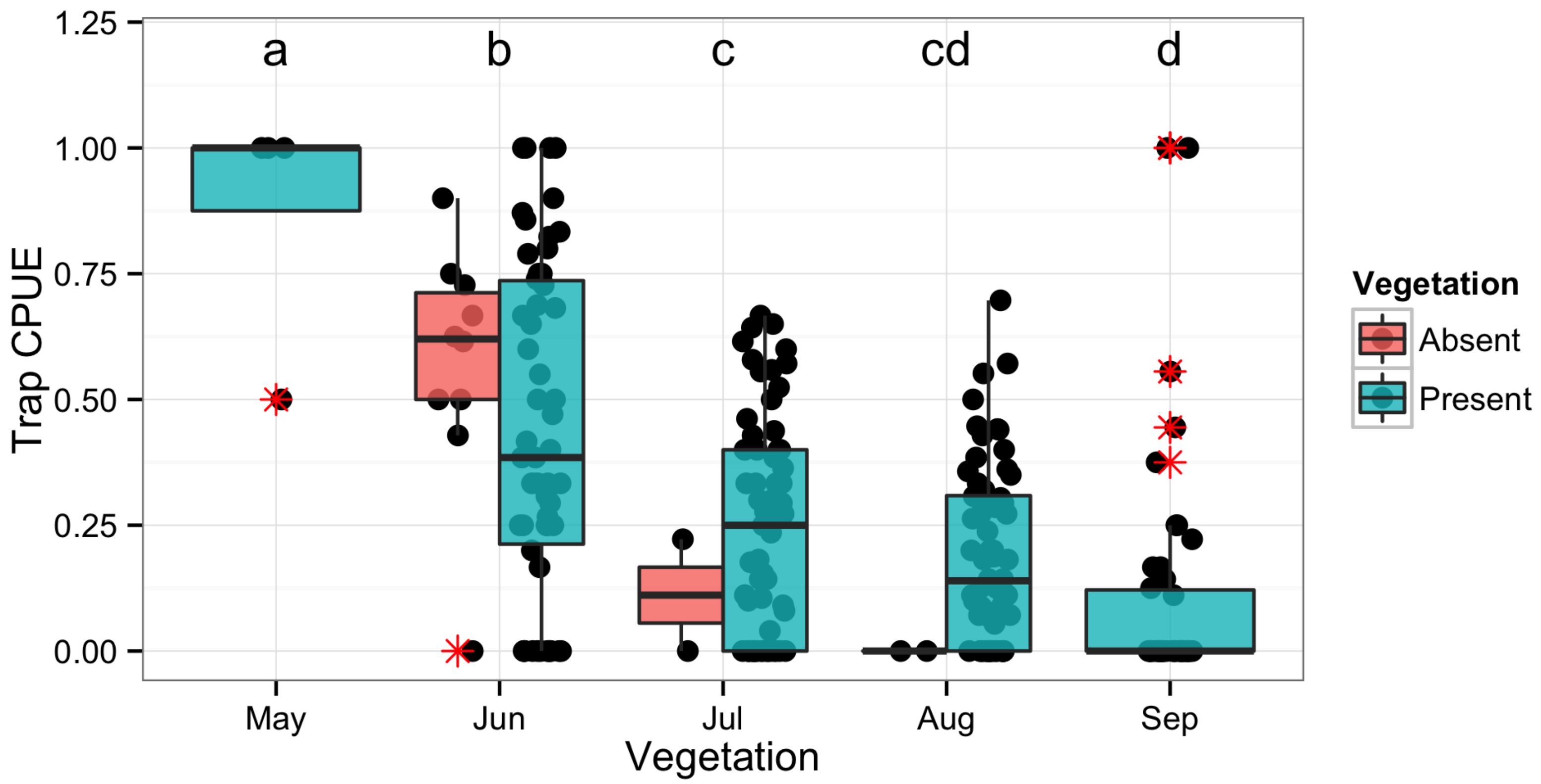

Figure 27. Trap CPUE of American eel by monthly vegetation (presence/absence) captured in traditional eel traps in Oakland Lake, Mahone Bay, Nova Scotia. Same letters indicate no significant difference between monthly trap CPUE at alpha = 0.05 after accounting for presence/absence in a 2-way ANOVA. Each dot represents a trap.

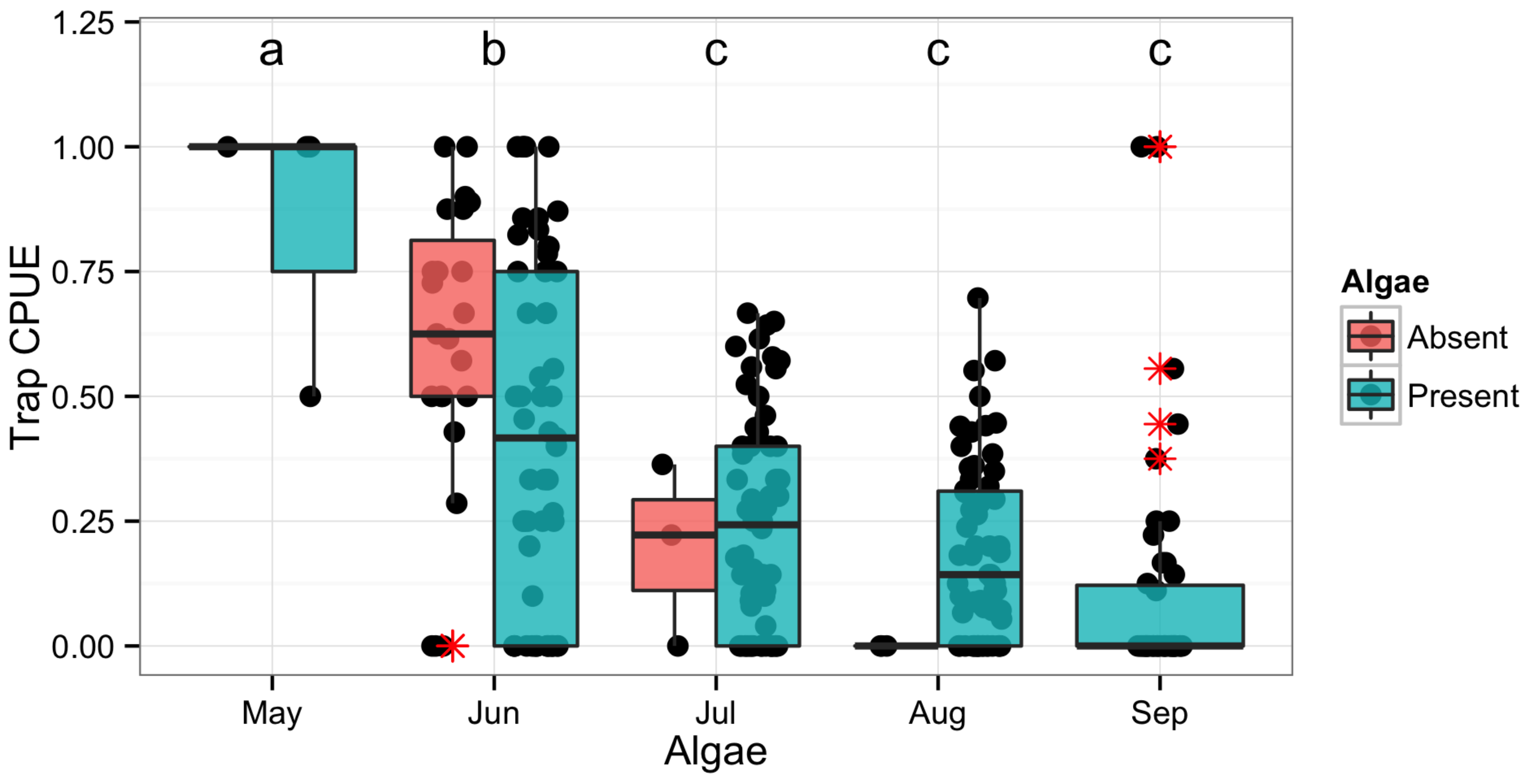

Figure 28. Trap CPUE of American eel by monthly algae (presence/absence) captured in traditional eel traps in Oakland Lake, Mahone Bay, Nova Scotia. Same letters indicate no significant difference between monthly trap CPUE at alpha = 0.05 after accounting for presence/absence in a 2-way ANOVA. Each dot represents a trap.

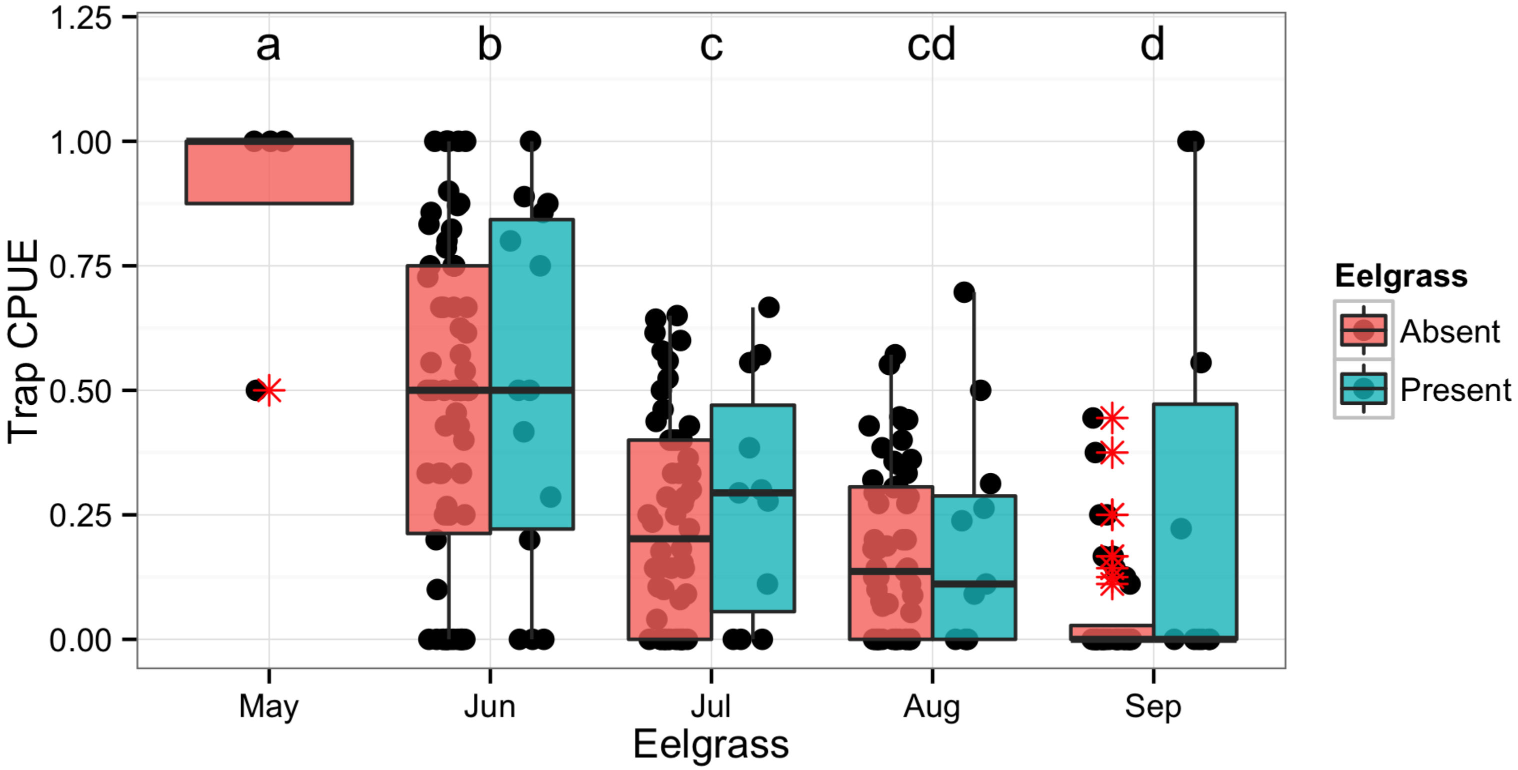

Figure 29. Trap CPUE of American eel by monthly eelgrass (presence/absence) captured in traditional eel traps in Oakland Lake, Mahone Bay, Nova Scotia. Same letters indicate no significant difference between monthly trap CPUE at alpha = 0.05 after accounting for presence/absence in a 2-way ANOVA. Each dot represents a trap.

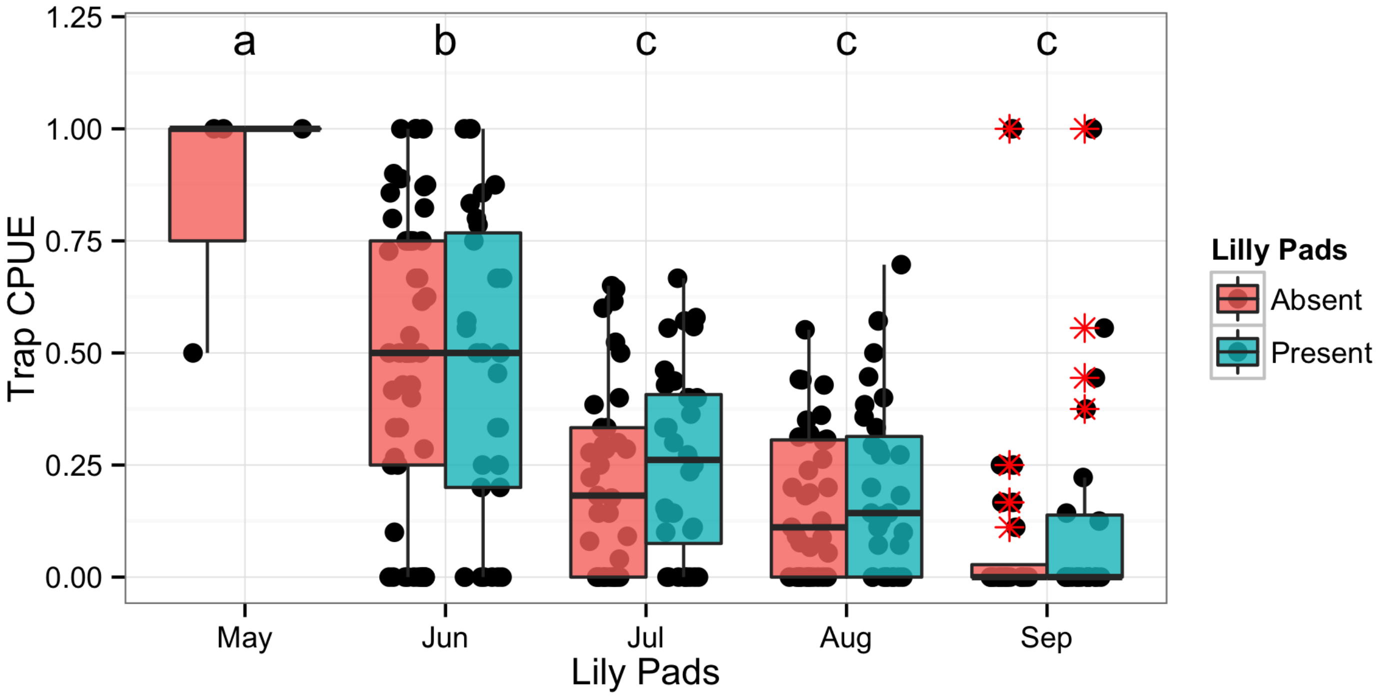

Figure 30. Trap CPUE of American eel by monthly lily pads (presence/absence) captured in traditional eel traps in Oakland Lake, Mahone Bay, Nova Scotia. Same letters indicate no significant difference between monthly trap CPUE at alpha = 0.05 after accounting for presence/absence in a 2-way ANOVA. Each dot represents a trap.

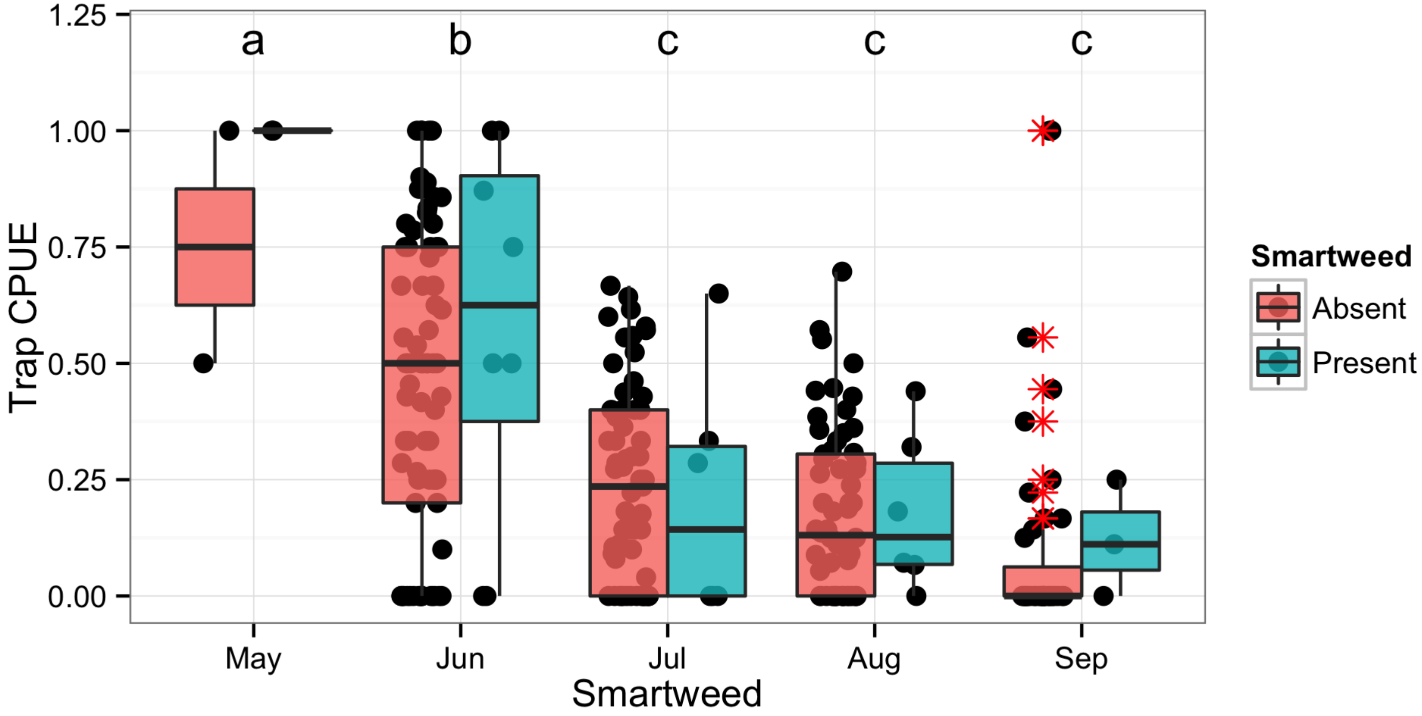

Figure 31. Trap CPUE of American eel by monthly smartweed (presence/absence) captured in traditional eel traps in Oakland Lake, Mahone Bay, Nova Scotia. Same letters indicate no significant difference between monthly trap CPUE at alpha = 0.05 after accounting for presence/absence in a 2-way ANOVA. Each dot represents a trap.

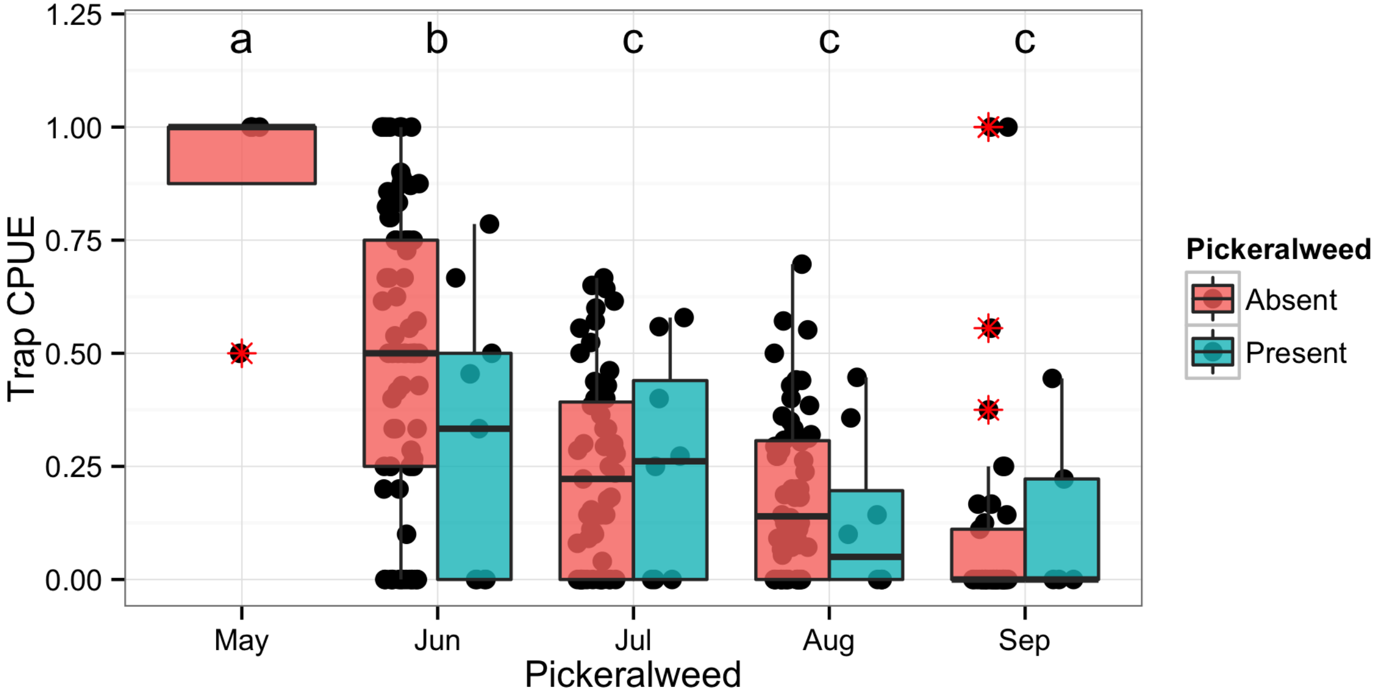

Figure 32. Trap CPUE of American eel by monthly pickerelweed (presence/absence) captured in traditional eel traps in Oakland Lake, Mahone Bay, Nova Scotia. Same letters indicate no significant difference between monthly trap CPUE at alpha = 0.05 after accounting for presence/absence in a 2-way ANOVA. Each dot represents a trap.

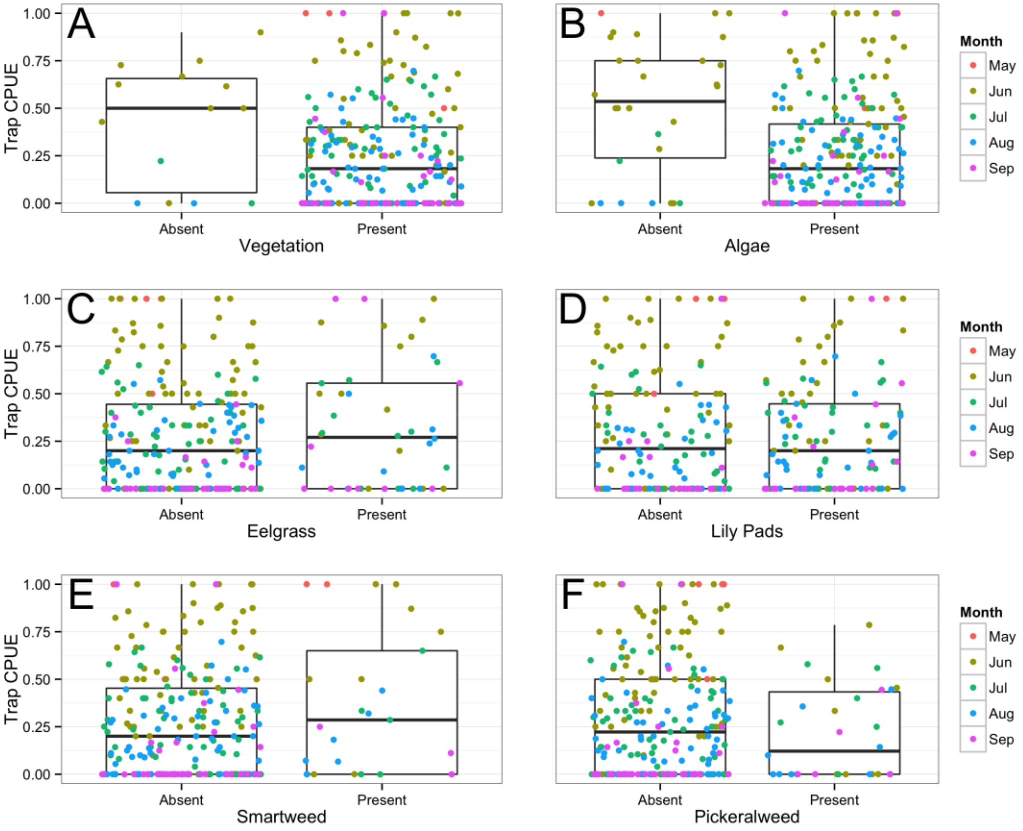

Figure 33. Trap CPUE of American eel by vegetation and vegetation type (presence/absence) including algae, eelgrass, lily pads, smartweed and pickeralweed in Oakland Lake, Mahone Bay, Nova Scotia. Each dot represents a trap.

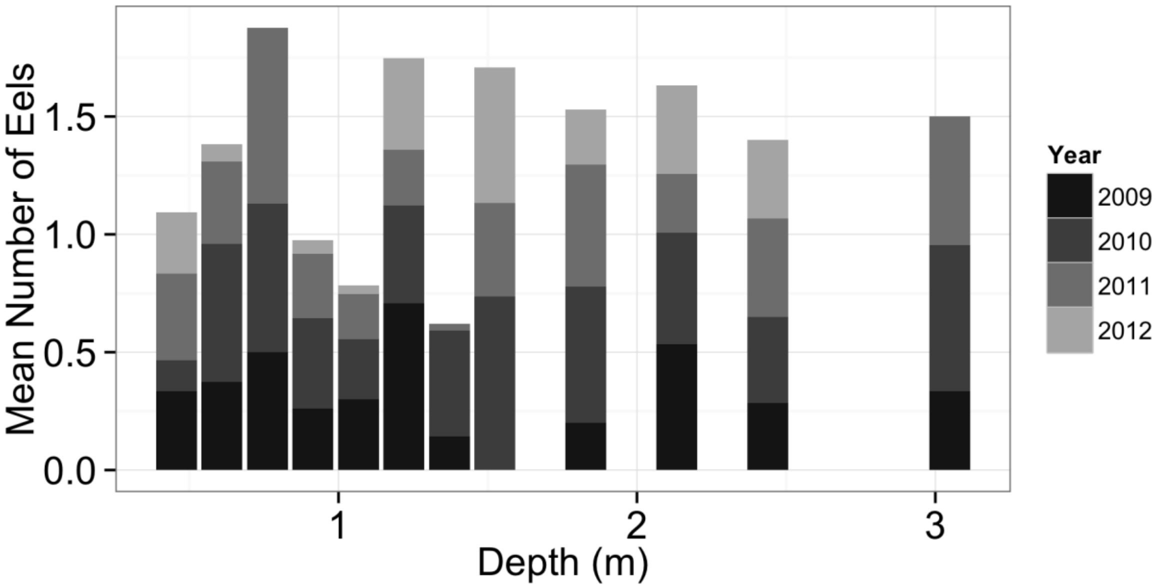

Figure 34. Mean number of American eels captured in traditional eel traps within each year (2009 – 2012) by depth in Oakland Lake, Mahone Bay, Nova Scotia.

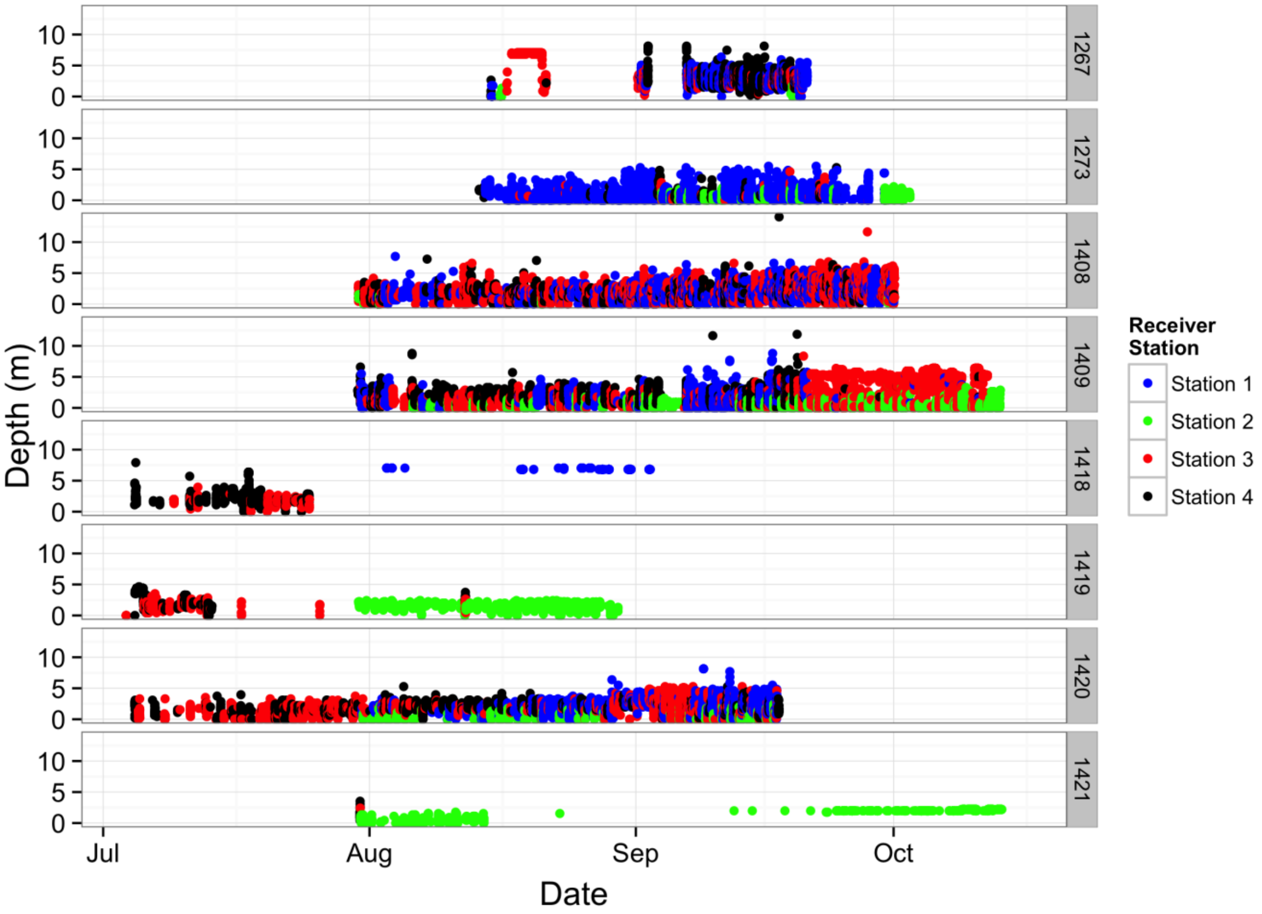

Figure 35. Detected depths (m) of eight acoustically tagged eels in 2012 in Oakland Lake, Mahone Bay, Nova Scotia

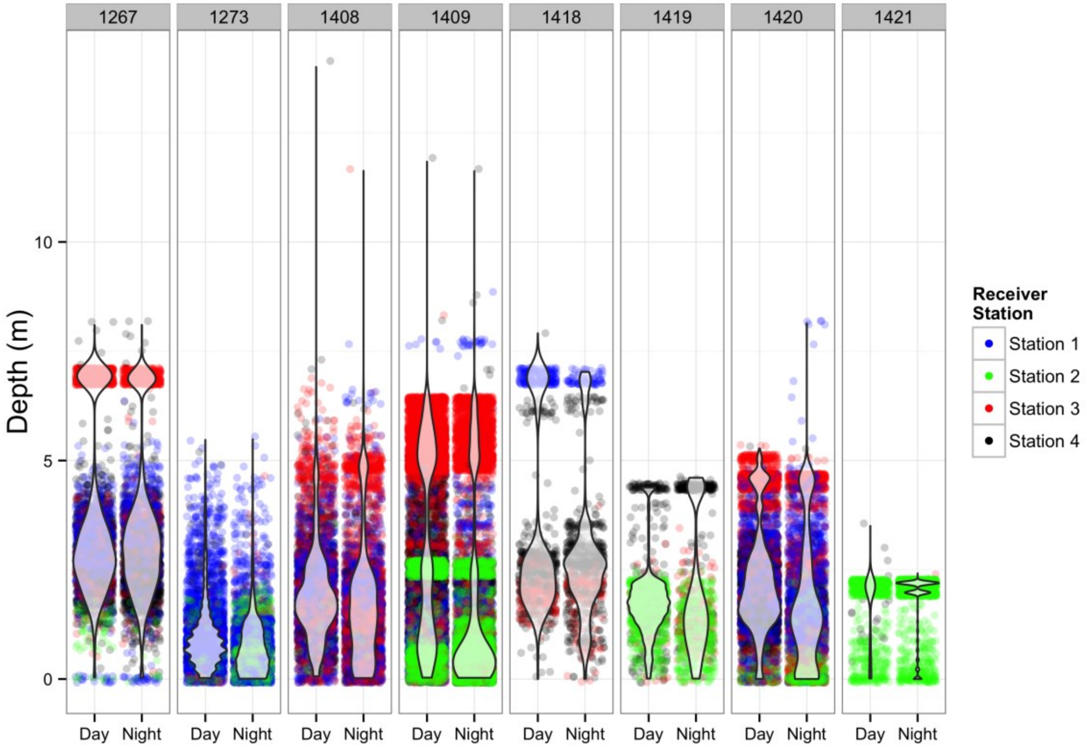

Figure 36. Detected depths (m) of acoustically tagged American eel in 2012 in Oakland Lake, Mahone Bay, Nova Scotia. Each facetted block represents the number of detections for individual eels.

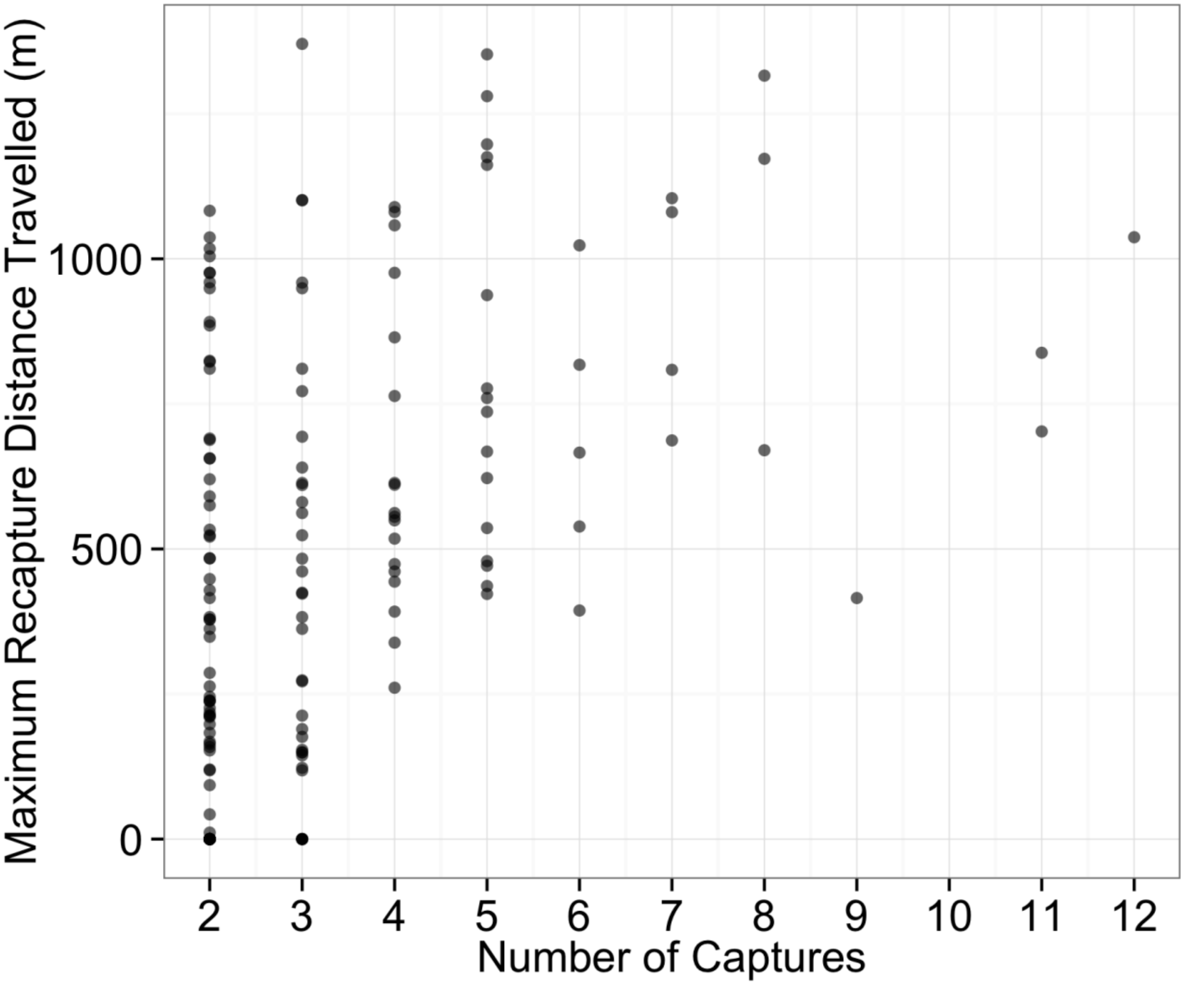

Figure 37. Number of individual eel captures by the maximum recapture distance (m) travelled from original trap site in traditional eel traps across all four years (2009 – 2012) in Oakland Lake, Mahone Bay, Nova Scotia. Each dot represents an eel. Darker dots indicate a higher number of eels captured with the same maximum recapture distance travelled.

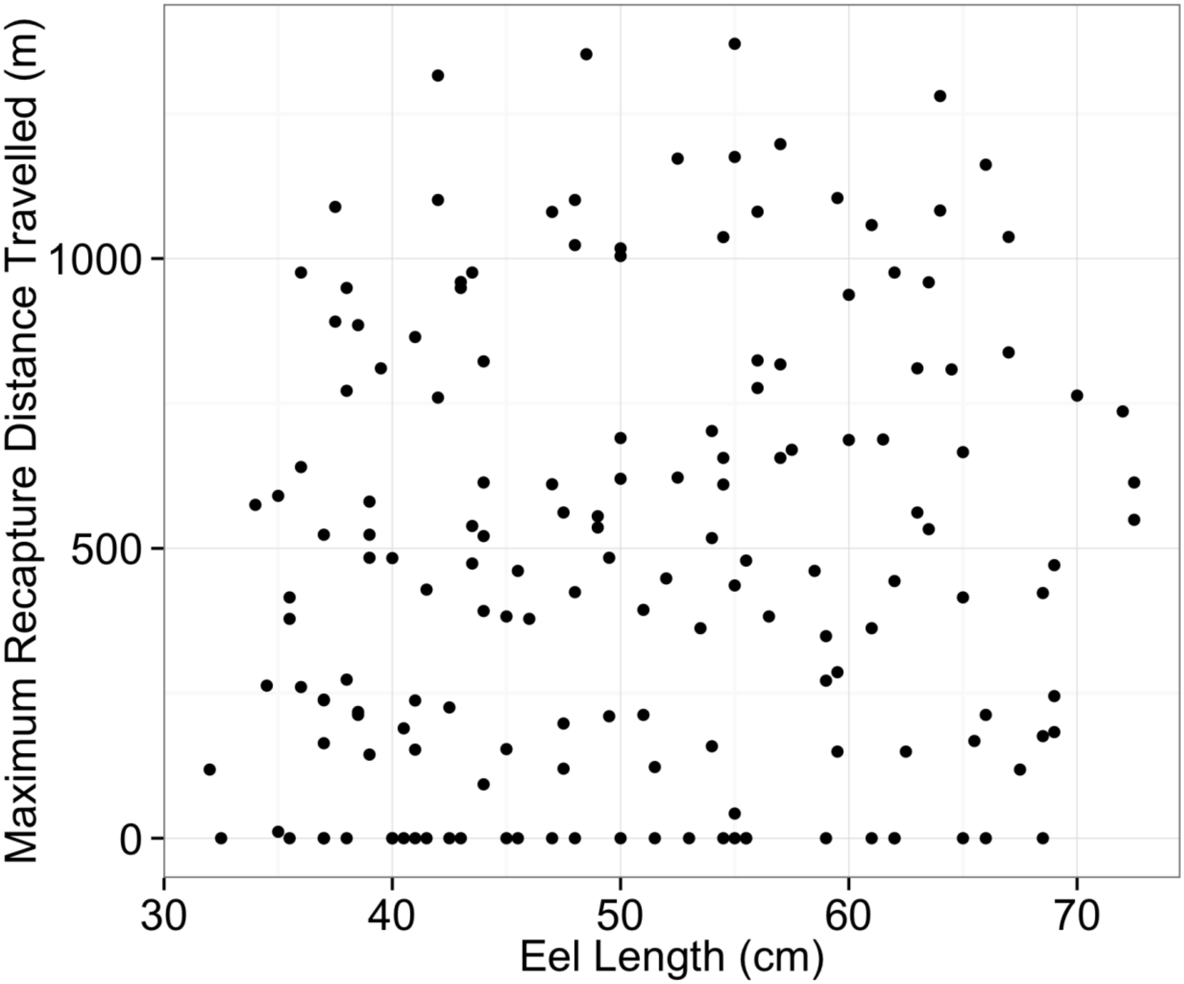

Figure 38. Maximum recapture distance (m) travelled by eel length (cm) of eels captured in traditional eel traps across all four years (2009- 2012) in Oakland Lake, Mahone Bay, Nova Scotia.

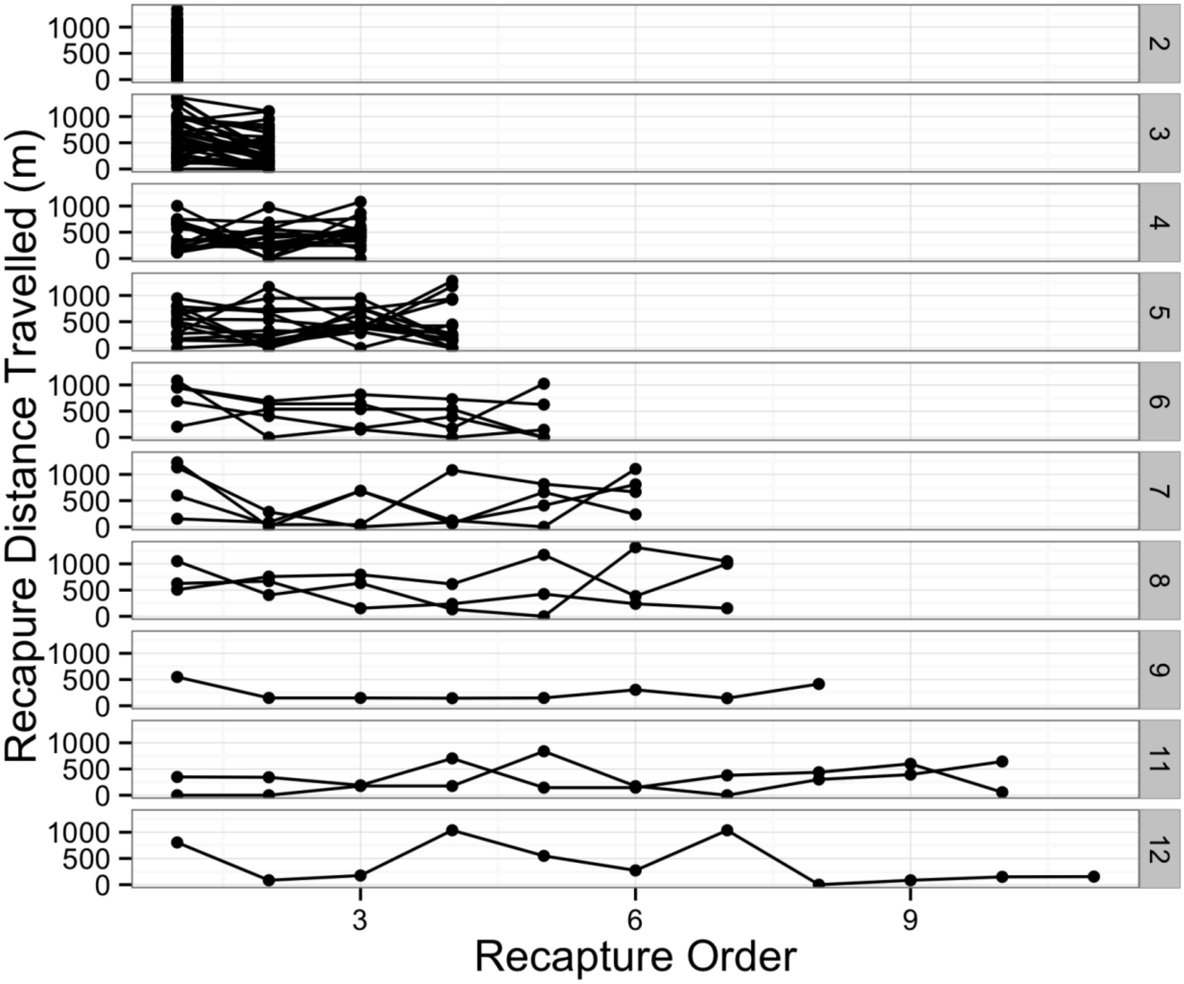

Figure 39. Number of individual eel recaptures in order of recapture history by recapture distance travelled (m) from original trap site in traditional eel traps across all four years (2009 – 2012) in Oakland Lake, Mahone Bay, Nova Scotia. Numbers on the right indicate the number of times an eel was captured.

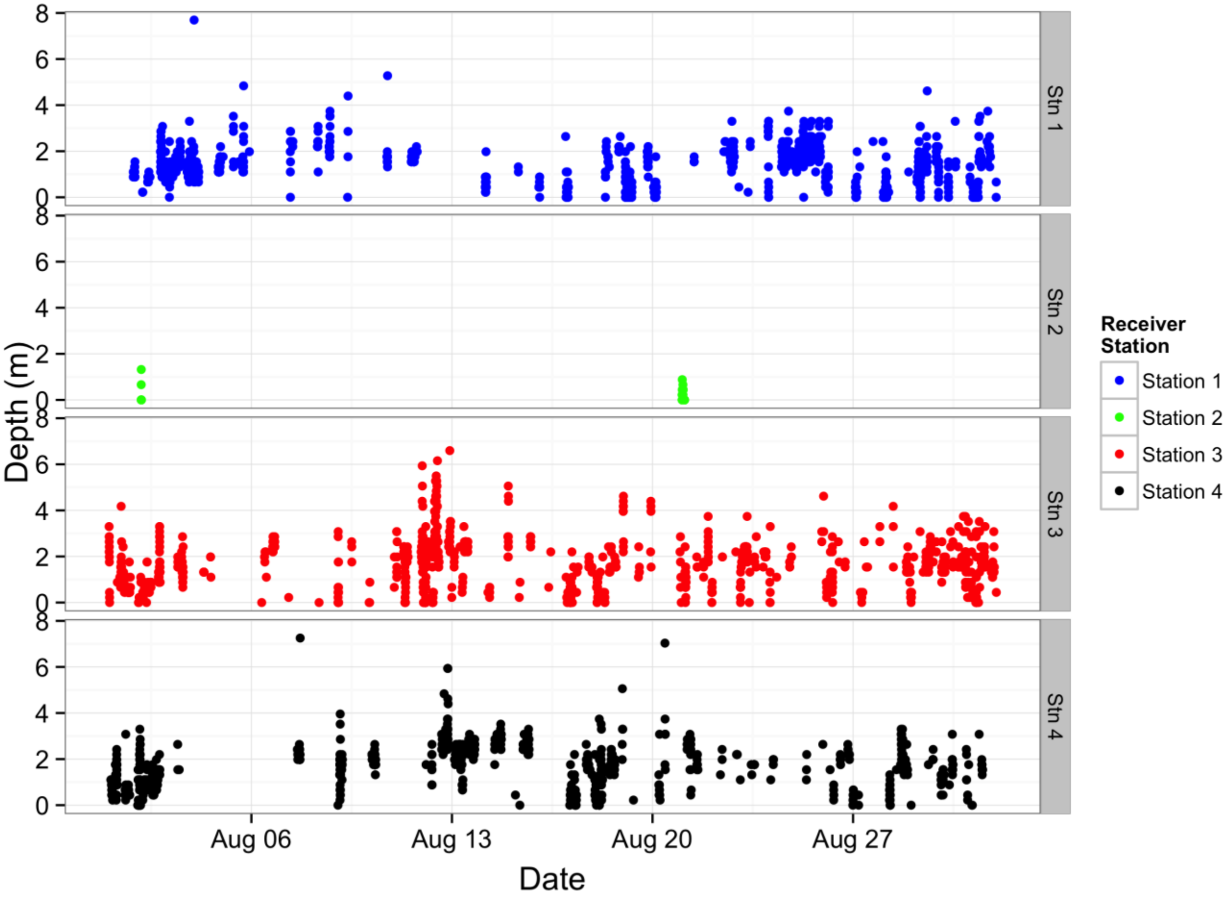

Figure 40. Detected movement of acoustically tagged eel, 1408 (42 cm, 540 g), in Oakland Lake, Mahone Bay, Nova Scotia from 30 July – 2 October 2012.

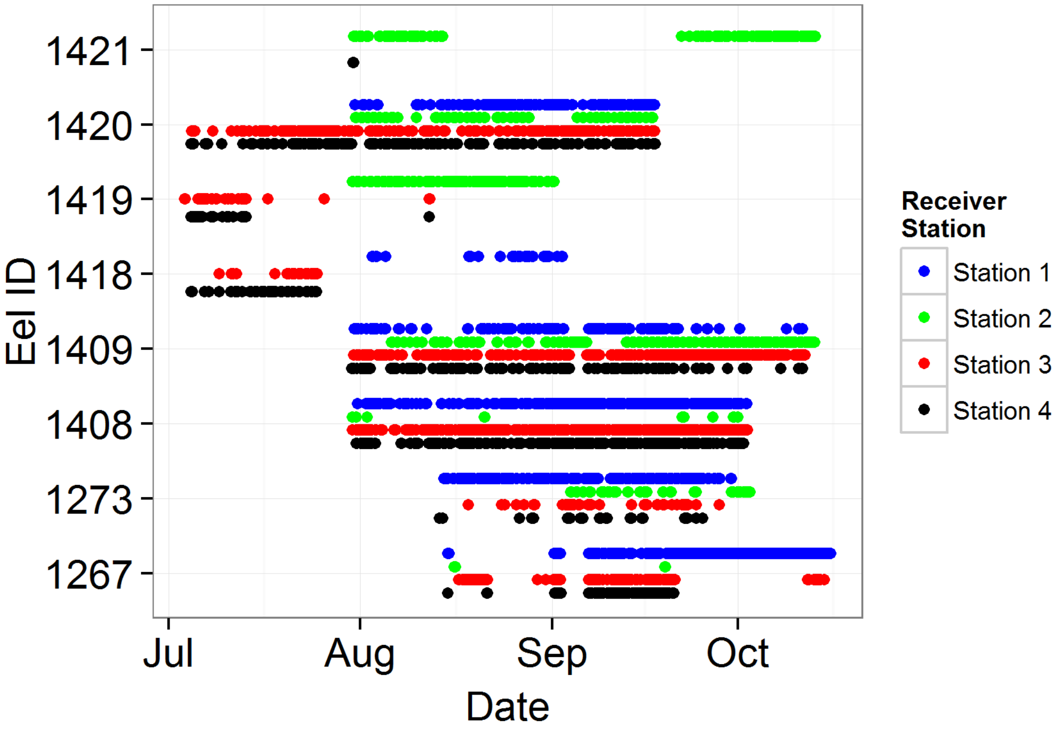

Figure 41. Acoustically tagged American eel detections at four receiver stations located around Oakland Lake, Mahone Bay, Nova Scotia in 2012.

Chapter III

Local Population Estimates and Trap Efficiency

Introduction

The American eel, *Anguilla rostrata*, population has shown widespread declines within its range (Hightower and Nesnow, 2006) yet, accurate information on local population demographics including abundance and density are limited (Bozeman, 2011). Currently in Canada, eels are assessed as a single designatable unit (DU) (COSEWIC, 2012). This is because the most recent molecular analysis shows no neutral genetic differences in the species range suggesting polygynandrous (promiscuous) mating behaviour is occurring on a regular basis (Bernatchez et al., 2011). The regions of the DNA that were tested come from non-coding parts of the genome and therefore have no effect on phenotype. If interbreeding were to rarely occur in American eels, different sequences could, over time, end up being part of those neutral regions (M. Snyder, pers. comm.). There are many American eel abundance indices occurring within local populations in Canada and the United States. Cairns et al. (2014) reports the available long-term monitoring indices of the American eel in Canada including: Moses Saunders Dam, Beauharnois Dam, Chambly Dam, St Lawrence Estuary, Quebec City (single location), Newfoundland, Miramichi River, East River Chester and East River Sheet Harbour. Overall, results of Cairns et al. (2014) continue to support the conclusions by COSEWIC (2012) of a general abundance decline of American eels in Canada within the last 32 years. On small scales such as in Ontario, declines as much as 99 % or more have been found within the indices of both recruitment and standing stock (Cairns et al., 2014).

Standing stock and silver eel abundances have been declining in Newfoundland and St. Lawrence Basin, respectively. The Southern Gulf of St. Lawrence is the only location where the standing stock abundance has shown an increasing trend over the past 32 year (Cairns et al., 2014).

Cairns et al. (2014) suggests local populations over a short period (16 years) have shown relative improvement in abundance for the indices with the exception of standing stock abundances in three of the four geographic locations (Lake Ontario, Newfoundland, Atlantic Coast of Nova Scotia, and Bay of Fundy). Increasing recruitment trends were found in the St. Lawrence Basin, Upper St. Lawrence/Lake Ontario. Increasing standing stock abundances for estuarine and marine locations were found in areas of the Southern Gulf of St. Lawrence. Local populations that showed variations in abundance with no statistically significant results included the elver recruitment index from the East River, Chester, standing stock index from the southern Gulf of St. Lawrence freshwater standing stock index and the silver eel abundance index from the St. Lawrence Basin (Cairns et al., 2014). Overall American eel abundance trends are varied at the scale of local populations, which may influence how American eels should be assessed in the future. Information on population demographics and dynamics within specific watersheds is needed to more accurately represent local American eel populations and to, in turn, better estimate their current global population status.

Recently, there has been great concern for population declines of both American and the closely related European eel, *Anguilla anguilla*. In the case of European eel, evidence suggests a sharp decline in elver recruitment is a main factor influencing population decline (Anon 2003; ICES 2007). In population dynamics, it is important to consider elver recruitment as a contributing factor to local American eel populations. Although there are many threats to both American and European eels including pollution, habitat loss, parasite and disease introduction and migration barriers (Bevacqua et al., 2009), the primary focus tends to be on commercial fishing. Nine American eel elver licences are currently issued in the Maritimes Region, which could potentially impact local populations. Some license holders are required to monitor elver migration and relative abundance yearly. Therefore, in addition to long-term monitoring of elvers on various rivers it is essential to link elver indices to adult abundances.

Few local American eel populations are monitored, leaving researchers with little information regarding population demographics or dynamics in local watersheds. Long-term monitoring of local eel populations can produce watershed-specific information including immigration (elvers), emigration (silver-phase eels), and mortality rates to help estimate population size and characterize population dynamics. A better understanding of fishing impacts would benefit from long-term monitoring of adults in watersheds where commercial fishing occurs or in parallel with watersheds near commercially fished systems. One on-going elver recruitment index in Eastern Canada occurs on the East River, Chester, Nova Scotia. It began in 1996 using Irish style elver traps with the exception of one break between 2003 – 2006, it has continued onward since (COSEWIC, 2012). Annual elver abundance estimates are variable (Bradford et al., 2010; Cairns et al., 2014); however, elver abundance estimates since 2008 have been similar to estimates between 1996 – 2002 (Bradford et al., 2010; Cairns et al., 2014). Annual elver runs increased between 2010 and 2013 (Cairns et al., 2014). In 2009 another on-going elver index began in St. Jean River estuary in Quebec using fyke nets; however, no trends in abundance have been detected to date. (COESWIC 2012).

An elver monitoring station was in operation on Oakland Stream from 2010 to 2012. This stream is approximately 25 km along the coast from East River, Chester and is useful as a parallel index for elver recruitment. Oakland Lakes' small and enclosed headwater to Mahone Bay estuary is a more practical study location for adult eel monitoring. Oakland Lake is an ideal long-term study location for a local American eel population because it is a protected watershed with relatively few anthropogenic activities, with easy access for research, and has only one stream for eel passage to and from the Mahone Bay estuary. Because of the single stream, elver abundances (a proxy for recruitment) and silver-phase emigration are relatively easy to measure through custom-built traps. Elver abundances from Oakland Lake can be compared with East River elver abundances in order to compare a non-fished site with a commercial fishing site, but Oakland Lake can also serve as a study site for local population characterization including habitat use. The Oakland Lake ecosystem is a relatively small watershed providing an ideal setting to study long-term population demographics and dynamics.

A complete population demographic and dynamic analysis requires long-term monitoring to describe the ways in which population changes over time through births, deaths, immigration and emigration. Trapping adult American eels is one approach to capture eels in a local population, and capture-mark-recapture is a useful technique for population demographic studies and to study habitat use. Trapping migrating adults provides emigration data on silver-phase American eels enroute to their spawning ground that can also be compared with yellow eel trapping.

Commercial fishing of large eels in the Maritimes is restricted to areas including, Saint John River, the south and southwestern shores of Nova Scotia, the southeastern portion of Cape Breton Island and the majority of the southern Gulf of St. Lawrence (Department of Fisheries and Oceans Canada, 1996). The large eel commercial fishery uses three main types of gear including fyke nets, weirs and baited pots, although spears are used in some locations. The type of gear used is dependent on habitat type and the desired stage of eel (Department of Fisheries and Oceans Canada, 1996). Weirs typically fish silver-phase eels in rivers, fyke nets are prohibited in inland waters and primarily capture yellow or silver eels in estuarine waters. Traditional eel traps tend to be set in the still water of lakes and estuaries to capture yellow and silver-phase eels (Department of Fisheries and Oceans Canada, 1996). Pots are baited, checked and moved often to maximize commercial fishing catch.

While commercial fishing techniques for trapping American eel are well established, their use for long-term monitoring does not include empirical information on trap efficiency, or trap-related behaviour. For example, underwater camera surveys suggest eels learn to escape traps (Cox, 2012). Investigating the feasibility of long-term monitoring using a capture-mark-recapture (CMR) technique with traditional trapping techniques in Oakland Lake will provide useful information on trap efficiency and sampling protocol, which can be used to characterize various population demographics. Analyzing recruitment (immigration) via elver abundance, emigration of silver-phase eels, and adult abundances (population estimates) should provide valuable information on American eel population demographics in Oakland Lake and a basis for analyzing population dynamics in larger watersheds. The study objectives for this chapter include:

1. Estimate local population sizes on a yearly basis in Oakland Lake using a closed population estimation method (Schnabel).
2. Assess the use of trap monitoring for conducting long-term monitoring of eels and how these factors relate to population demographics, and eel behaviour including:
    a. Estimating trap efficiency based on fishing time (trap soak time),
    b. Estimating optimal trap effort and capture event timing.

Materials and Methods

American Eel abundances were monitored in Oakland Lake, Mahone Bay, Nova Scotia (a protected watershed) during the spring and summer months from 2009 – 2012. Eels were captured using baited traps set in various trap sites and recorded using spatial coordinates as UTMs. Eel pots consisted of large traditional style eel traps (2009 – 2012) typically used in the adult eel commercial fishery. Traps were checked approximately every second day. Captured eels were separated and placed into holding bags, and taken to shore sites where they were sampled. Eels were scanned for a PIT (Passive Integrated Transponder) tag prior to being anesthetized with a clove oil solution. If untagged, eels were anesthetized, and injected with a PIT tag. If the anesthesia exposure period was inadequate, eels were returned to the clove oil for an additional few seconds. After tagging and biological sampling (length, weight measurements), eels were placed in fresh water and moved back and forth to pass oxygenated water over their gills. Once fully recovered, eels were released to the wild. For a more detailed and in-depth review regarding study area, sampling, and other protocols refer to Chapter II: General Demographics and Habitat Use.

Capture Events

Population estimations based on capture-mark-recapture techniques require assignment of "capture events". Under a lockstep trapping schedule, in which all traps in a study are checked on the same days, capture events are simply the days when traps are checked. However, in the present study capture events could not be defined simply as days or weeks because individual eel traps were checked unequally within these arbitrary periods. For example, a trap may have been checked twice within the same sample period that another trap was checked only once. During sampling periods some traps were not fishing (e.g. blown on shore, stolen), or were not checked because their buoys were sunken or because of poor weather. Because trap checking did not follow a uniform schedule, , two methods were defined to standardize capture events as ‘variable’ or ‘fixed’ depending on the analysis. Under both schemes, only traps that were present and operating for the entire capture event were considered.

Variable capture events were defined as periods during which a set percentage of a set number of eel traps was checked. For example, if 28 traps were available, check traps until 50% of traps (i.e. 14) are checked. The first capture event included the first day of sampling and subsequent days until the set percentage of traps was checked. The second capture event began on the day following the end of the first capture event. Using this methodology, capture events varied in their period (number of days) because individual traps had variability in their fishing time. When capture events were based on a lower percentage of traps (e.g. 50 %), it resulted in more capture events, each having shorter periods, than when based on a higher percentage of checked traps (e.g. 90 %).

Sampling days occurring at the end of each year were truncated and not included in analyses if the set percentage of traps could not be checked within the given period.

Fixed capture events were defined as periods during which a set number of traps were checked within a set number of days. The first capture event of each year included the first day of sampling and subsequent days until the set number of days were reached. The second capture event began on the day following the end of the first capture event. Sampling days occurring at the end of each year were truncated and not included in analyses if traps could not be checked within the given period.

The number of captured and recaptured individuals in a given capture event was calculated using three rules:

1. If a trap was checked more than once in a single capture event, the number of captured or recaptured eels was defined as their respective sums.
2. If an individual eel was captured multiple times in a single capture event, it was considered multiple recaptures.
3. Eels recaptured during the target year (e.g. 2010) that had been marked in a previous year (e.g. 2009) were considered 'new' eels for the target year.

Local Population Estimates

Because the American Eel population is panmictic, the term 'local population' is ecologically defined as a geographically confined sub-population and this terminology is applied to eels here. As well, the term 'population' will be adopted as equivalent to 'local population' where the term is used in explaining analyses.

Closed Population Size Estimation

Closed populations are assumed to be confined geographically and demographically meaning the population size is not changing through immigration, emigration, births or deaths (Steven et al., 2005). Most populations are not closed, but changes over short periods are often small enough that assuming a closed population is a reasonable approximation, and the effects of violating the assumptions are minimal (Steven et al., 2005). Because elver immigration (and subsequent recruitment of juvenile eels) into and mature adult emigration out of Oakland Lake occur at the start and end of each study year, a closed population is a reasonable assumption within a year. Therefore, Oakland Lake will be treated as a closed population *within* each of 2009, 2010, 2011 and 2012. Estimates of population size (*N*) were calculated using the method defined by Schnabel (1938).

Abundance estimates were completed using FSA – a package for fisheries analysis in R. Closed populations were estimated using the Schnabel method using the {mrClosed} function. Confidence limits were estimated using the stats {confint} function. Custom scripts co-created by Danielle Quinn (Acadia University) and myself were used for sensitivity analyses using randomizations of numbers of traps within the variable and fixed capture events. These scripts were previously built and used for a MITACS internship of which I was the main intern. My involvement in the script writing was confirming logic and methods, especially yearly changes in methods. Running the code required using ACE-net and associated privileges so my involvement was minimal. I summarize the simulation outcomes here with additional details of the methods and place them in context with my three years of monitoring eels and the subsequent 4th year

(2012) of data obtained from the American Eel Study of Bluenose Coastal Action Foundation and the Atlantic Elver Fishery. As well, I was involved with monitoring elver migrations (2009 – 2011) and adult eel out-migrations (2009), both of which I will also discuss in context with trap monitoring.

The Schnabel (1938) method, incorporated sequential capture events, and was calculated using the equation:

$$N = \frac{\sum M_i C_i}{\sum R_i}$$

where i is a capture event, M_i is the total number of previously marked individuals at event i, C_i is the number of individuals captured at event i, and R_i is the number of marked individuals (recaptures) captured at event i. Baseline population estimates were based on the number of eels captured each sampling day (where each sampling day was considered a capture event) regardless of the number of available traps per year. The mean population estimate, by year, using the Schnabel method was used as a baseline for subsequent sensitivity analyses and is referred to hereafter as “baseline population estimates”.

Sensitivity Analysis of Closed Population Estimates

Sensitivity analyses used variations in measures of sampling effort to examine the variability in corresponding population estimates. A sensitivity analysis determines how different values of an independent variable (sampling effort) will impact a particular dependent variable (population estimate) under a given set of assumptions or under varying combinations and levels of independent variables. The sensitivity analysis consisted of randomly selecting traps and applying population estimate analyses to subsets of data including only those selected traps. Bootstrapping, or resampling, was done to assign measures of variance to sample estimates. The objective of this analysis was to estimate trap efficiency based on fishing time and estimate optimal trap effort and capture event timing to determine an efficient and cost-effective long-term sampling protocol with minimal effort for a CMR study. Consideration was given to 1) how many traps should be checked, and 2) how often traps should be checked, to produce population estimates comparable to baseline population estimates.

Sensitivity Analysis 1: Variable Capture Events

Variable capture events were defined using the methods described above with the following details. For each year, Z number of randomly selected traps (where $Z = 2, 4, 6, \ldots, 30$) were chosen as a subset of the CMR data without replacement. Capture events were based on Z traps, in which X (where $X = 50, 55, 60, \ldots 90$ %) of Z traps were checked. Inherently, if a greater percentage of traps (X) were checked, more time is required and the trade-off was that there would be fewer capture events. For each year (2009 – 2012), this process was bootstrapped 100 times for each Z and X combination. For example, 10 traps were randomly selected and the period when 50 % of those 10 traps were checked defined a capture event.

Sensitivity Analysis 2: Fixed Capture Events

Fixed capture events were defined using the methods described above. For each year, Z number of randomly selected traps (where $Z = 2, 4, 6, \ldots, 30$) were chosen as a subset of the CMR data without replacement. Capture events were defined by D number of days (where $D = 1, 2, 3, \ldots, 10$). For each year (2009 – 2012), this process was bootstrapped 100 times for each Z and D combination. For example, 10 traps were randomly selected and checked over a two day period defined a capture event. Bootstrapped results for both variable and fixed capture events were visualized in R using ggplot2.

Trap Efficiency

The relationship between standardized fishing times and resulting captures were visualized in R using ggplot2 to investigate fishing time. The relationship of fishing time to capture frequency was calculated by linear regression; however, many zeros skews this relationship.

Immigration of Elvers

Two Irish style elver traps were placed at the mouth of Oakland Stream in the spring of 2010, 2011 and 2012. Traps were typically set in April when elvers began their upstream migration and generally remained until the end of June to mid-July when the run was complete. These gravity-fed traps each contain a ramp for elvers to ascend when migrating upstream. Elvers travel up these ramps because they are attracted to the low velocity flows of freshwater. The traps were designed to capture elvers along stream edges where water flow is low. Once elvers ascended the ramp they were flushed into a holding box where they could be removed and counted volumetrically or individually depending on abundance. If measured volumetrically, elvers were placed in a graduated cylinder with a mesh bottom allowing excess water to drain. Elvers were volumetrically measured to the nearest 10 mL, removed from the graduated cylinder and counted individually to get a total count per mL. Remaining abundances were calculated volumetrically based on count per mL calculated for each day. An elver run was deemed complete when captures decreased to approximately zero to five elvers over the span of one to two weeks. Elver traps gave daily migration estimates providing information on immigration. The protocol was similar to that used for the East River elver index. A comparison between the Oakland Stream index and East River elver index can be made to provide further insight into any immigration trends.

Emigration of Adults

A custom-built trap was placed within Oakland Stream in 2009 (1 September – 28 October), 2011 and 2012 (10 September – 24 October) and fished for 29, 26 and 45 days, respectively, to determine downstream out-migration presumably of sexually maturing silver eels. A funnel was installed that spanned the width of the stream (71 cm) directing the flow of water into a 68.5 cm (Width) x 81 cm (Depth) x 114 cm (Height) rectangular cage with a small mesh size (2.5 cm x 2.5 cm). This trap was checked daily until the out migration was complete. Eels were removed from the mesh trap with a net, scanned to determine if a PIT tag was present and, if so, the PIT tag number was recorded. Eels were measured, weighed and released back in to the stream to continue migrating. In 2009, the trap washed out between 9 – 12 October due to increased water levels caused by rain. The trap was redesigned in 2012 and replaced. The redesign included small holes in the funnel to reduce water pressure and prevent washout or breakage.

Trapping downstream migratory eels gives an estimate of how many sexually maturing eels leave Oakland Lake each year and the run timing of this migration. It will also provide an estimate of population turnover and relate it to population size and recruitment. Trapping also provides a count of the proportion of tagged eels in the local population during out migration. The proportion of tagged to untagged eels adds to the information on abundance and provides migrating eel size distributions to compare with eels captured in Oakland Lake. Measurements may also provide an indication of the relative size of sexually mature eels. Because full records of lengths, weights, and tag returns were not available for this study and publically available data were limited it is important to note these data exist and could provide valuable insight into the local American eel population in Oakland Lake.

Results

Sensitivity Analyses of Closed Population Estimates

Baseline population estimates ranged from 87 to 161 eels in traditional eel traps across years, with a mean annual estimate of 114 (Table 10). Annual baseline population estimates varied because of the variable number of days (therefore, capture events) and eels captured within each year.

Sensitivity Analysis 1: Variable Capture Events

Overall, selecting more traps leads to a non-linear increase in mean population estimates, with estimates approaching an asymptote near or exceeding baseline population estimates (Figure 42). Annual baseline population estimates and population estimates from 2009 – 2011 have similar trends compared with 2012. From 2009 – 2011 estimates were comparable within a given year using capture events with lower percentages of traps checked (e.g. < 65 %). When a low number of traps were selected, mean population estimates were low suggesting a minimum number of traps were required for accurate estimates.

From 2009 – 2011, when a greater number of traps were selected per capture event, mean population estimates increased and become relatively stable after about 10 –

20 traps, regardless of percent checked. In 2012, mean population estimates increased and never appeared to become stable. Confidence intervals increased as the number of traps increased, but beyond the inflection point as the number of traps continued to increase, confidence intervals narrowed. Theoretically, the difference between the baseline population estimates and bootstrapped population estimates can be used to determine how many traps are needed to find equivalent estimates. If the confidence intervals of bootstrapped population estimates overlap baseline population estimates, then the estimates are not statistically different at alpha = 1-CI level (du Prel et al., 2009) indicating that fewer traps could be used to obtain the same estimate.

Sensitivity Analysis 2: Fixed Capture Events

Overall, selecting more days leads to a non-linear increase in mean population estimates, with mean estimates approaching an asymptote near or exceeding baseline population estimates (Figure 43). Annual baseline population estimates and population estimates from 2009 – 2011 have similar trends compared with 2012. Similar to variable capture events, low numbers of traps produced low population estimates.

From 2009 – 2011, when a greater number of traps were selected per capture event, mean population estimates increased and appeared to become relatively stable after 10 – 20 traps, regardless of the period of capture events. In 2012, mean population estimates increased and never become stable even with a high number of traps. Confidence intervals increased as the number of traps increased, but beyond the inflection point as the number of traps increased past 20 traps, confidence limits narrowed. Similar to variable capture events, fixed capture event periods decreased as the number of days (*D*) increased. Increasing days allows a greater number of traps to be checked however, increasing the number of days also leads to fewer fixed capture events, which, under the sampling conditions and protocols, makes population estimates less stable. Theoretically, these simulations can be used to determine the optimal capture event period (days between checking traps) to find an equivalent population estimate. For example, the more days between checking traps (longer capture event period), results in more trap checks in a given capture event. If a relatively high number of capture events is still realized, population estimates are more stable.

Trap Efficiency

Fishing times varied across all four study years and were significantly different from one another ($p < 0.001$) except for 2009 and 2011 ($p = 0.669$) (Figure 44). When many eels were captured and sampled on a single day, fewer traps could be checked due to time constraints with PIT tagging and biological sampling. Therefore, traps had various fishing times within and among years ranging from 1 – 13 days. The longest fishing time of 13 days was in 2011 and was likely due to a lost trap that was later found. Overall, mean fishing time was 3.3, 5.8, 3.4 and 2.2 for 2009, 2010, 2011 and 2012, respectively. Within each year from 2009 – 2012, a higher number of eels captured appeared after traps fished for 2 – 3 days, but no relationship existed between the number of eels captured and fishing time (Figure 45).

Immigration of Elvers

Comparing immigration from another watershed is a good proxy to determine adult population abundance trends when watershed area and/or volume are taken into account. Immigration estimates of total run size to the East River, Chester, Nova Scotia, have varied from approximately 450,000 elvers in 1999 to 1.9 million elvers in 2012

(Cairns, et al., 2014). Although the East River is a much larger watershed, the elver count trend over years is reflected in Oakland Lake (Figure 46). The drainage basin of East River is approximately 134 km^2 (Jessop et al., 2002) compared to Oakland Lake which has a drainage basin of approximately 4 km^2 (D. Mackenzie, pers. comm.). In 2010, abundance of elvers immigrating into East River was 633 times the abundance of elvers immigrating into Oakland Stream. In 2011, abundance of elvers immigrating into East River was 270 times the abundance of elvers immigrating into Oakland Stream. In 2012, abundance of elvers immigrating into East River was 358 times the abundance of elvers immigrating into Oakland Stream.

Emmigration of Adults

During the fall of 2009, 2011 and 2012 a custom-built trap in Oakland Stream captured 221, 283 and 405 eels, respectively, of which all were assumed to be leaving Oakland Lake. Of those eels two were tagged in 2009, one in 2010, and 13 in 2011 (Crnec, 2012). The increasing trend in out-migrating eels follows the increase in population estimates (Table 10). The low number of tagged eels suggests a high proportion of smaller eels were captured in the custom- built trap. Those small eels would likely not have been tagged in Oakland Lake based on the results from Chapter II where overall mean eel length caught in traditional eel traps was 48.4 ± 11.0. Size information from the 2009, 2011 and 2012 custom-built trap in Oakland Stream is not available; however, in 2013, 526 silver eels were captured of which, 380 were < 45 cm (Pernette, 2013).

Discussion

Baseline Population Estimates

Inter-annual variations in population estimates may be affected by the overall sampling period for the year. For example, because 2009 had a shorter overall sampling period than other years, fewer capture events were possible overall regardless of capture events being variable or fixed. Another factor was the possibility of learned behavior in eels. This factor could present itself in two ways. First, eels may have learned how to enter a trap knowing food was available, and revisited traps because they provided a food source. Second, eels learned how to escape traps, and this occurred before eels were "captured". Differing fishing times may also influence the number of eels captured. For example, the attractiveness of a baited trap should decrease with fishing time because eels capable of escaping would likely eat the bait, but the longer a trap fishes the more time eels have to find it, eat, and find a way to escape. If a trap fishes for less time, eels may not have enough time to find it, may be captured while still eating, or may get captured simply because of poor timing (being in the trap when it is hauled) whether they learned to escape or not. Finally, traps may only be efficient at catching eels of a certain size distribution (see Chapter II). Smaller eels are able to move freely through the trap mesh (Cox, 2012). Therefore, if mean eel length and mass were smaller in one target year versus another, this may only indicate that smaller individuals entered traps, ate, and escaped leaving little or no bait for larger eels, thus capturing larger eels may be less likely.

Baseline population estimates are lower than expected given the number of eels out-migrating. Therefore, population estimates may be confined to the larger sized eels in

Oakland Lake. Smaller eels particularly less than 30 cm could easily escape through the larger mesh of traditional style eel pots. Pernette (2013) found a large proportion of eels leaving Oakland Stream in 2013 were < 45 cm suggesting many eels in Oakland Lake are small and are not captured. In the future, placing a smaller mesh barrier around traditional eel pots and/or adding minnow traps for long-term monitoring (longer than one study year) may enhance collections allowing for more accurate population estimates on different size distributions of American eel. Other evidence of traps being ineffective at holding eels has been seen through underwater camera surveys (Cox, 2012). Filming traditional style eel pots in 2012 showed American eel entering baited eel pots, eating the bait and swimming around until they found the funnel opening to escape. Potentially, there could be a large number of American eels entering traps, but not accounted for because of escapement. In addition to unaccounted for eels, a Schnabel estimate is only used for calculating closed populations therefore, the population estimates will be inflated if there is a high degree of immigration or emigration. However, the closed assumption for this study holds given that immigrating elvers even after 4 – 5 years are unlikely to be large enough to be captured, and emigrating eels do not leave until after sampling was completed. If an overall population estimate is wanted, a different method is needed such as open population using capture histories *across* several years. When capture histories are analyzed across years variables including deaths, births, immigration and emigration are accounted for and therefore, will not unnecessarily inflate the population estimate.

Generally, more eels did appear to be caught after traps fished for 2 – 3 days, likely because the majority of traps only fished for approximately three days within each year with the exception of 2010. However, traps that fished for more days did not affect the number of eels captured. Based on overlapping confidence intervals between bootstrap and baseline population estimates, it appears a minimum of 10 traps should be checked per capture event. At fewer than 10 traps, mean population estimates were lower than baseline estimates. This probably reflects a decrease in the probability of capturing a marked individual because of decreased effort. The initial increase in confidence intervals was expected because capture event periods using fewer traps results in shorter capture event durations, and therefore, more variability in randomized selection of traps. This result is at odds with increasing the number of capture events, which should narrow confidence intervals around the estimate because more events are included in the calculation.

In summary, the more traps checked within a target year the more opportunity there is to capture eels. Through simulation, it was found that increasing traps to about 10 produced population estimates statistically equivalent to baseline population estimates (using all days), but confidence intervals were wide. After 10 traps, mean population estimates remained relatively constant with narrowing confidence intervals. Unfortunately, increasing trap checks (effort) results in longer sampling periods (days), and therefore fewer capture events, which may produce variable and potentially biased population estimates (Stevens et al., 2005). Increased sampling effort by adding traps resulted in population estimates approaching baseline in most years. The exception occurred in 2012 when sampling periodicity was not controlled by me. Essentially, across all four study years, biological sampling, tagging and trap type (traditional eel traps) remained the same suggesting trap sampling differed. From 2009 – 2011, trap sampling was done by me in a consistent manner. This protocol lead to increased effort (more trap checks) which apparently resulted in, less variable baseline population estimates, and more consistent patterns in bootstrap population estimates. A consistent sampling design and traps checked at regular intervals appears to have increased accuracy. In 2009 – 2011, each trap was checked approximately every second day; in 2012, trap checks were more variable in terms of sampling periods, not fishing time. If factors such as missing, lost or stolen traps, trap checks lost to poor weather conditions, and/or number of eels captured during a day (i.e. higher catches means fewer traps checked) were not an issue then consistency is met and populations estimates would be expected to follow similar patterns. Because population estimates were inconsistent in pattern and variability, especially in 2012, it underscores the need for consistency in sampling protocols for long term monitoring.

Recommendations for long-term monitoring

Based on the evidence in this study, the current sampling methods for long-term monitoring using traditional trapping techniques in Oakland Lake appears to underestimate the true American eel population size in Oakland Lake, but several recommendations for future long-term monitoring in Oakland Lake have been proposed.

1. Set a reasonable number of traditional traps (i.e. 15-20) that can be checked within a short period of time (< 1 day). This will result in less variable capture events, more consistent sampling and more accurate/stable population estimates.
2. Set the traditional eel traps close to shore within one quadrant of lake. Less time will be required to check all traps. Eels were captured in all habitat types with the exception of deep water therefore enough eels should be captured to obtain a population estimate.

3. Bait the traditional eel traps in the afternoon prior to checking. Check traps early in the morning the following day to reduce the amount of time eels have to enter and escape traditional eel traps.
4. Because eels are capable of escaping from traditional eel traps and smaller eels are capable of travelling freely through the mesh, an experimental trap design(s) may be beneficial to the study. Ideally a non-baited trap (reduce bias) that captures eels of all sizes would allow researchers to gain a better understanding of the true demographics and population size of eels in Oakland Lake. It is important to keep in mind that a trap that catches eels of all sizes may result in cannibalism if traps are not checked often.

Immigration of Elvers

Recruitment by eel count varies greatly between Oakland Stream and East River, but a similar trend exists relative to stream size. For instance, fewer elvers would migrate upstream into Oakland Lake each year than the East River, possibly because the watershed is smaller and therefore supports fewer fish. The East River watershed is approximately 33.5 times the size of the Oakland Lake watershed, and in theory could potentially sustain 33.5 times the mass of eels. Because density is thought to play an important role in determining sex of an individual (and therefore size), it is not reasonable to suggest East River could potentially sustain 33.5 times the number of eels than Oakland Lake. Well over this multiple of eels entered East River compared to Oakland Stream from 2010 – 2012.

The number of elvers immigrating upstream into freshwater appears to be dependent on the size of the watershed, yet because eels are panmictic, they are not likely to immigrate into the same watershed(s) as their parents. It is unclear how elver quantities immigrating into a watershed are determined. Using chemosensory cues, eels are believed to be attracted to freshwater (Creutzberg, 1961; Sorenson, 1986). Perhaps the amount of freshwater draining into an estuary attracts a proportional quantity of elvers. If a larger river has a greater flow rate than a smaller river, a greater attraction would exist and more eels would potentially enter.

Emmigration of Adults

Given the large number of eels emigrating from Oakland Lake during the fall of 2009, 2011 and 2012 it is unlikely the population estimates calculated for this study are accurate with respect to all sizes of eels. The population estimates may, however, be accurate for eels of a certain size distribution (e.g. >30 cm), because a very high proportion of the eels leaving Oakland Lake were small (Pernettte, 2013). Mean length of eels captured in minnow traps was 38.5 ± 5.00 cm (see Chapter II) suggesting small eels are in Oakland Lake, but do not frequently get caught in traditional eel traps.

Table 10. Annual mean baseline population estimates calculated from the number of eels captured each sampling day given the number of available traps per year (2009 – 2012) with 95 % confidence intervals (in parenthesis) and descending eel counts from Oakland Stream (2009, 2011 and 2012) in Oakland Lake, Mahone Bay, Nova Scotia.

Year	Population Estimate		Oakland Stream Eel Emigration Count
2009	90	(62 – 136)	221
2010	87	(72 – 108)	NA
2011	119	(99 – 149)	283
2012	161	(108 – 250)	405

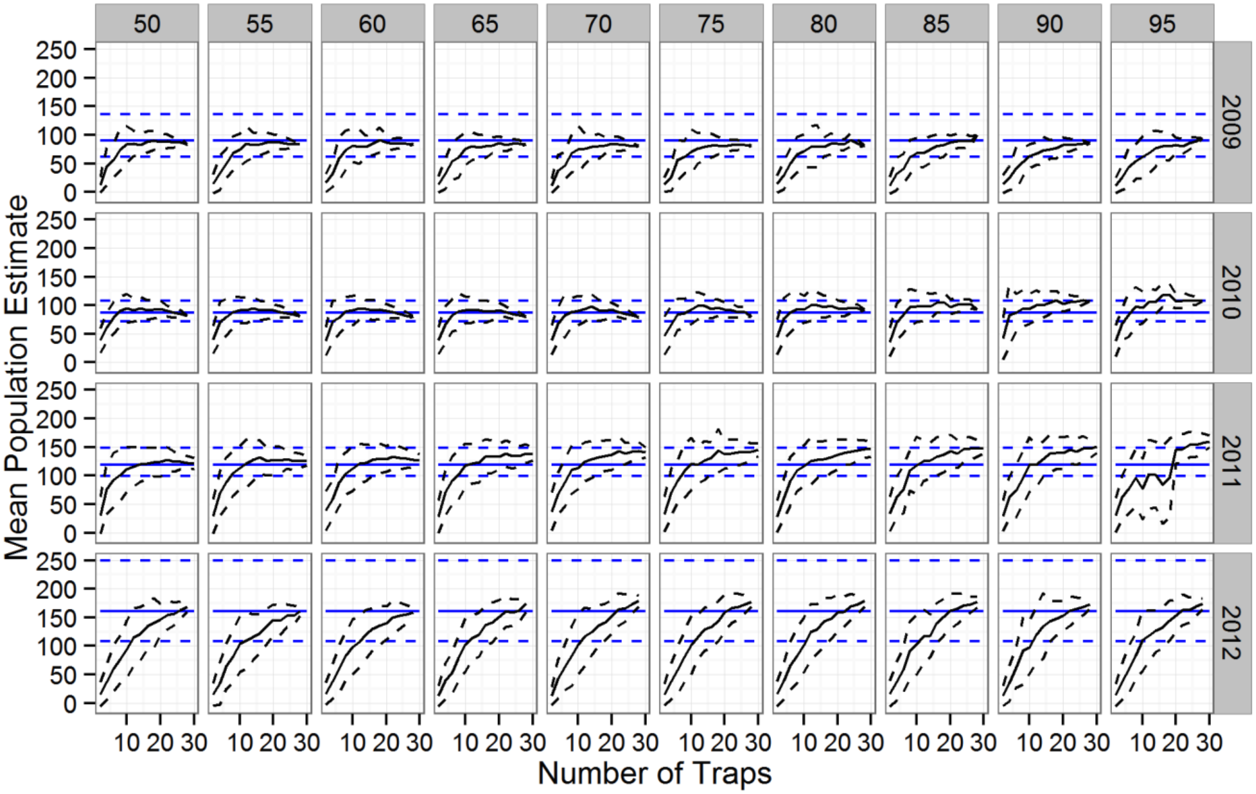

Figure 42. Sensitivity analysis of variable capture events across all four study years (2009 – 2012) in Oakland Lake, Mahone Bay, Nova Scotia where mean population estimates (black) were calculated based on sampling a set percentage of traps. Baseline population estimates (blue) were calculated using each sampling day. Dashed lines are 95% confidence intervals.

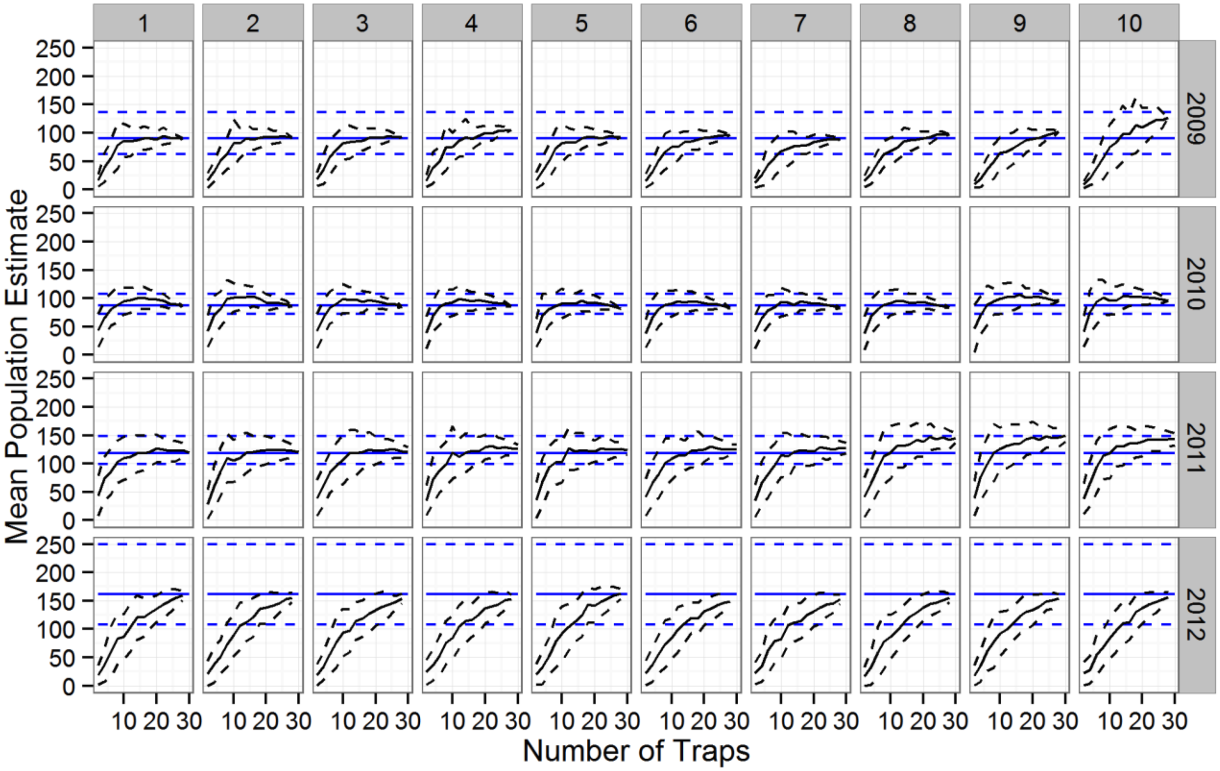

Figure 43. Sensitivity analysis of fixed capture events across all four study years (2009 – 2012) in Oakland Lake, Mahone Bay, Nova Scotia where mean population estimates (black) were calculated based on a set number of days. Baseline population estimates (blue) were calculated each day sampling day. Dashed lines are 95% confidence intervals.

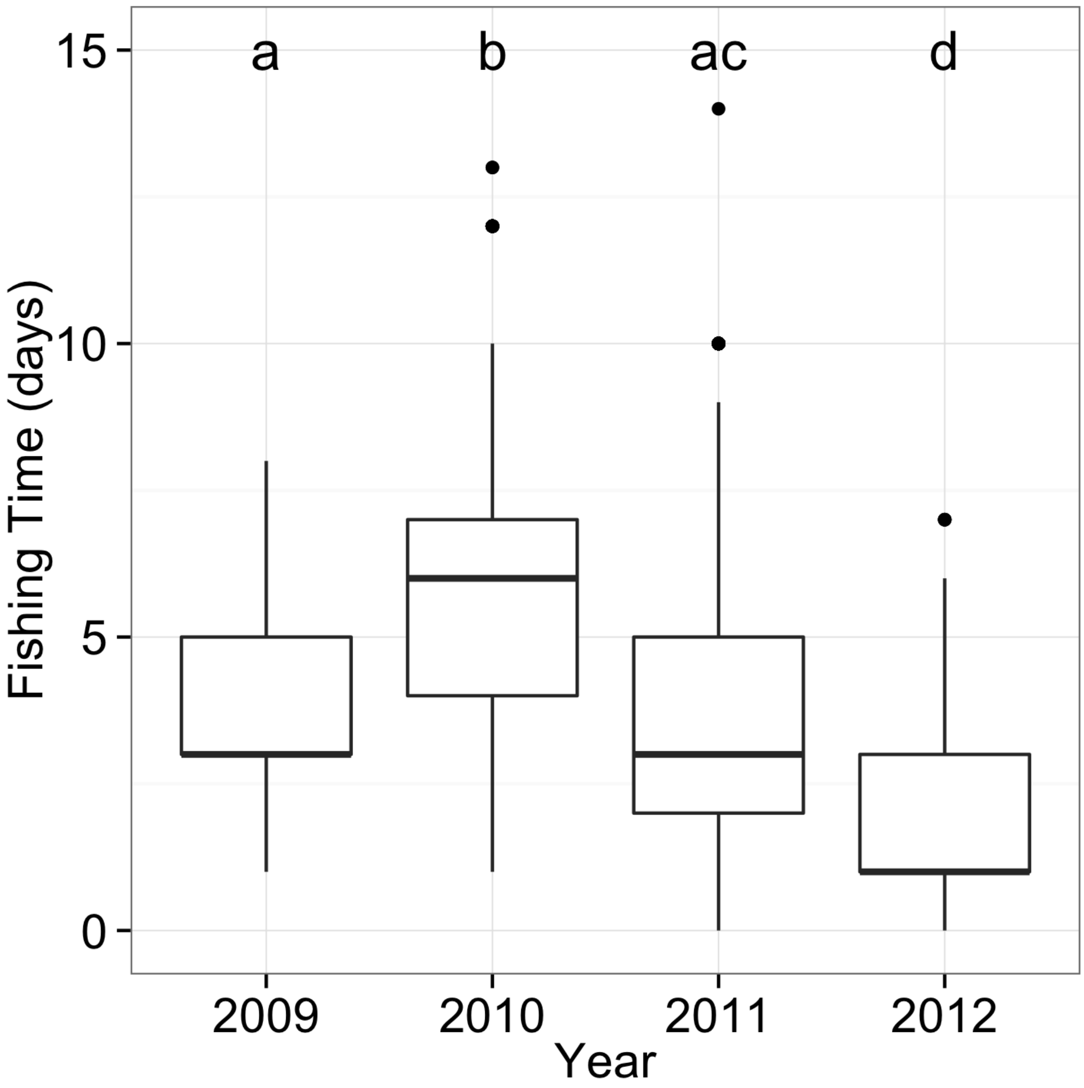

Figure 44. Fishing time (days) for traditional eel traps across all four years (2009 – 2012) in Oakland Lake, Mahone Bay, Nova Scotia. Same letters indicate no significant difference between fishing time and year at alpha = 0.05.

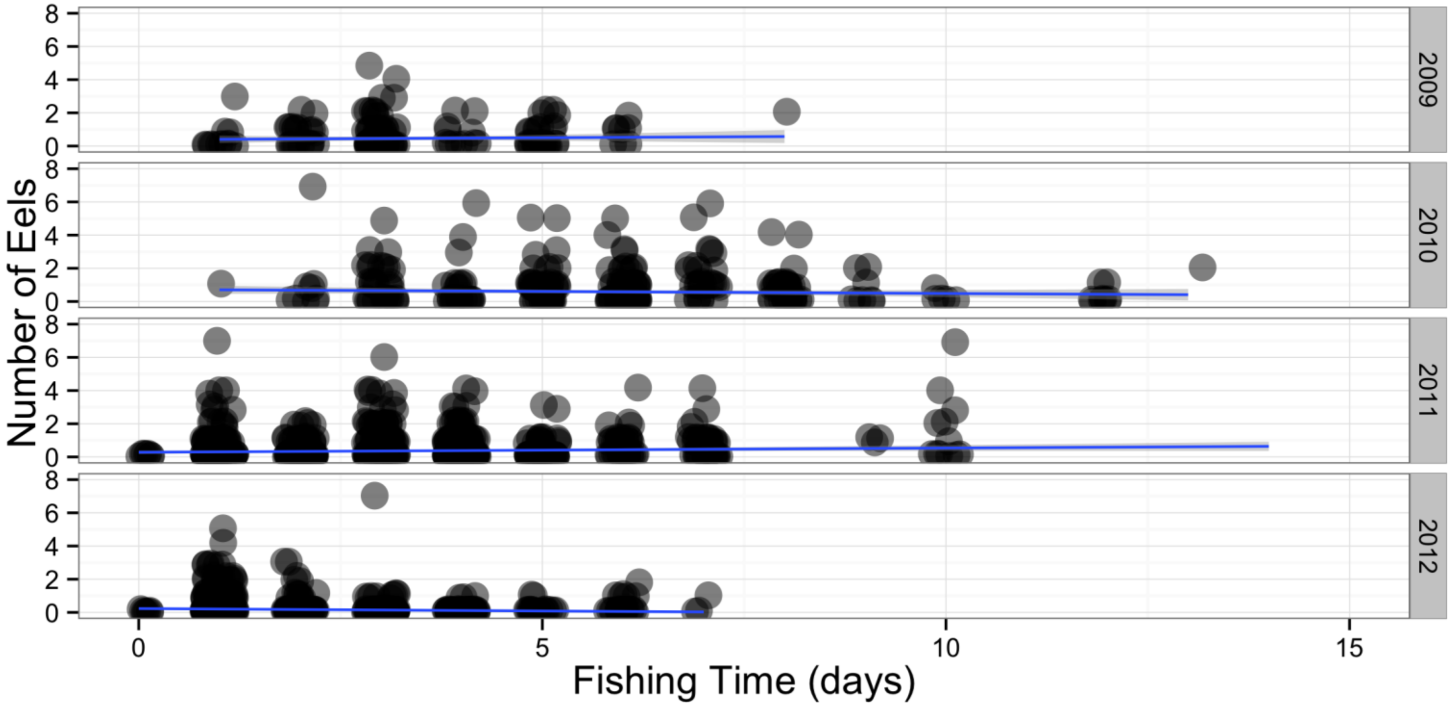

Figure 45. The number of eels captured in traditional eel traps by fishing time (days) across all four years, 2009 (R^2 adj= 0.015; p =0.765; y = -0.02164x + 1.56738), 2010 (R^2 adj= 0.004; p = 0.211; y = -0.06213 x + 2.01384), 2011 (R^2 adj= 0.004; p = 0.920 0.; y = -0.003507x + 1.616691), 2012 (R^2 adj= 0.012; p = 0.150 0.; y = -0.09533x+ 1.69531) in Oakland Lake, Mahone Bay, Nova Scotia.

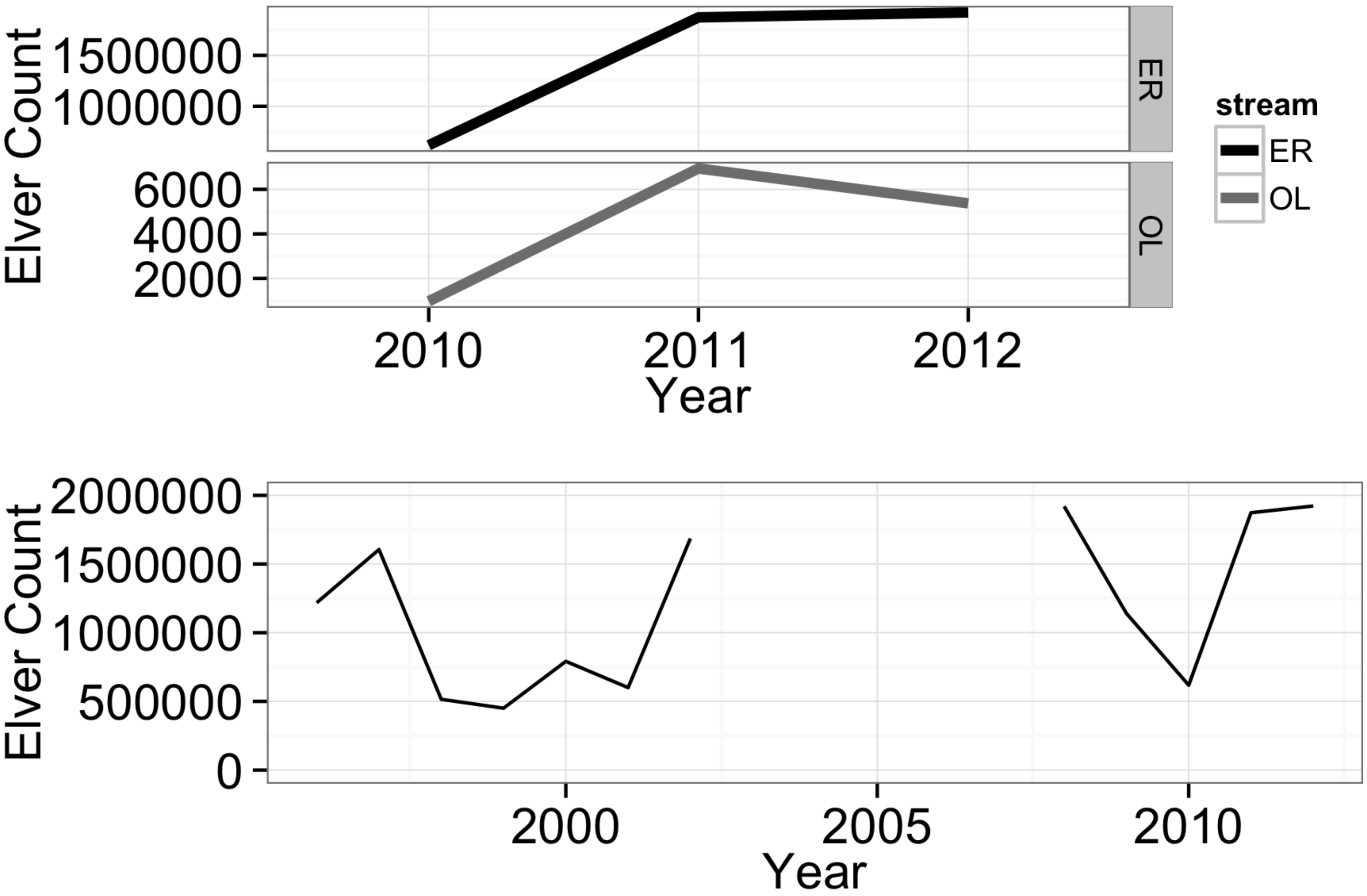

Figure 46. Total elver count from 2010 – 2012 of East River (ER), Chester, Nova Scotia and Oakland Stream (OL), Mahone Bay, Nova Scotia (top). Total elver count from 1996 – 2002 and 2008 – 2012 in East River, Chester, Nova Scotia (bottom).

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Appendix 1. Traditional eel trap sites with associated substrate type (%) across all four study years (2009 – 2012) in Oakland Lake, Mahone Bay, Nova Scotia.

Trap	Boulders	Cobble	Gravel	Sand	Detritus
1	0	0	0	0	1
2	0	1	0	0	0
3	0	1	0	0	0
4	0	0.1	0	0.9	0
5	0	0	0	1	0
6	0.8	0	0	0.2	0
7	0.8	0	0	0.2	0
8	0.8	0	0	0.2	0
9	0	0	0	0	1
10	0.3	0.3	0	0.4	0
11	0.2	0.8	0	0	0
12	0	0.8	0	0.2	0
13	0	0.8	0	0.2	0
14	0.3	0.7	0	0	0
15	0.4	0	0	0	0.6
16	0	0	0	0	1
17	0	0.1	0	0	0.9
18	0	0	0	0	1
19	0	1	0	0	0
20	0.9	0	0	0.1	0
21	0.9	0	0	0.1	0
22	1	0	0	0	0
23	0.4	0	0	0	0.6
24	0	0	0	0	1
25	0.4	0	0	0	0.6
26	0.9	0	0	0.1	0
27	0.7	0.3	0	0	0
28	0.7	0.3	0	0	0
29	0.1	0.6	0	0	0.3
30	0	0	0	0	1
31	0	0	0	0	1
32	0	0	0	0.3	0.7
33	0.5	0.5	0	0	0
34	0.5	0.5	0	0	0
35	0	0	0	0.2	0.8
36	0	1	0	0	0
37	0.5	0.5	0	0	0
38	0.5	0.5	0	0	0

39	0	0.5	0.5	0	0
40	0	0.5	0.5	0	0
41	0	0.5	0	0.5	0
42	0	0.3	0.1	0.5	0.1
43	0	0.5	0	0.5	0
44	0.3	0.1	0	0.6	0
45	0	0.9	0	0.1	0
46	0.2	0	0	0.8	0
47	0	0.9	0	0.1	0
48	0	0.4	0	0.6	0
49	0	0	0	0.1	0.9
50	0	0	0	0.2	0.8
51	0	0	0	0.2	0.8
52	0	0	0	0.2	0.8
53	0.2	0	0	0.4	0.4
54	0	0.8	0	0.2	0
55	0	0.8	0	0.2	0
56	0	0	0	0.8	0.2
57	0.8	0	0	0.2	0
58	0	1	0	0	0
59	0	0.3	0	0.7	0
60	0	0.3	0	0.7	0
61	0	0.6	0	0.4	0
62	0	0.6	0	0.4	0
63	0	0	0	0	1
64	0	0	0	0	1
65	0	0.8	0	0.2	0
66	0	0	0	0.4	0.6
67	0	0	0.2	0.8	0

Appendix 2. Traditional eel trap sites with associated with vegetation type across all four study years (2009 – 2012) in Oakland Lake, Mahone Bay, Nova Scotia.

Trap	Algae	Eelgrass	Lily Pads	Smartweed	Pickeralweed
1	0	0	0	0	0
1	1	0	0	0	0
2	1	1	0	0	0
3	1	0	0	0	0
3	1	1	0	0	0
4	1	0	0	0	0
5	1	0	0	0	0
6	1	0	0	1	0
7	1	0	1	0	1
8	1	0	1	0	1
9	0	0	1	1	0
9	1	0	1	0	1
10	1	0	0	0	0
11	1	0	0	0	0
12	1	0	0	1	0
13	1	0	0	1	0
14	1	0	1	0	0
15	0	0	0	1	0
15	1	1	1	0	0
16	1	1	1	0	1
17	1	1	1	0	0
18	0	0	0	0	0
18	1	0	1	0	0
19	0	0	0	0	1
19	1	0	1	0	0
20	0	0	0	0	0
21	0	0	0	0	0
22	0	0	0	0	0
22	1	0	1	0	0
23	1	0	0	1	0
24	0	0	0	0	0
24	1	0	0	0	0
25	1	0	1	0	0
26	0	0	0	0	0
26	1	0	0	0	0
27	0	1	0	0	0
27	1	0	1	0	0
28	1	0	1	0	0

29	1	0	1	1	0
30	0	0	0	0	0
30	1	0	0	0	0
31	1	0	0	0	0
32	0	0	1	0	0
33	0	0	1	0	0
33	1	0	0	0	0
34	1	0	0	0	0
35	1	1	1	0	0
36	0	0	0	0	1
36	1	0	1	0	0
37	1	0	0	0	0
37	1	0	1	0	0
38	1	0	1	0	0
39	1	0	0	0	0
39	1	1	0	0	0
40	1	1	0	0	0
41	0	1	0	0	0
41	1	1	0	0	0
42	1	0	0	0	0
43	1	1	1	0	0
44	0	1	0	0	0
44	1	0	0	0	0
45	1	0	1	0	0
46	1	0	0	0	0
46	1	0	1	0	1
47	0	1	0	0	0
47	1	0	0	1	0
48	0	0	0	0	0
48	1	0	0	0	0
49	0	0	1	0	0
49	1	0	1	0	0
50	1	0	1	0	1
51	1	0	1	0	1
52	0	0	0	1	0
52	1	0	1	0	1
53	1	0	0	0	0
53	1	1	0	0	0
54	1	0	0	0	0
55	0	0	1	0	0
55	1	0	0	0	0
56	1	0	0	0	0
56	1	0	1	0	0

57	1	0	0	0	0
57	1	1	1	0	0
58	1	0	0	0	0
58	1	0	1	0	0
59	0	0	0	0	0
59	1	0	1	0	0
60	0	0	0	0	0
60	1	0	1	0	0
61	1	0	0	0	0
62	1	0	0	0	0
63	1	0	0	0	0
64	1	0	0	0	0
65	1	0	1	0	0
66	1	0	0	0	0
67	1	0	0	0	0