A STUDY OF DARTER (PERCIDAE) ASSEMBLAGES IN SEVERAL TRIBUTARIES OF THE OTTAWA RIVER, QUÉBEC, CANADA

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ABSTRACT

The purpose of this study was to examine the habitat preference (or use), distribution and growth of darters (Channel Darter *Percina copelandi*, Logperch *Percina caprodes*, Fantail Darter *Etheostoma flabellare*, Tessellated Darter *Etheostoma olmstedi* and Johnny Darter *Etheostoma nigrum*) in tributaries of the Ottawa River, Québec, Canada. The Channel Darter's habitat can be characterised by coarse heterogeneous substrate with water velocities greater than 0.25 ms^{-1} in zones with low bank slopes. Its distribution is limited to five tributaries of the Ottawa River, downstream from the first physical barrier. The Logperch and Fantail Darter's habitats were similar to that of the Channel Darter, although the Fantail Darter was present in shallower waters. The Tessellated Darter was spatially partitioned from the others; the species seems to be a habitat generalist. The Johnny Darter was the least abundant darter and seems to prefer coarse heterogeneous substrate. The majority of growth in length was attained during the first year in all species. Growth rates were affected by the presence of parasites in the Channel Darter and Fantail Darter, non-parasitized individuals growing faster than parasitized individuals. Growth rates also differed among males and females in the Channel Darter, males growing faster than females.

Keywords: Age, Channel Darter, Distribution, Fantail Darter, Growth, Habitat partitioning, Habitat use, Johnny Darter, Logperch, Species at risk, Tessellated Darter

RÉSUMÉ

L'objectif de cette étude était d'examiner l'habitat, la distribution et la croissance des dards (Fouille-roche gris *Percina coplandi*, Fouille-roche zébré *Percina caprodes*, Dard barré *Etheostoma flabellare*, Raseux-de-terre gris *Etheostoma olmstedi* et Raseux-de-terre noir *Etheostoma nigrum*) dans des tributaires de la rivière des Outaouais au Québec, Canada. L'habitat du fouille-roche gris est caractérisé par un substrat grossier et hétérogène avec une vitesse de courant plus élevée que 0.25 ms^{-1} et par de petites pentes de berge. Sa distribution est limitée à cinq tributaires de la rivière des Outaouais, en aval des premières barrières physiques. L'habitat du fouille-roche zébré et du dard barré ressemble à celui du fouille-roche gris, sauf que le dard barré préfère des eaux peu profondes. Le raseux-de-terre gris était séparé des autres dards; l'espèce semble être généraliste. Le raseux-de-terre noir était le dard le moins abondant et semble préférer un substrat grossier et hétérogène. Toutes les espèces ont connu une croissance rapide durant leur première année. Le taux de croissance était affecté par la présence de parasites chez le fouille-roche gris et chez le dard barré, les espèces non-parasitées ayant une croissance plus rapide que les individus parasités. La croissance était aussi plus rapide chez les mâles que chez les femelles pour le fouille-roche gris.

Mots clés: Age, Croissance, Dard barré, Distribution, Espèce en péril, Fouille-roche gris, Fouill-roche zébré, Raseux-de-terre gris, Raseux-de-terre noir, Ségrégation d'habitat, Utilisation d'habitat

GENERAL INTRODUCTION

Human activities can have negative impacts on various ecosystems throughout the world, often resulting in dramatic changes in patterns of species composition, abundance and diversity (Faeth et al, 2005; Jenkins, 2003). The conservation of biodiversity has become an increasingly critical problem (McCusker et al., 2010) especially in running waters which encompass diverse and unique species, habitats, and ecosystems of great economic value (Angermeier and Winston, 1999). Over the past few decades, the alarming rate at which overall freshwater biodiversity has been declining suggests that freshwater ecosystems are more threatened than marine and terrestrial systems (Jenkins, 2003). Freshwater fish is one of the four freshwater taxonomic groups at the top of the IUCN Red List of Threatened Species; many species of fish are listed as rare, endangered, or threatened based on observed declines in population size or habitat loss (Hoffmann et al, 2010; Xenopoulos and Lodge, 2006). In North America alone, between 1989 and 2008, the number of freshwater fish species at risk almost doubled up to 40% of species (Magurran, 2009).

These declines in biodiversity and species richness can be attributed to several anthropogenic factors such as habitat loss and degradation, the spread of invasive species, overexploitation, and pollution (Jenkins, 2003; Magurran, 2009). In order to protect and manage freshwater fish assemblages, it is essential to identify which factors influence their distribution and abundance (Maloney and Weller, 2011; Pinto et al, 2009) Consequently, fish assemblage studies are now increasingly used to determine the relative importance of the abiotic and biotic factors in defining the structure, dynamics, and function of freshwater fish assemblages through space and time. This knowledge acquisition is useful in determining the best practices for the conservation of threatened freshwater fish species and their habitat.

Assemblages of freshwater fishes are determined by the interactions of numerous abiotic and biotic factors (Cottenie, 2005; Crow et al, 2010; Emmrich et al, 2011; Sargeant et al, 2011; Welborn et al, 1996). In ecology, an assemblage refers to a group of various species coexisting in a particular defined area. Abiotic factors such a substrate, water velocity and river widths tend to outweigh biotic factors within large riverine systems (Jackson et al., 2001). However, habitat partitioning has been documented at smaller spatial scales as a result of biotic factors such as interspecific competition and predation (Fausch et al., 1994; Herder & Freyhof, 2006; Jackson et al., 2001; McIntosh, 2000; Schluter, 2003; Schluter & McPhail, 1992; Townsend & Crowl, 1991; Young, 2004). The combination of abiotic and biotic factors within a river ecosystem affects assemblage patterns, influencing the abundance, richness, diversity, and composition of freshwater fish species.

Several studies have shown that freshwater fish demonstrate distinct preferences for different aquatic habitat variables, resulting in differences in fish assemblages (Baber et al, 2002; Eadie and Keast, 1984; Erõs et al, 2009; Gorman & Karr, 1978; Grossman et al., 1998; Rosenfield and Hatfield, 2006; Schlosser, 1982; Tonn and Magnuson, 1982). As fish species require different physical and hydrological conditions for spawning and survival throughout their development, these preferences can differ spatially and temporally (Langford et al, 2012, Rosenfield and Hatfield, 2006, Schlosser, 1982). Habitat types such as riffles, runs, and pools are characterised by differences in water velocity, depth, and turbulence, which results in differences in fish assemblages (Pinto et al, 2009). Several researchers have found water velocity, water depth, and dominant substrate type to be the main habitat variables that affect fish assemblages (e.g. Gorman & Karr, 1978; Pinto et al, 2009; Rifflart et al, 2009). Other studies have shown that other variables can also be important, such as refuge availability and proximity to the riparian zone (e.g. Richards et al, 1996; Rifflart et al, 2009). Aquatic plants provide habitat and shelter for fish and serve as important feeding areas (Gozlan et al., 1999, Heino, 2008). Water quality can also influences the structuring of fish assemblages. Water quality properties such as oxygen, pH, conductivity, and temperature have been shown to limit the occurrence and abundance of certain fish species (Kilgour and Barton, 1999). Lastly, the complexity of the habitat has been shown to be correlated with the diversity of the fish assemblage. Heterogeneous habitats can for example provide more refuge from harsh environmental conditions and predators than homogeneous habitats and can therefore support a higher diversity and abundance of fish (Gorman & Karr, 1978).

River characteristics are influenced by the landscape through which they flow, and landscape therefore indirectly affect fish assemblages (Maloney and Weller, 2011). Many rivers have been impaired by urbanization and agricultural practices (USEPA 2000, USEPA 2006, Maloney and Weller, 2011). These anthropogenic alterations of landscapes affect the structure and function of riverine systems (Paukert and Makinster, 2009; Waters, 1995). Consequences of land use activities include differences in sediment flux and organic matter inputs (Pimental et al, 1995), water pollution (Allan, 2004), and changes in water temperature. These factors can ultimately affect the distribution and composition of fish assemblages (Paukert and Makinster, 2009) and alter biodiversity (Hobbs and Huenneke, 1992, Hornung and Reynolds, 1995) as many fish species are sensitive to sediment pollution, requiring clean substrates during their life cycle (Sutherland et al, 2002).

Freshwater fish assemblages are also the result of biotic interactions (Welborn et al, 1996). Biotic interactions, such as predation and competition, can affect the growth, reproduction, and survival of a species (Gilliam et al, 1993; Grossman et al, 1998). For instance, interspecific competition for shared resources such as food and spawning sites, can lead to cascading consequences at the assemblage level (Wellborn et al. 1996). Dietary guilds have been shown to affect the distribution of fish species along a river or stream. Generalist fish species that feed on a wide range of invertebrates are expected to be distributed in upstream reaches while omnivores, herbivores, and piscivores are expected to be more abundant downstream (Schlosser, 1982; Vannote et al., 1980). Biotic interactions can also influence the microhabitat use of freshwater fishes (McIntosh, 2000; Jackson et al., 2001). Several studies have shown significant effects of competition on habitat selection and in turn on the assemblage patterns of invertebrates (Beckerman, 2000; Kohler, 1992), and fish (Langeland et al. 1991; Young, 2004) in streams (Nakano et al. 1999; Rodrıguez 1995; Rosenzweig 1987). This competition is condition-specific, depending for example upon the availability of resources within a stream (Dunson and Travis, 1991; Taniguchi, 2000). Competition between fish is often a result of a size asymmetry between species (Young, 2004). Dominant species are generally larger and displace subordinate species from a mutually preferred habitat (Connell 1983; Diamond 1978; Hairston 1980; Jaeger 1971; Morse 1974; Pacala and Roughgarden 1982; Robinson and Terborgh 1995; Schoener 1983, Thompson and Fox, 1993). Predation can also have an effect on assemblage patterns. Piscivorous predatory fish for example, have been shown to have strong negative effect on cyprinid distribution in an assemblage (Chapleau et al, 1997). Predation on eggs and juveniles can affect spawning site selection, limiting species distributions (Marsh-Matthews 2000; Mills et al., 2004). Knowledge of species interactions and how they affect assemblage structures are critical for the development of predictive models in community organization.

Darters (Percidae: Estheostomatini) are a diverse group of cryptically-coloured bottom-dwelling fish, encompassing over 200 species. Several of these species are considered to be at risk (Jelks et al, 2008) mainly as a result of the fragmentation, destruction and pollution of freshwater habitats (Allan and Flecker, 1993). Most darters are small benthic fish rarely exceeding 8.0 cm in total length (Pratt and Lauer, 2013; Pflieger 1997; Trautman 1981), are insectivores (Alford and Beckett, 2007; French and Jude, 2001; Kissick, 1987; van Snik Gray et al, 1997) and are habitat specialists (Gorman and Karr, 1978; Roberts and Angermeier, 2007; Stauffer et al, 1996; van Snik Gray and Stauffer, 1999; White and Aspinwall, 1984). In general, substrate type, water velocity and water depth are important determinants of both darter habitat use and partitioning (Chipps et al, 1994; Kessler et al, 1995; Paine et al, 1982; Pratt and Lauer, 2013; Schlosser and Toth, 1984; Stauffer et al, 1996; Welsh and Perry, 1998). In Canada, the lack of information on the habitat and biology of several darter species limits the recovery potential of these species.

The channel darter (*Percina copelandi*) has been designated as Threatened in Canada by the Committee on the Status of Endangered Wildlife since 1993 (COSEWIC) and is listed as protected under schedule 1 (part 3: endangered species) of the federal Species at Risk Act (SARA). Due to a lack of information, the recovery potential of the species remains uncertain. The purpose of this study is to examine the habitat use, habitat partitioning, distribution and growth of a darter assemblage coexisting in the Ottawa River watershed in Québec. More specifically, five species of darters from two genera, including the channel darter, are the focus of this study (Figure 1).

GENERAL METHODOLOGY

Study Area. – The study area is located in Southern Québec, Canada (45°50'84"N, 75°64'34"W, WGS 84), and is comprised of the Ottawa River catchment (mean discharge: 1937 m^3s^{-1}). The Ottawa River basin stretches from its source at Lake Capimitchigama, in the Laurentian Mountains of central Québec (47.72 N, -75.67 W), and flows west of Lake Timiskaming (47.38 N, -79.50 W) for approximately 1,271 km in length. It is bordered on either side by the provinces of Ontario and Québec, draining a total area of about 146,300 km^2. Its tributaries originate in the Canadian Shield where they have clear waters and coarse substrate (Reyjol et al, 2008). As the tributaries cross the alluvial plain to reach the Ottawa River, water transparency tends to decline (Reyjol et al, 2008). The studied tributaries are surrounded by several municipalities in Québec such as Calumet, Arundel, Huberdeau, Fasset, Notre-Dame du Bonsecours, Montebello, Plaissance, Saint-Sixte, Saint-André Avellin, Ripon, Lochaber, Thurso, Masson-Angers, Buckingham, Val-des-Bois, Gatineau, Chelsea, Wakefield, La Pêche, Luskville, and Quyon. Consequently, there exists a great range of landscape types surrounding the rivers, such as forests and protected areas, as well as landscapes altered due to anthropogenic activities such as housing developments, extensive riverbank reinforcement, as well as agricultural practices. The climate of the region is temperate, with cold winters and hot summers.

Data Collection. – Fish sampling was performed with a portable electrofishing unit (LR-24 F00512 Smith-Root, Inc., Vancouver, WA, USA) and a large dip net. Electric fishing was conducted on foot along river banks, in shallow water (< 0.8 m) as well as from a canoe depending on the accessibility of the shallow edges of the rivers. The working voltage of the electrofishing unit ranged from 250-500 V depending on water conductivity. Backpack electrofishing has proven to be an effective mean of capturing small, benthic and cryptic fish species (Copp, 1989; Cowx et al, 2001; Jurajda et al, 2009) such as darters (Boucher et al, 2009; Kessler and Thorps, 1993; Pratt and Lauer, 2013). In addition, darters are mostly sedentary, especially during non-reproductive periods (Winn, 1958). Lastly, as the species of interest in this study are all from the same family, are of similar size and exhibit similar behavior, sampling bias between species is minimal. Overall, electric fishing is a cost-efficient method that minimizes the destruction of habitat and mortality of fish (Persat and Coop, 1990).

Direct observations (snorkeling) have been used to study habitat use and partitioning in darters (Chipps et al, 1994; Stauffer et al, 1996; Welsh and Perry, 1998). This method requires good water visibility, a requirement which was not met for the majority of sites sampled within the tributaries of this study. Seines have also been used to sample darters (Paine et al, 1982), although this method seems to be more efficient in smaller streams (Karr, 1981) and when sampling a small number of stations. Electrofishing allows for an efficient sampling of undercut banks and under large woody debris, where fish could escape standard seines (Karr, 1981).

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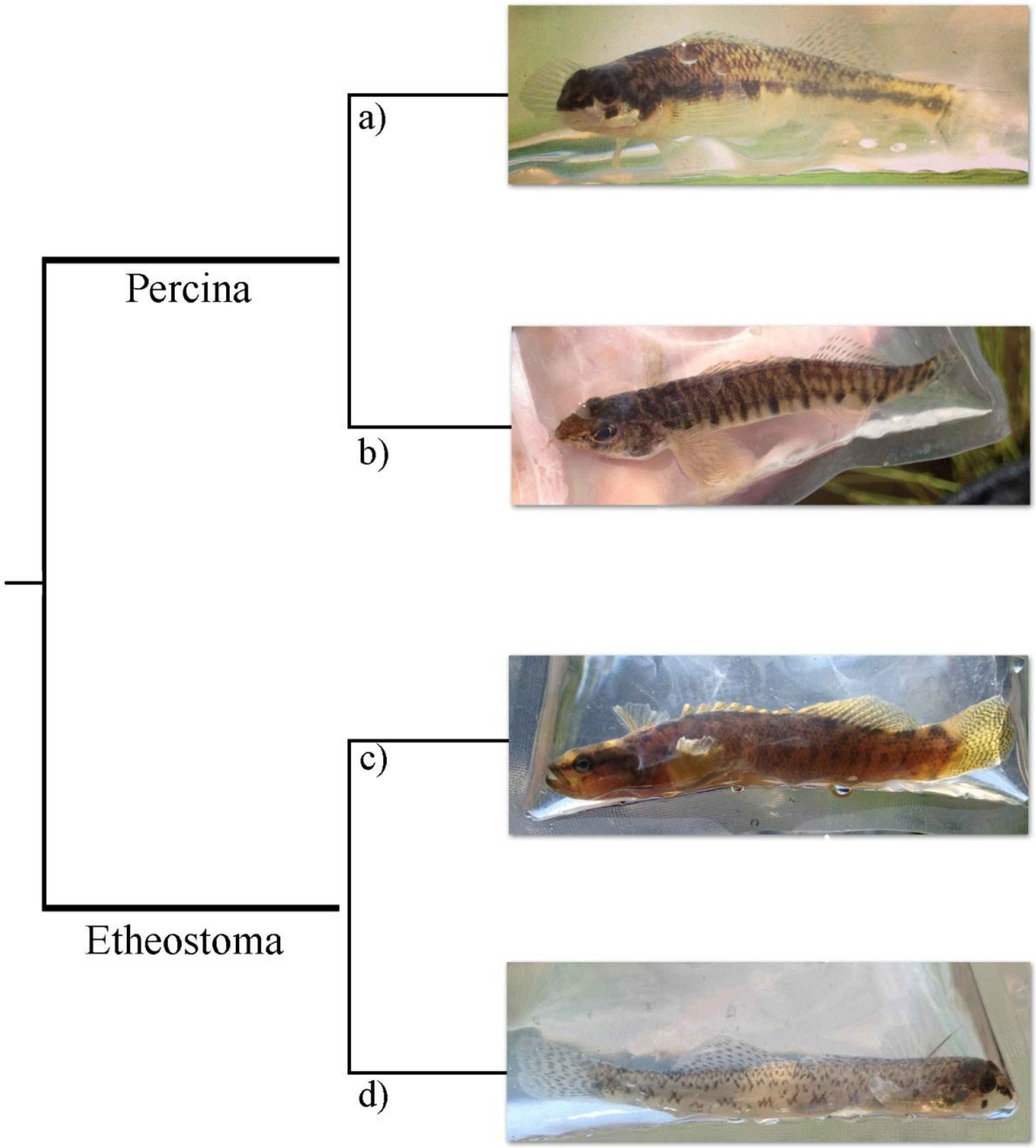

Figure 1. Darters captured within several tributaries of the Ottawa River included the (a) Channel Darter *Percina copelandi*, (b) Logperch *Percina caprodes*, (c) Fantail Darter *Etheostoma flabellare* and (d) Tessellated and Johnny Darters *Etheostoma olmstedi* and *nigrum*.

CHAPTER 1: HABITAT USE AND PARTITIONING AMONG FIVE SPECIES OF DARTERS (PERCIDAE) IN FOUR TRIBUTARIES OF THE OTTAWA RIVER (QUÉBEC, CANADA).

ABSTRACT

Habitat use and partitioning was studied for five darter species (Channel Darter *Percina copelandi*, Logperch, *Percina caprodes*, Fantail Darter *Etheostoma flabellare*, Tessellated Darter *Etheostoma olmstedi* and Johnny Darter *Etheostoma nigrum*) in four tributaries of the Ottawa River in Québec, Canada. Analyses of niche breadth and overlap indicated that species differed in their degree of specialization in habitat use; the Tessellated Darter was a habitat generalist whereas the other four species tended towards habitat specialization. Logistic regressions and a canonical correspondence analysis (CCA) were used to determine which habitat variables were important in both predicting the presence of species as well as in segregating them. Habitat use varied primarily with substrate type and heterogeneity, water velocity, the distance from the Ottawa River and bank slope. No clear segregation was present between *Percina* and *Etheostoma* genera. The presence of the Channel Darter, the Logperch and the Fantail Darter were highly correlated, the species demonstrating similar preferences for habitat variables. The relative abundance of the Johnny Darter was less than those observed for the other species, suggesting that the species may inhabit smaller rivers or streams than those studied. The Channel Darter was the least widely distributed species, its upstream distribution in rivers being associated with the presence of impassable physical barriers.

Keywords: Canonical correspondence analysis (CCA), Distribution, *Etheostoma*, fish, logistic regression, niche, *Percina*, use-availability

RÉSUMÉ

L'utilisation et la partition de l'habitat ont été étudiées pour cinq espèces de dards (Fouille-roche gris *Percina coplandi*, Fouille-roche zébré *Percina caprodes*, Dard barré *Etheostoma flabellare*, Raseux-de-terre gris *Etheostoma olmstedi* et Raseux-de-terre noir *Etheostoma nigrum*) dans quatre tributaires québécois de la rivière des Outaouais, Canada. Des analyses d'ampleur et chevauchement de niches ont indiqué que les espèces diffèrent dans leur degré de spécialisation d'utilisation d'habitat; le raseux-de-terre gris est un généraliste alors que les quatre autres espèces ont tendance à être des spécialistes.. Des régressions logistiques et une analyse canonique des correspondances (ACC) ont été utilisées pour déterminer les variables d'habitat qui sont importantes pour prédire la présence et la partition d'habitat des espèces. L'utilisation d'habitat variait principalement selon les types et l'hétérogénéité de substrat, la vitesse du courant, la distance de la rivière des Outaouais et la pente de la berge. Il n'y avait pas de séparation claire entre les genres *Percina* et *Etheostoma*. La présence du fouille-roche gris, fouille-roche zébré et du dard barré étaient fortement corrélés, les espèces démontrant des préférences similaires d'habitat. L'abondance relative du raseux-de-terre noir était plus faible que pour les autres espèces, ce qui suggère que l'espèce habite peut-être de plus petits cours d'eau que ceux étudiés. Le fouille-roche gris était l'espèce la moins grandement répartie sur le territoire sa distribution en amont des rivières étant limitée par la présence de barrières physiques.

Mots clés: Analyse canonique des correspondences (ACC), Distribution, *Etheostoma*, niche, *Percina*, poisson, régression logistique, utilisation-disponibilité

INTRODUCTION

Human activity can have negative impacts on various ecosystems throughout the world, often resulting in changes in patterns of species composition, abundance and diversity (Jenkins, 2003). The alarming rate at which freshwater biodiversity has been declining suggests that freshwater ecosystems are among the most threatened environments in the world (Jenkins, 2003; Malmqvist and Rundle, 2002; Richter et al, 1997). Darters (Percidae: Etheostomatini) are a speciose group of freshwater fish encompassing over 200 species, many of which are considered imperiled (Jelks et al, 2008). Although darters are an important component of North America's freshwater fish fauna, inhabiting various types of microhabitats (Moyle and Cech, 1988; Winn, 1958), few studies focus on these species as they are not economically important. Darters, however, play various roles within the trophic organization of freshwater communities as they consume a wide variety of benthic invertebrates (Alford and Beckett, 2007), are hosts to freshwater mussels larvae (Jones et al, 2004; Yeager and Saylor, 1995; Zanatta and Wilson, 2011) and are important prey to fish that are of interest to sport and commercial fishing practices (Fullhart et al, 2002; Kapuscinski et al, 2012). Furthermore, darters can be good indicators of stream diversity and integrity (Pratt and Lauer, 2013) as many species are sensitive to habitat alterations. Consequently, studies on darter assemblages are necessary in order to better understand the habitat requirements of these species and help prioritize river monitoring efforts and management decisions.

Niche use results from the combination of environmental factors favored by a species within a particular biotic setting (Crow et al, 2010). Several studies have shown that freshwater fish demonstrate distinct preferences for different habitats, resulting in differences in fish assemblages (Erõs et al, 2009; Gorman and Karr, 1978; Grossman and Freemand, 1998;

Rosenfeld and Hatfield, 2006; Schlosser and Toth, 1984; Tonn and Magnuson, 1982). Factors such as current velocity, substrate type and aquatic vegetation have been shown to be important determinants of habitat use. Local and landscape variables, such as bank slope and land use, can also affect the assemblage and distribution of fish (Paukert and Makinster, 2009; Waters, 1995). Anthropogenic alterations of the landscape bordering running water, resulting from urbanization and agricultural practices, are thought to negatively alter riverine systems by increasing sediment inputs, altering substrates, and increasing water pollution (Allan, 2004; Pimental et al, 1995).

While abiotic factors tend to be important in limiting the distributions of species throughout riverine systems, biotic factors affect the success of species at smaller spatial scales and can lead to microhabitat and resource partitioning. Many darter species occur sympatrically in riverine systems, requiring them to segregate along a resource axis to avoid intense interspecific competition (Greenberg, 1991). Species partitioning can occur by habitat (Pratt and Lauer, 2013; Schlosser and Toth, 1984; Stauffer et al, 1996; Welsh and Perry, 1998), by feeding behaviour (van Snik Gray et al, 1997) and by time of activity (Smart and Gee, 1979). In general, large ecological differences have been found between species in the genera *Etheostoma* and species in the genera *Percina* (Greenberg, 1991; Stauffer et al, 1996; Welsh and Perry, 1998).

Although a number of studies have been directed on microhabitat use and resource partitioning in darters (Chipps et al, 1994; Kessler and Thorp, 1993; Paine et al, 1982; Pratt and Lauer, 2013; Schlosser and Toth, 1984; Stauffer et al, 1996; Welsh and Perry, 1998), information on such patterns is limited for the populations located in Southern Québec. The primary purpose of this study was to describe habitat use for five species of darters found in four tributaries of the Ottawa River, Québec, Canada. More specifically the objectives were to (1) characterize each darter`s habitat use, (2) determine which environmental variables are important in predicting the presence of the species, and (3) examine habitat partitioning among the darter assemblage. Determining which factors are important in defining the structure and dynamics of these darter assemblages, through time and space, will enhance our understanding of how they will be affected by anthropogenic stressors and can be useful when making decisions on their protection and management.

MATERIALS AND METHODS

Study Area and Species. – The study area is located in Southern Québec, Canada, and comprises of four tributaries of the Ottawa River: Saumon River (previously Kinonge River), Petite-Nation River, Blanche River (Thurso) and Blanche River (Gatineau). The four tributaries contain a diverse fish fauna including five darter species; the Channel Darter (*Percina copelandi*), the Common Logperch (*Percina caprodes*), the Fantail Darter (*Etheostoma flabellare*), the Tessellated Darter (*Etheostoma olmstedi*) and the Johnny Darter (*Etheostoma nigrum*). The Channel Darter is currently a threatened species in Canada (COSEWIC, 2002), it`s decline being attributed to increased siltation and impoundment of rivers, resulting in loss of clear-water habitat (Boucher et al, 2009; Reid and Mandrak, 2008).

Fish Sampling. – Data were collected using a modified version of point abundance sampling by electrofishing (PASE) technique (Levert, 2013). PASE is commonly used in freshwater research as it provides accurate estimates of a fish assemblage, it is minimally destructive to the habitat, and it is cost-efficient as well as labour-efficient (Persat and Copp, 1990). In addition, PASE provides a standardized method of collecting multiple small discrete samples, rendering it an ideal method to sample a diversity of habitats and permitting comparisons within and between these habitats on a spatial and temporal scale (Copp, 2010; Persat and Copp, 1990).

Rivers were subdivided into sectors of 100 m, starting at their confluence with the Ottawa River and moving upstream to the first physical barrier (i.e. falls or dam). In accordance with the PASE method, about 100-300 m of intact un-fished area was left between each 100 m fished reach. In each reach, four stations were randomly selected and sampled. Stations varied in their distance from the start of the reach (0-90 m), their depth within the water column (0.1-0.8 m) and their sampled area (range: 1- 30 m^2, mean: 5.2 m^2, standard deviation: 3.3). Sampling effort, at each station, was determined as a function of (1) homogeneous habitat from the sampler's perspective and (2) accessibility, with the objective to maximize the total sampled area. Sampling was done using a portable electric fishing device (LR-24 F00512 Smith-Root, Inc., Vancouver, WA, USA) and a fine-mesh dip net. Each fish shocked and caught in a station was identified to species, measured, and sorted according to sexual maturity before being returned to the water. Specimens which were difficult to identify were brought back to the laboratory for confirmation with the use of a microscope. Data collection occurred in spring (June), summer (July-August) and fall (October-November) in order to observe temporal variations in habitat use.

Environmental Variables. – The general habitat characteristics were quantified for each sampled station, such as average water depth (m), average distance to bank (m) and the presence of woody debris (absent=0, present=1). Primary substrate type was classified as; (1) organic matter, (2) silt < 0.125 mm, (3) sand 0.125-5 mm, (4) gravel 5-40 mm, (5) pebble 40-80 mm, (6) cobble 80-250 mm, (7) boulder 250-500 mm, (8) big boulder >500 mm, (9) or bedrock >1000 mm (Boudreault, 1984). From this classification, an index of mean substrate particle size was established using the modified Wentworth classification (Cummins, 1962; Leeder, 1982). Primary substrate was treated as an ordinal variable (class) for some of the analyses, and as a continuous variables (mean particle size) for others. Substrate heterogeneity was classified as; (1) one substrate, (2) two substrate where one dominates, (3) two equally dominant substrates, (4) three unequally dominant substrates and (5) three equally dominant substrates or more than three substrates. Vegetative cover underwater as well as periphyton cover on substrate or vegetation were classified as either; (1) 0%, (2) 0-25%, (3) 25-50%, (4) 50-70%, (5) 75-100%. Water velocity (ms^{-1}; Global water Flo Probe, Vel001) and water temperature (°C; Waterproof Combo PH/EC Tester, HI 98129) were also measured. Bank slope was calculated as the ratio of water depth over the distance from the bank at each station. Lastly, land use was assessed for each reach using a combination of ArcGIS 10 (ESRI, Redlands, CA), Google Maps and Canadian Topographic Maps (Natural Resource Canada). Primary land use was classified as; (1) forested land, (2) rangeland, (3) wetland, (4) agricultural land or (5) urban land.

Statistical Analyses. – Although darter density was measured quantitatively (i.e. number of individuals per area sampled), binary presence-absence data was used in all statistical analyses To determine each species' preference for the different environmental variable, usage-availability ratios were first observed visually and then usage and availability ranks were evaluated using the method proposed by Johnson (1980). This method allows the results to be comparable with those of other studies, regardless of the array of components deemed available to the animals by the investigator (Johnson, 1980). First, each environmental variable (x) was subdivided into different classes (j); for example bank slope's first class consists of the range 0-10 %. For each class j of the variable x, the usage percentage (Eq. 1) and availability percentage (Eq. 2) was calculated, ranked, and the difference between the two was determined.

$$(1) \quad Usage_j = \frac{\#\ stations\ of\ class\ j\ frequented\ by\ species}{total\ \#\ of\ stations\ frequented\ by\ species} x100$$

$$(2) \quad Availability_j = \frac{\#\ of\ stations\ of\ class\ j}{total\ \#\ of\ stations} x100$$

For each environmental variable, a class is favored by a species if its usage rank is larger than its availability rank, and avoided if the inverse is true (Johnson, 1980). Classes for which the usage and availability percentages were less than 5% were not evaluated (Levert, 2013).

To further quantify the degree of specialization of each species for an environmental variable, a modified version of Hurlbert's standardized niche breadth (B_x) was measured by first calculating Levin's measure of niche breath (Eq. 3) and standardizing it (Eq. 4), where *B'* is Levin's measure of niche breath, p_j is the proportion of stations in which a species was utilizing class *j* of the environmental variable *x* (i.e. $\text{Usage}_j/100$), a_j is the proportion of the total available stations in which the class *j* was found (i.e. $\text{Availability}_j/100$), and a_{min} is the smallest available proportion of all classes belonging to *x* (Hurlbert, 1978).

$$(3) \quad B' = \frac{1}{\Sigma(p_j^2/a_j)}$$

$$(4) \quad B_x = \frac{B' - a_{min}}{1 - a_{min}}$$

Finally, niche overlap (*O*) of all habitat variables between two species (*m* and *k*) was quantified using Pianka's index (Eq. 5), where p_{jm} and p_{jk} are the proportions resource *j* is of the total resources used by species *m* and *k* respectively (Pianka, 1974).

$$(5) \quad \mathrm{O_{mk}} = \frac{\Sigma_i^n \mathrm{p_{jm} p_{jk}}}{\sqrt{\Sigma_i^n \mathrm{p_{jm}^2} \Sigma_i^n \mathrm{p_{jk}^2}}}$$

Niche breadth and niche overlap are expressed on a scale of 0 to 1.0, where high niche breadth values are indicative of habitat generalization for resource *x* and low niche breadth values are indicative of habitat specialization (Hurlbert, 1978). Generalist species are able to thrive is a variety of environmental conditions, allowing them to exploit whichever habitats are readily available, whereas specialist species are only able to thrive in a narrow range of environmental conditions (Morris, 1996). High niche overlap is indicative that both species utilize resources in proportion to their availability and low niche overlap is indicative that both species share no resources (Pianka, 1974).

Logistic regression models were used to identify the variables associated with each species presence, allowing for a quantitative comparison of niche use. The logistic regression model is an approach used when the response variable is binary, transforming the outcome probability (i.e. probability of presence being 1) onto the logit scale (Eq. 6).

$$(6) \quad logit(p) = \ln\left[\frac{p}{(1-p)}\right]$$

I examined the relationships between each darter's presence and the following environmental variables: (1) water depth, (2) mean primary substrate size (continuous variable), (3) substrate heterogeneity, (4) mean vegetative cover, (5) mean periphyton cover, (6) presence of woody debris, (7) water velocity, (8) bank slope, (9) the distance from the confluence with the Ottawa River (inversely proportional to the distance to the first physical barrier) and (10) land use. In addition, as the sampled area within a station could affect the probability of a species being captured, it was also analysed in the model (11). As interactions between the environmental variables and both river and period could provide information on how the predictive variables differ both in space and time, they were included into the full model (Eq. 7). Various models were created using backward, forward and stepwise selection. For each species, an optimal model containing the predictive variables of its presence was selected by minimizing Akaike Information Criterion (AIC) and minimizing the complexity of the model (number of variables). The McFadden's pseudo R-squared values were calculated for the final models. Using the final logistic regression equations, the expected probability of presence (i.e. Y=1) was computed for a given value of each environmental variable and plotted as a measure of effect size (Eq. 7). Curves were derived for an environmental variable by holding all other variables in the models constant at their average values.

$$(7) \quad p = \frac{1}{1+\exp(-logit)}$$

To analyze other aspects of the darter assemblage, multivariate statistical methods were also used. A canonical correspondence analysis (CCA) was used to create an ordination based on the species presence data which could be related to the habitat variables at stations in which at least one species was present (N=369). This is a direct gradient analysis, relating a set of species to their environment, therefore allowing for an independent assessment of the importance of the habitat variables in segregating the five darter species (ter Braak, 1986). To account for multicollinearity, a correlation matrix was created for the set of environmental variables. Using a Pearson product moment correlation (r) threshold of 0.4, redundant variables were removed to form a reduced dataset. CCA was used on the full data set of environmental variables as well as the reduced data set to observe whether explanatory power was lost.

All generalized linear models and multivariate statistics were performed using R 3.0.2 (R Development Core Team, Vienna Austria). The logistic regressions were performed using the *pscl* package (Jackmand, 2012) and the CCA was carried out using the *vegan* package (Oksanen et al, 2013).

Darter Inventory. – An inventory of the shoreline distribution of darters within several other tributaries of the Ottawa River was also conducted. Tributaries were chosen using Canadian Topographic Maps (Natural Resources Canada, 1998) and included several streams and rivers from Rouge River in the East to Quyon River in the West. Darters were collected using the backpack electrofishing unit. Consequently sampling was limited to waters less than 0.8 m. Site selection and sampling effort varied (area range 2.5 - 60 m^2 per site; average 15.6 m^2 per site) from one tributary to the next as a function of (1) tributary size, (2) past records of capture, (3) accessibility (e.g. obstacles, water depth, bank slope) and (4) with the objective to cover as much territory as possible. The sites included areas upstream of the four rivers which had previously been sampled in 2011 and 2012, as well as smaller tributaries of these rivers. The general habitat characteristics were again quantified for each site, and each captured fish was measured, identified to species and returned to the water.

To get a measure of the predictive power of the five logistic regression models, the expected and observed probabilities of the presence of each species were analyzed using the inventory data. The expected probability of presence were calculated using generalized logistic regression models, in which each coefficient was averaged for the effect of river and period when relevant. The probability was then calculated for each site using the measured environmental variables. Lastly, for the variable with the greatest effect size for each species, the mean expected probability was calculated for each class of that variable and compared to the mean observed usage.

RESULTS

Fish Capture. – A total of 2018 fish were collected during 70 days of sampling in 2011 and 2012, representing 9 families and 32 species (Table 1). Of these, 1064 belong to Percidae, 1027 being darters. Non-darter species that had high abundances among all sites, in decreasing order, included the Pumpkinseed (*Lepomis gibbosus*), Bluntnose Minnow (*Pimephales notatus*), Longnose Dace (*Rhinichthys cataractae*), and Smallmouth Bass (*Micropterus dolomieu*). No evidence of darter spawning readiness was observed; no release of eggs or milt under slight pressure of the abdomen. Sampling was done mainly in the pre- and post-spawning period (Levert, 2013). Although sampling with the portable electrofisher allowed the capture of various lengths of darters (range 32 – 77 mm), no young-of-the-year were collected.

Channel Darters, Logperches, Fantail Darters and Tessellated Darters were collected in all four tributaries, their highest abundance being in Saumon River (Table 2). The Johnny Darter, which had the lowest abundance (N=40), was not collected from Petite-Nation River. Darters were caught in 35% of stations, within 119 reaches. Among those, station-level darter abundances ranged between 1 and 17 individuals, with a mean of 3 individuals per station. The five darters species where not found simultaneously in any of the stations. Among all rivers, the presence of the Channel Darter was highly positively correlated with that of the Fantail Darter and the Logperch (Table 3), occurring in 46% and 39% of the same stations respectively. The presence of the three species was also positively correlated with that of the Johnny Darter, even though the species was not common. The presence of the tessellated darter was negatively correlated with the four other species, especially the Fantail Darter. These associations were similar within all rivers (Appendix, Table A1).

Habitat Availability. – Riffles, runs and pools were present in all four tributaries, riffle-like habitats typically located at the base of waterfalls, except for Saumon River. Station-level habitat characteristics varied within and among stations (Appendix A, Table A2). The comparison of habitat use and availability demonstrated that the Channel Darter, Logperch and Fantail Darter preferred habitats were characterised by medium to large substrate (sand - boulder), high substrate heterogeneity, water velocities greater than 0.25 ms^{-1} and small bank slopes (Appendix A, Tables A3-A5). The Fantail Darter's preferred habitat is also characterised by shallow water. The Tessellated Darter's preferred habitat is characterised by smaller substrate (sand and gravel), high substrate heterogeneity and bank slopes greater than 10% (Appendix A, Table A6). Finally, the Johnny Darter's preferred habitat is characterised by sand and gravel substrates, moderate substrate heterogeneity, small vegetative cover, water velocities greater than 1.0 ms^{-2} and bank slopes greater than 20% (Appendix A, Tables A7).

The Channel Darter and Fantail Darter demonstrated low niche breadth values ($B_j < 0.6$) for primary substrate, substrate heterogeneity, water velocity and bank slope (Table 4) indicating that they are specific to particular habitats in regards to these variables. Similarly the Logperch had low niche breadth values in regards to those same variables except for bank slope. The Johnny Darter had low niche breadth for primary substrate, periphyton cover and water velocity. The Tessellated Darter appears to be a habitat generalist, having high niche breadth values for most variables. Pianka's indexes demonstrated that all species had a certain degree of niche overlap (Table 5). Niche overlap was highest ($O > 0.80$) for the Channel Darter, Logperch and Fantail Darter. There was also a high overlap of the Johnny Darter's niche with that of the Channel Darter, Logperch and Tessellated Darter.

Logistic Regression. – The combination of habitat variables retained in the models differed for each of the five species (Table 5, Appendix A; Tables A8-A12). In the case of the Channel Darter, the model included three significant predictive variables of its presence (Eq. 8); substrate heterogeneity ($ß_7$ = 0.42, *P*-value <0.001), bank slope ($ß_8$ = -0.06, *P*-value <0.001), and sampled area ($ß_{11}$ = 0.18, *P*-value <0.001). There was also a significant interaction between water velocity and river (χ^2 = 18.36, *P*-value <0.001). Water velocity seems to be a predictor of Channel Darter presence in all rivers but the Saumon River (Figure 3c). The McFadden pseudo-R^2 values indicated that 40% of the variation in the presence of the Channel Darter is explained by the model.

$$(8)\ Presence\ \mathrm{P. copelandi} = -3.95 + (0.42 * heterogeneity) + (0.71 * velocity) - (0.06 * slope) + (0.18 * area) - (0.33 * BlancheThurso) + (0.09 * PetiteNation) + (0.63 * Saumon) + (3.12 * BlancheThurso{:}velocity) + (1.50 * PetiteNation{:}velocity) - (0.86 * Saumon{:}velocity)$$

In the case of the Logperch, the model included three significant predictive variables of its presence (Eq. 9); primary substrate ($ß_2$ = 0.01, *P*-value = 0.004), water velocity ($ß_7$ = 0.62, *P*-value = 0.005) and sampled area ($ß_{11}$ = 0.18, *P*-value <0.001). The magnitude of the effect of primary substrate varied from one river to the next (χ^2=11.57, *P*-value = 0.009), the effect being the greatest in Saumon River and nearly no effect being present in Blanche River (Gatineau) (Figure 4b). The McFadden pseudo-R^2 values indicated that 20% of the variation in the presence of the Logperch is explained by the model.

$$(9)\ Presence\ \mathrm{P. caprodes} = -7.63 + (0.01 * Substrate) + (0.62 * velocity) + (0.18 * area) + (3.68 * BlancheThurso) + (3.90 * PetiteNation) + (4.29 * Saumon) - (0.01 * PetiteNation{:}substrate) - (0.01 * Saumon{:}substrate)$$

The Fantail Darter`s model included five significant predictive variables of its presence (Eq. 10); water depth ($ß_1$ = -3.96, *P*-value <0.001), substrate heterogeneity ($ß_3$ = 0.68, *P*-value

<0.001), periphyton cover ($ß_6$ = 0.03, *P*-value <0.001), water velocity ($ß_7$ = 1.03, *P*-value <0.001), and sampled area ($ß_{11}$ = 0.12, *P*-value <0.001) (Figure 5 a-d). The McFadden pseudo-R^2 values indicated that 46% of the variation in the presence of the Fantail Darter is explained by the model.

$$(10) \quad Presence\ \mathrm{E.flabellare} = -4.81 - (3.96 * depth) + (0.68 * \mathrm{heterogeneity}) + (0.03 * \mathrm{periphyton}) + (1.03 * \mathrm{velocity}) + (0.12 * \mathrm{area}) - (0.53 * \mathrm{BlancheThurso}) - (1.02 * \mathrm{PetiteNation}) + (1.39 * \mathrm{Saumon})$$

In the case of the Tessellated Darter, the model included four significant predictive variables of its presence (Eq. 11); water depth ($ß_1$ = -1.22, *P*-value = 0.029) , the presence of woody debris ($ß_6$ = 0.710, *P*-value <0.001), water velocity ($ß_7$ = -2.04, *P*-value <0.001) and the distance from the Ottawa River ($ß_9$ = -0.05, *P*-value = 0.054).The magnitude of the effect of the distance from the Ottawa River varied from one river to the next, the relationship being negative in all rivers but Blanche River (Thurso) (Figure 6d). There were also significant interactions between land use and river (χ^2 = 25.51, *P*-value <0.001), land use being a predictor of Tessellated Darter presence in Blanche River (Gatineau), Petite-Nation River and Saumon River. The McFadden pseudo-R^2 values indicated that 13% of the variation in the presence of the Tessellated Darter is explained by the model.

$$(11) \quad Presence\ \mathrm{E.olmstedi} = -0.34 - (1.22 * depth) + (0.71 * woodydebris) - (2.04 * velocity) - (0.05 * distance) - (0.04 * landuse) - (1.28 * BlancheThurso) - (1.75 * PetiteNation) + (2.06 * Saumon) + (0.18 * BlancheThurso{:}\,landuse) + (0.35 * PetiteNation{:}\,landuse) - (0.61 * Saumon{:}\,landuse) + (0.11 * BlancheThurso{:}\,distance) - (0.06 * PetiteNation{:}\,distance) - (0.30 * Saumon{:}\,distance)$$

Finally, in the case of the Johnny Darter, the model included two significant predictive variables of its presence (Eq. 12); substrate size ($ß_2$ = -0.020, *P*-value = 0.0294) and substrate heterogeneity ($ß_3$ = -0.982, P-value = 0.0018). The magnitude of the effect of both substrate size and substrate heterogeneity varied from one period to the next (χ^2 = 15.74, P-value = <0.001, χ^2 = 4.67, P-value = <0.096). The effect of primary substrate on the probability of the Johnny Darter being present was much greater than the effect of substrate heterogeneity or woody debris (Figure 7a-c). There was also significant interactions between the presence of woody debris and period (χ^2 = 6.26, P-value = 0.04). The probability of Johnny Darters being present increased with the presence of woody debris, especially in period 2 (summer). The McFadden pseudo-R^2 values indicated that 27% of the variation in the presence of the Tessellated Darter is explained by the model.

$$(12) \quad Presence\ \mathrm{E.\,nigrum} = -6.56 - (0.02 * substrate) + (0.98 * heterogeneity) + (0.90 * woodydebris) + (1.59 * BlancheThurso) - (17.31 * PetiteNation) + (1.45 * Saumon) - (1.39 * Summer) - (3.32 * Fall) + (0.03 * Summer{:}substrate) + (0.02 * Fall{:}substrate) - (1.38 * Summer{:}heterogeneity) + (0.01 * Fall{:}substrate) + (3.66 * Summer{:}woodydebris) + (2.34 * Fall{:}woodydebris)$$

Canonical Correspondence Analysis. – The CCA was used to extract synthetic gradients that maximize the habitat partitioning among species from the environmental variables. Some of the environmental variables were highly correlated and therefore removed from the full dataset. Substrate heterogeneity and water velocity were correlated with primary substrate and the distance from the Ottawa River (Appendix A, Table A13). Primary substrate and distance were retained in the reduced data set. A comparison of the results from the full and reduced CCAs demonstrated that there was a small drop in eigenvalues and species-environment scores (Table 6), substrate heterogeneity and water velocity loading the highest on the first axis. The full CCA was accepted and interpreted.

The first three axes of the CCA accounted for 81.7%, 10.2% and 5.6% of the variance respectively, for a total of 97.5%. The Tessellated Darter had the highest loading on the first axis, followed by the Fantail Darter and the Channel Darter. The environmental scores associated with this first axis, and thus the separation between the Tessellated Darter and the other two species, were substrate heterogeneity, water velocity, the distance from the Ottawa River and primary substrate. The Tessellated Darter was negatively associated with these variables, contrary to the Fantail Darter and Channel Darter. On the second axis, the Johnny Darter had the highest species score which corresponded positively with the presence of woody debris and negatively with land use. The Logperch was the species that had the highest loading on the third axis, separating it from the Johnny Darter, the first being positively associated with water depth and primary substrate. The results of the first two axis of the CCA are displayed in an ordination diagram (Figure 8) in which species, stations and habitat variables are represented with letters, points and vectors respectively. This diagram permits for a direct interpretation of the relationship between the species distribution and the environmental gradients. The relative lengths of the environmental vectors are proportional to the importance of the variable in segregating the darter species (ter Braak, 1986).

Darter Distribution. – A total of 290 sites were sampled within 24 tributaries of the Ottawa River (Table 7). A sixth species of darters, the Iowa darter (*Etheostoma exile*), was captured within two of these tributaries; the Brasserie Stream and the Quyon River. The Channel Darter seemed to be the least widely distributed species, being captured in only two watercourses; the Tête de la Baie Plaissance, a tributary of the Petite-Nation River, and the Gatineau River. The species was not captured upstream of the barriers in the Saumon River, Petite-Nation River, Blanche River (Thurso) and Blanche River (Gatineau). In addition, although it is very abundant in the Gatineau River downstream and upstream of the Alonzo bridge, it has not been captured upstream of the Rapides-Farmer Generating Station (Levert et al, 2013). The other four species were found in various other rivers and streams, including upstream of the first physical barrier in the Saumon River and Blanche River (Gatineau). No darters were captured upstream of the Petite-Nation River and Blanche River (Thurso).

Classification error for sites where species were not present (i.e. presence=1 but probability of presence > 0.5) ranged from 0% in the Johnny Darter to 23% in the Channel Darter (Table 8). Classification error for sites where species were present (i.e presence = 0 but probability of presence < 0.5) ranged from 31% in the Channel Darter to 100% in the Johnny Darter. Overall classification error of species for all sites ranged from 4.1 to 31.7%. A comparison of the mean expected probability of presence and observed presence for each class of a habitat variable can be seen in Figures 9 and 10. Although most expected curves are either sigmoidal or somewhat linear, the observed curves are more bell-shaped for the Channel Darter and Fantail Darter, bimodal for the Logperch and multimodal for the Tessellated and Johnny Darters. The relationships however, between the presence of darters and the environmental variables, are relatively similar than what was predicted by the models in all species but the Johnny Darter, as it was captured in sites with larger primary substrates than expected.

DISCUSSION

This study presents data on the habitat and distribution of five species of darters coexisting within several tributaries of the Ottawa River in Québec, Canada. The sampling protocols allowed for the collection of data in various habitats spread over a large area of study.

Potential sampling bias with the portable electrofishing unit was minimized by focusing on darters which are small, benthic and cryptic and can thus be effectively captured with this method (Copp, 1989). The relative abundance of darters captured within the four tributaries sampled in 2011 and 2012 was greater than any other group or family, darters making up about 50% of the total catch. No young-of-the-year darters were captured however and it is unclear whether the absence of these juveniles (age 0+) is indicative of sampling selectivity by the portable electrofisher or simply that juveniles inhabit different habitats than adults (age ≥ 1+). In the case of the Banded Darter (*Etheostoma zonale*) for example, juveniles have been shown to occupy shallower habitats with higher water velocities than adults (Stauffer et al, 1996).

Habitat Use. **–** The Channel Darter's habitat, in waters less than 0.8m, can be characterised by heterogeneous substrate composed of sand to big boulder and water velocities greater than 0.25 ms^{-1} in areas with low bank slopes. This characterisation is consistent with riffle-like habitats, which were typically found at the base of waterfalls, chutes or dams within the rivers, thus resulting in a positive association with the distance from the Ottawa River. Heterogeneous substrate provides feeding areas for benthic species such as the Channel Darter as well as shelter from predators and from the current.

Levert (2013) used a hierarchical analysis nested at three levels (station, reach and river) to analyse the preferential habitat of the Channel Darter using similar data on the four tributaries. The density (individual/m^2) of Channel Darters was positively associated with substrate type and negatively associated with the log of bank slope. Levert (2013) also found Channel Darter density to be positively associated with water velocity at the river level. This positive relationship is only present in the Blanche River (Thurso) and therefore water velocity would not seem to be an important predictive variable of the Channel Darter in all other streams and rivers.

As substrate heterogeneity was highly correlated with substrate type, it is possible that the first is masking the effect of the second in the logistic regression and vice versa in the hierarchical analysis. The Channel Darter appears to be a specialist and show preferences for both variables.

The Logperch's habitat, in waters less than 0.8m, can be characterised by heterogeneous substrate composed primarily of boulder with moderate water velocities ranging from 0.25 to 0.75 ms^{-1} in areas with low bank slopes. These results indicate that the species may be more specialized in regards to primary substrate than previously thought (Stauffer et al, 1996). The Fantail Darter's habitat, in waters less than 0.8m, can be characterised by shallow waters (0.2 m), heterogeneous substrate composed primarily of gravel and pebble, but also boulder, with water velocities greater than 0.25 ms^{-1} in areas of low bank slopes. Similar to the Channel Darter, both of these species were often found in riffle-like habitats, at a distance from the Ottawa River, which is consistent with many other studies on the Fantail Darter (Chipps et al, 1994; Paine et al, 1981; Pratt and Lauer, 2013).

The Tessellated Darter's habitat, in waters less than 0.8m, can be characterised by shallow and slow moving waters over sand or gravel substrate with woody debris and some vegetation present. This species seems to be a generalist, showing no real specialization in regards to environmental variables. It was most often captured in pool-like areas downstream of the rivers, bordered by forested land rather than agricultural or urban land. It was the only species that was frequently found in stations with silt substrate (usage 71%), which is the most available substrate in all rivers but avoided by most other species.

The Johnny Darter's habitat, in waters less than 0.8m, is characterised by heterogeneous substrate composed primarily of sand. The low abundance of the Johnny Darters captured within the four rivers (N=40), not one individual being captured in the Petite-Nation River, prevented detailed characterisation of its preferred habitat. Johnny Darters have been shown to inhabit weed beds in smaller rivers and streams than the Tessellated Darter (Chapleau and Pageau, 1985; Paine et al, 1982).The presence of woody debris was also positively associated with the presence of the Johnny Darter, but only in the summer. This could be explained by factors related to the Johnny Darter's life history strategies. As the majority of the Johnny Darter individuals were captured during late spring or early summer, one could hypothesize that the species migrate from smaller tributaries of the four rivers in order to reproduce, which occurs in late May to June, for which they need to dig in substrate to create nests (Grant and Colgan, 1984). As the Johnny Darter was most common in stations where the Logperch and Fantail Darter were also present, the species does not seem to be displaced by the other species.

Sampled area was a significant predictor of presence in the case of the Channel Darter, Logperch and Fantail Darter. These species where often found in long stretches of homogenous riffle-like habitat, which allowed for a greater area to be sampled in each station. These areas were however also harder to sample as the abundance of crevices among the substrate and the high water velocity made it harder to successfully capture fish in the dip net and required larger areas to be sampled in order to determine which species were present. Finally, as sampling did not exceed 0.8m in depth, a limitation of sampling with a portable electrofishing device, it is important to note that the possibility of species occurring in deeper habitats cannot be refuted.

Habitat Partitioning. **–** Many studies have found habitat use in coexisting darters to vary primarily with water depth, substrate size, and current velocity (Chipps, et al, 1994; Pratt and Lauer, 2013; Schlosser and Toth, 1984; Stauffer et al, 1996; Welsh and Perry, 1998). Although primary substrate and water velocity were important in the habitat partitioning of all five species, depth seemed only important in the partitioning of the Logperch and Johnny Darter. This lack of an effect of depth could be a result of the sampling protocol and the limited sampled depths in this study. Substrate heterogeneity, the distance from the Ottawa River and the bank slope were also important, especially in partitioning the Tessellated Darter from the Fantail Darter and Channel Darter. As darters are benthic, it is natural that they are influenced by the size, type and composition substrate. The Tessellated Darter, which seems to be a habitat generalist, was spatially segregated from all four other darter species within the four tributaries. Although the Tessellated Darter showed some preference for sand and gravel substrates, it was mostly found in silt habitats. This potential habitat shift could be a result of competitive exclusion by the other darters in order to reduce niche overlap. The Tessellated Darter has previously been found to seek out alternative habitats in the presence of other darter species (van Snik Gray and Stauffer, 2001; van Snik Gray et al, 2005).

Unlike other studies, complete segregation among *Percina* and *Etheostoma* species was not observed. On the contrary, the occurrence of the Fantail Darter was highly correlated with that of the Channel Darter and the Logperch and the results of the CCA demonstrated that these species relate similarly to the environment. In general, these species were found in high densities in riffles areas. This ecological overlap may indicate that resources are not limiting or that other factors such as their position within the water column, feeding behaviour, resource dimension use and time of activity may play an important role in minimizing interactions between these three darter species coexisting in the same habitat. *Percina* species have been observed to occur primarily above the substrate, whereas *Etheostoma* species have been observed to occur under and between substrate (Stauffer et al, 1996; Welsh and Perry, 1989). In addition, *Percina* species are generally larger and thought to be better swimmers than *Etheostoma* species, which combined with their cryptic coloring, reduces their risk of predation in deeper habitats (Greenberg, 1991). Channel Darters are benthic feeders, feeding on organisms between and behind rocks whereas the Logperch is a more aggressive predator, using its elongated snout to exhibit stone-rolling foraging behaviour (Winn, 1953). The Fantail Darter on the other hand has a narrow and flexible body with an upturned mouth, making it well-adapted for crevice microhabitats where organisms can be removed from the sides and undersides of cobble (Chipps et al, 1994; Schlosser and Toth, 1984). Both *Percina* species showed neither preference nor avoidance of water depths, whereas the Fantail Darter preferred water depths ranging from 0-20 cm. Although the Johnny Darter was found in a minimal number of stations, its occurrence was also positively associated with that of the Fantail Darter, the Logperch and the Channel Darter. The Johnny Darter is also a benthic forager, using its subterminal mouth to capture sedentary prey (Paine et al, 1982). These differences in feeding behaviour and resource dimensions used could explain how the species are coexisting within similar habitats.

***Distribution.* –** The distribution of the Channel Darter within several tributaries of the Ottawa River seems to be limited to the five large rivers in which it has previously been found (Boucher et al, 2009; Comptois et al, 2004; Levert, 2013); Saumon River, Petite-Nation River, Blanche River (Thurso), Blanche River (Gatineau) and Gatineau River. In addition, the upstream distribution of the Channel Darter is limited by physical barriers, a phenomenon which has been documented for the species in Ontario (Reid et al, 2005). Further investigation of the suitability of habitats upstream or natural barriers and in other tributaries could be important to determine whether the local distribution of this endangered species could be expanded through introductions.

The Logperch, Fantail Darter, Tessellated Darter and Johnny Darter were all present upstream of the first physical barrier in either, or both, the Saumon River and Blanche River (Gatineau). The differences in the occurrence of riffle-dwelling darters upstream of barriers may reflect differences in the timing of their post-glacial colonization (Reid et al, 2005), the Channel Darter gaining access to the drainage later than the other species (Bailey and Smith, 1981). The Logperch and Tessellated darters were the most widely distributed darters, present in 13 and 15 rivers and streams of various sizes respectively. Although the Johnny Darter is thought to be the most widely distributed member of its genus with a broad tolerance for habitat types (Propst and Carlson, 1989) it was only present in 7 rivers and streams. Overall, the classification error of all five species was greater for presences than absences. This can happen when analyzing presence-absence data, where absences may prevent the models from correctly identifying areas suitable for a species to spread (Cianfrani et al, 2010). Further analysis of species habitat using presence-only data could provide more reliable predictions of each species distribution.

In conclusion, I studied the habitats and distribution of five species of darters coexisting within four tributaries of the Ottawa River in Québec, Canada. Substrate size and heterogeneity, water velocity, the distance from the Ottawa River and bank slope were important variables in describing niche use and partitioning. Habitat partitioning among these species also suggests that factors related to their life history strategies may affect patterns of segregation; morphological and behavioural differences between coexisting darters possibly playing an important role in the structuring of these benthic assemblages. These conclusions will help with the effective management and conservation of these benthic species, which can be particularly susceptible to habitat degradation related to human activities. Sampling of deeper habitats and an examination of other environmental variables could provide further understanding of the habitat preferences of these species and better the implementation of stream restoration efforts and policy making.

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TABLES

Table 1. Breakdown of fish species captured in 2011 and 2012 within the four tributaries of the Ottawa River, Québec, Canada.

Family	**Common Name**	**Genus Species**	**Abundance**
Atherinopsidae	Brook silverside	*Labidesthes sicculus*	7
Catostomidae	White Sucker	*Catostomus commersoni*	10
	Shorthead Redhorse	*Moxostoma macrolepidotum*	2
	Silver Redhorse	*Moxostoma anisurum*	1
Centrarchidae	Pumpkinseed	*Lepomis gibbosus*	248
	Smallmouth Bass	*Micropterus dolomieu*	100
	Rock Bass	*Ambloplites rupestris*	77
	Bluegill	*Lepomis macrochirus*	29
Cyprinidae	Bluntnose Minnow	*Pimephales notatus*	151
	Longnose Dace	*Rhinichthys cataractae*	102
	Spotfin Shiner	*Notropis spilopterus*	50
	Mimic Shiner	*Notropis vollucelus*	45
	Emerald Shiner	*Notropis atherinoides*	41
	Fallfish	*Semotilus corporalis*	31
	Eastern Silvery Minnow	*Hybognathus regius*	9
	Blacknose Shiner	*Notropis heterolepis*	5
	Golden Shiner	*Notemigonus crysoleucas*	2
	Sand Shiner	*Notropis stramineus*	1
	Creek Chub	*Semotilus atromaculatus*	1
Ictaluridae	Brown Bullhead	*Ictalurus nebulosus*	15
	Margined Madtom	*Noturus insignis*	1
Lotidae	Burbot	*Lotta lotta*	2
Percidae	Fantail Darter	*Etheostoma flabellare*	351
	Tessellated Darter	*Etheostoma nigrum*	253
	Channel Darter	*Percina copelandi*	224
	Logperch	*Percina caprodes*	159
	Johnny Darter	*Etheostoma nigrum*	40
	Yellow Perch	*Perca flavescens*	36
	Sauger	*Sander canadensis*	1
Petromyzontidae	American Brook Lamprey	*Lampetra appendix*	45
	Northern Brook Lamprey	*Ichthyomyzon fossor*	7
	Lamprey sp.		5
Umbridae	Central Mudminnow	*Umbra limi*	12

Table 2. Abundance (number captured) and frequency of occurrence (proportion of stations were the species was detected) of five species of darters sampled in 2011 and 2012. Sampling took place during three seasons in four tributaries of the Ottawa River, Québec, Canada.

Species	**Period**	**Saumon River**		**Petite-Nation River**		**Blanche River (Thurso)**		**Blanche River (Gatineau)**		**Species Total**
		Captured	Freq	Captured	Freq	Captured	Freq	Captured	Freq	
Channel Darter	Spring	46	0.140	25	0.047	18	0.103	15	0.041	104
	Summer	13	0.062	27	0.089	19	0.068	22	0.134	81
	Fall	19	0.103	8	0.065	1	0.015	11	0.069	39
Total		78		60		38		48		224
Logperch	Spring	28	0.129	26	0.054	2	0.029	0	NA	56
	Summer	17	0.148	16	0.089	15	0.098	2	0.030	50
	Fall	26	0.103	18	0.117	7	0.060	2	0.028	53
Total		71		60		24		4		159
Fantail Darter	Spring	184	0.292	0	NA	2	0.029	14	0.122	200
	Summer	69	0.247	2	0.025	2	0.015	26	0.119	99
	Fall	38	0.103	1	0.013	0	NA	13	0.056	52
Total		291		3		4		53		351
Tessellated Darter	Spring	37	0.164	33	0.162	10	0.118	12	0.135	92
	Summer	11	0.111	4	0.038	38	0.182	20	0.179	73
	Fall	7	0.103	12	0.130	24	0.269	45	0.361	88
Total		55		49		72		77		253
Johnny Darter	Spring	17	0.041	0	NA	7	0.044	0	NA	24
	Summer	0	NA	0	NA	5	0.030	5	0.045	10
	Fall	2	0.103	0	NA	4	0.015	0	NA	6
Total		19		0		16		5		40
Darter Total		514		172		154		187		**1027**

Table 3. Tetrachoric correlation matrix for the occurrence of the Channel Darter (*Percina copelandi*), the Logperch (*Percina caprodes*), the Fantail Darter (*Etheostoma flabellare*), the Tessellated Darter (*Etheostoma olmstedi*) and the Johnny Darter (*Etheostoma nigrum*) sampled within four tributaries of the Ottawa River, Québec, Canada (N=1133).

	P. copelandi	***P. caprodes***	***E. flabellare***	***E. olmstedi***	***E. nigrum***
P. copelandi	1.00	-	-	-	-
P. caprodes	0.66	1.00	-	-	-
E. flabellare	0.59	0.30	1.00	-	-
E. olmstedi	-0.24	-0.09	-0.40	1.00	-
E. nigrum	0.29	0.34	0.36	-0.01	1.00

Table 4. Hulbert's standardized niche breadth (B_x) for the 8 habitat variables and Pianka's niche overlap index (*O*) for the 5 darter species sampled in 2011 and 2012 within four tributaries of the Ottawa River, Québec, Canada.

	P.copelandi	***P. caprodes***	***E. flabellare***	***E. olmstedi***	***E. nigrum***
Water Depth	0.90	0.97	0.80	0.93	0.69
Primary Substrate	0.32	0.44	0.23	0.89	0.46
Substrate Heterogeneity	0.44	0.57	0.29	0.91	0.71
Vegetative Cover	0.73	0.82	0.61	0.91	0.92
Periphyton Cover	0.84	0.87	0.93	0.97	0.58
Woody Debris	0.98	0.95	0.72	0.87	0.73
Water Velocity	0.35	0.51	0.29	0.84	0.49
Bank Slope	0.34	0.70	0.40	0.94	0.80
P.copelandi	-	-	-	-	-
P. caprodes	0.96	-	-	-	-
E. flabellare	0.97	0.93	-	-	-
E. olmstedi	0.63	0.74	0.56	-	-
E. nigrum	1.00	0.80	0.69	0.83	-

Table 5. Results of the five final logistic regression models for each darter species demonstrating the estimated coefficients and p-values for all significant habitat variables present in the model. This summary table was extracted from the full results demonstrated in tables A11-A15 of Appendix A.

	P. copelandi		***P. caprodes***		***E. flabellare***		***E. olmstedi***		***E. nigrum***	
Variables	**Estimated Coefficients**	**p-value**	**Estimated Coefficients**	**p-value**	**Estimated Coefficients**	**p-value**	**Estimated Coefficients**	**p-value**	**Estimated Coefficients**	**p-value**
Depth	-	-	-	-	-3.96	<0.001	-1.216	0.0293	-	-
Sub1	-	-	0.01	0.004	-	-	-	-	-0.020	0.0294
Hetero	0.42	<0.001	-	-	0.68	<0.001	-	-	0.982	0.0018
Peri	-	-	-	-	0.03	<0.001	-	-	-	-
Woody	-	-	-	-	-	-	0.709	8.630^{-5}	-	-
Velocity	-	-	0.62	0.005	1.03	<0.001	-2.036	0.0003	-	-
Slope	-0.06	<0.001	-	-	-	-	-	-	-	-
Area	0.18	<0.001	0.18	<0.001	0.12	<0.001	-	-	-	-

*p-value significant at $\alpha \leq 0.05$

Table 6. Results of the canonical correspondence analysis (CCA) demonstrating the accumulated constrained eigenvalue, proportion of variance explained, and cumulative proportion of variance explained for both the full and reduced data sets. For each axis (canonical component) the species scores and environmental scores are also demonstrated.

		Full CCA			**Reduced CCA**		
		Axis I	Axis II	Axis III	Axis I	Axis II	Axis III
Model	Eigenvalues	0.573	0.071	0.039	0.467	0.062	0.034
	Proportion Explained	0.817	0.102	0.056	0.805	0.107	0.059
	Cumulative Proportion	0.817	0.919	0.975	0.805	0.912	0.971
Species Scores	P. copelandi	0.571	0.246	-0.013	0.563	0.214	-0.023
	P. caprodes	0.200	0.112	0.348	0.238	0.028	0.346
	E. flabellare	0.862	-0.301	-0.145	0.709	-0.255	-0.168
	E. olmstedi	-0.980	-0.104	-0.036	-0.899	-0.075	-0.037
	E. nigrum	-0.201	0.919	-0.314	-0.169	0.965	-0.314
Habitat Scores	Temperature	-0.002	0.163	0.091	0.003	0.158	0.121
	Water Depth	-0.209	0.128	0.664	-0.220	0.072	0.774
	Primary Substrate	0.525	0.042	0.464	0.587	-0.084	0.400
	Heterogeneity	0.783	-0.067	0.023	NA	NA	NA
	Vegetative Cover	-0.461	0.141	-0.301	-0.512	0.251	-0.159
	Periphyton Cover	0.071	0.144	-0.196	0.078	0.171	-0.181
	Woody Debris	-0.475	0.560	-0.255	-0.516	0.685	-0.051
	Water Velocity	0.773	-0.278	-0.167	NA	NA	NA
	Bank Slope	-0.493	-0.280	0.179	-0.550	-0.255	0.246
	Distance	0.594	0.135	-0.041	0.659	0.071	-0.145
	Land Use	-0.490	-0.481	0.003	-0.550	-0.450	-0.050

Table 7. Presence and absence (1/0) of six species of darter (Channel Darter *Percina copelandi*, Logperch *Percina caprodes*, Fantail Darter *Etheostoma flabellare*, Tessellated Darter *Etheostoma olmstedi*, Johnny Darter *Etheostoma nigrum* and Iowa Darter *Etheostoma exile*) captured within several tributaries of the Ottawa River, Québec, Canada. For each watercourse, the number of visits in indicated (N).

Watercourse	**Municipality at juncture**	**Flows Into**	**N**	***P. copelandi***	***P. caprodes***	***E. flabellare***	***E. olmstedi***	***E. nigrum***	***E. exile***
Rouge River	Grenville	Ottawa River	14	0	1	0	1	0	0
Beaven Stream	Arundel	Rouge River	1	0	0	0	1	0	0
Saumon River[A]	Fasset	Ottawa River	38	0	0	1	1	1	0
Pesant Creek West	Fasset	Saumon River	8	0	0	0	1	0	0
Pesant Creek East	Fasset	Saumon River	4	0	0	0	0	0	0
Petite-Nation River[A]	Plaissance	Ottawa River	27	0	0	0	0	0	0
Tête de la Baie Plaissance	Plaissance	Petite-Nation River	17	1	1	1	1	0	0
de la Loutre Stream	Plaissance	Petite-Nation River	4	0	0	0	1	0	0
Blanche River[A]	Thurso	Ottawa River	13	0	0	0	0	0	0
Gauthier Stream	Thurso	Blanche River (T)	3	0	0	0	0	0	0
Brady Stream	Thurso	Blanche River (T)	4	0	0	0	0	0	0
MacClean Stream	Thurso	Blanche River (T)	3	0	1	0	1	1	0
Lièvre River	Buckingham	Ottawa River	12	0	1	1	1	0	0
Blanche River[A]	Gatineau	Ottawa River	17	0	1	1	0	1	0
Gatineau River	Gatineau	Ottawa River	81	1	1	1	1	0	0
Brasserie Stream	Gatineau	Gatineau River	9	0	1	0	1	1	1
Lemay Stream	Gatineau	Gatineau River	1	0	0	0	0	0	0
Discharge Lemay Lake	Gatineau	Lemay Lake	2	0	0	0	0	0	0
Chelsea Stream	Chelsea	Gatineau River	6	0	0	0	0	0	0
de la Pêche River	Wakefield	Gatineau River	3	0	1	0	0	0	0
Brady Stream	Luskville	Faris Stream	3	0	1	0	1	1	0
Alarie Stream	Luskville	Crique Chartrand	2	0	0	0	0	0	0
Bradley Stream	Luskville	Ottawa River	6	0	0	0	0	1	0
Quyon River	Quyon	Ottawa River	12	0	1	0	1	0	1
Total			290	2	10	5	12	6	2

[A]Data presented for the Saumon River, Petite-Nation River, Blanche River (Thurso) and Blanche River (Gatineau) is for sites located upstream of the first physical barrier to fish migration

Table 8. Classification error of five species of darter (Channel Darter *Percina copelandi*, Logperch *Percina caprodes*, Fantail Darter *Etheostoma flabellare*, Tessellated Darter *Etheostoma olmstedi* and Johnny Darter *Etheostoma nigrum*) captured within several tributaries of the Ottawa River, Québec, Canada.

Species	Absent (0)			Present (1)			Overall Classification Error (%)
	P < 0.5	P ≥ 0.5	Error (%)	P < 0.5	P ≥ 0.5	Error (%)	
P. copelandi	181	54	22.9	17	38	30.9	31.7
P. caprodes	205	38	15.6	37	10	78.7	24.1
E. flabellare	230	11	4.6	45	4	91.8	19.3
E. olmstedi	229	4	1.7	55	2	96.5	20.3
E. nigrum	278	0	0	12	0	100	4.1

Figures

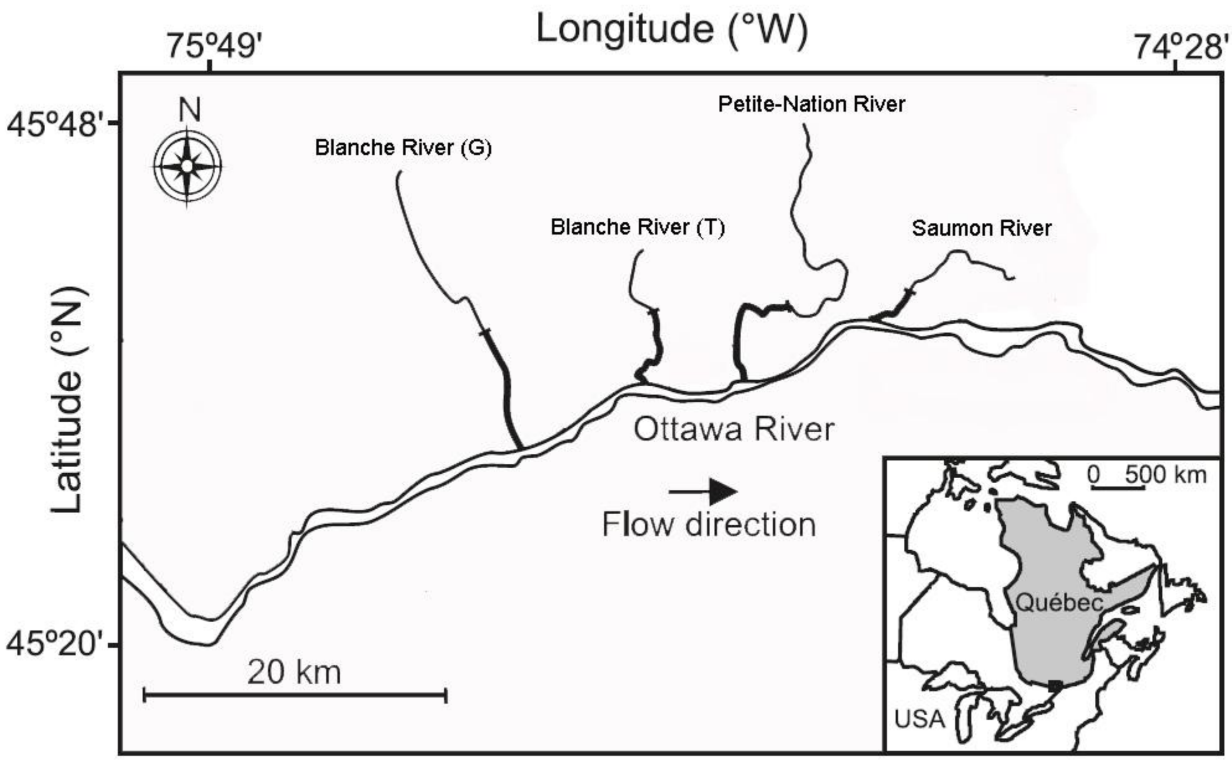


Figure 1. Four tributaries of the Ottawa River (Québec, Canada) sampled in 2011 and 2012 from the Ottawa River to the first physical barrier to fish migration (adapted from Reyjol et al, 2008).

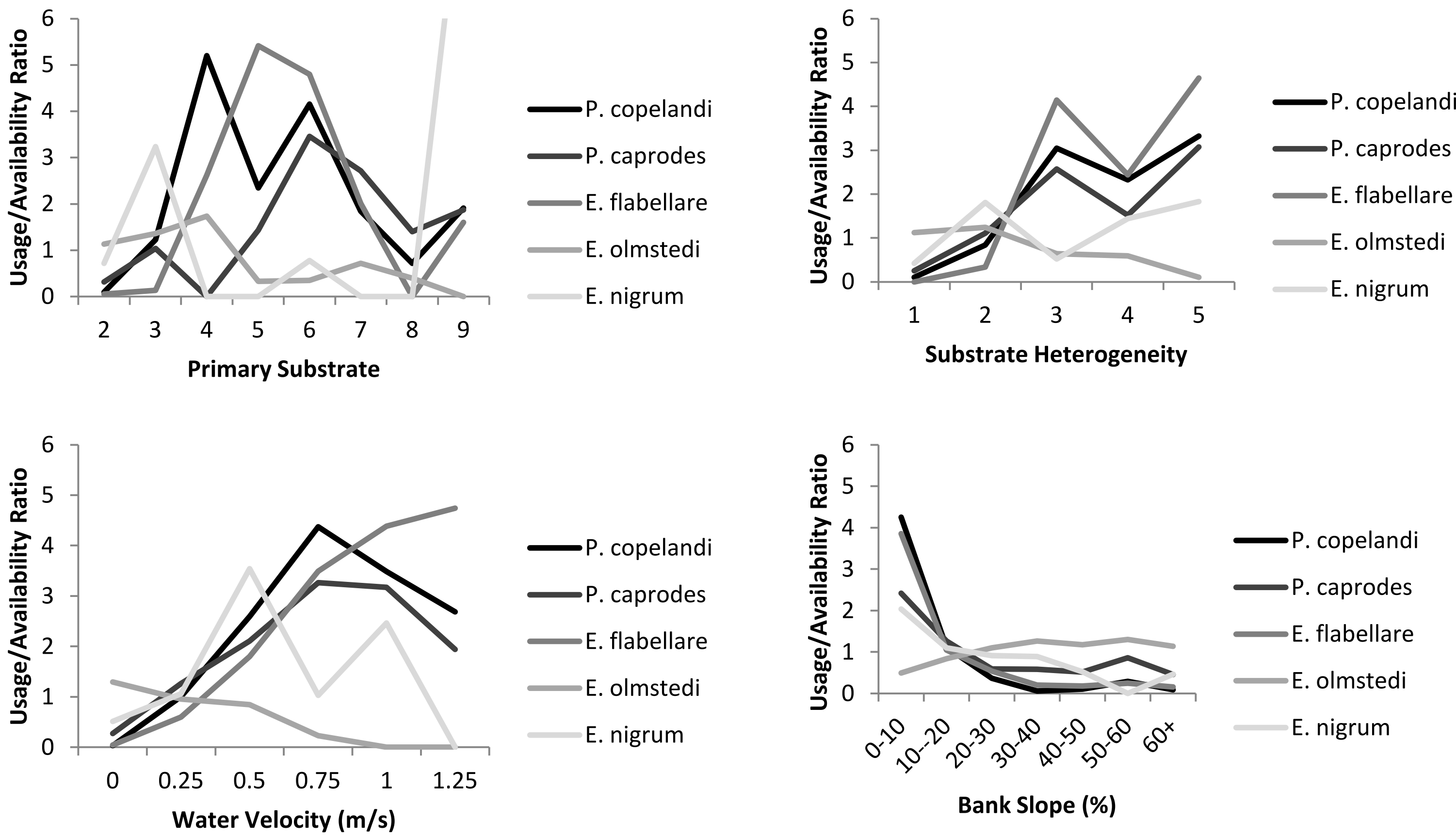


Figure 2. Representation of the usage over availability ratio of five species of darters (Channel Darter *Percina copelandi*, Logperch *Percina caprodes*, Fantail Darter *Etheostoma flabellare*, Tessellated Darter *Etheostoma olmstedi* and Johnny Darter *Etheostoma nigrum*) for four habitat variables measured within four tributaries of the Ottawa River, Québec, Canada: (a) primary substrate type (from silt (2) to bedrock (9)), (b) substrate heterogeneity (low (1) to high (5)), (c) water velocity (ms^{-1}) and (d) bank slope (%) (N = 1133).

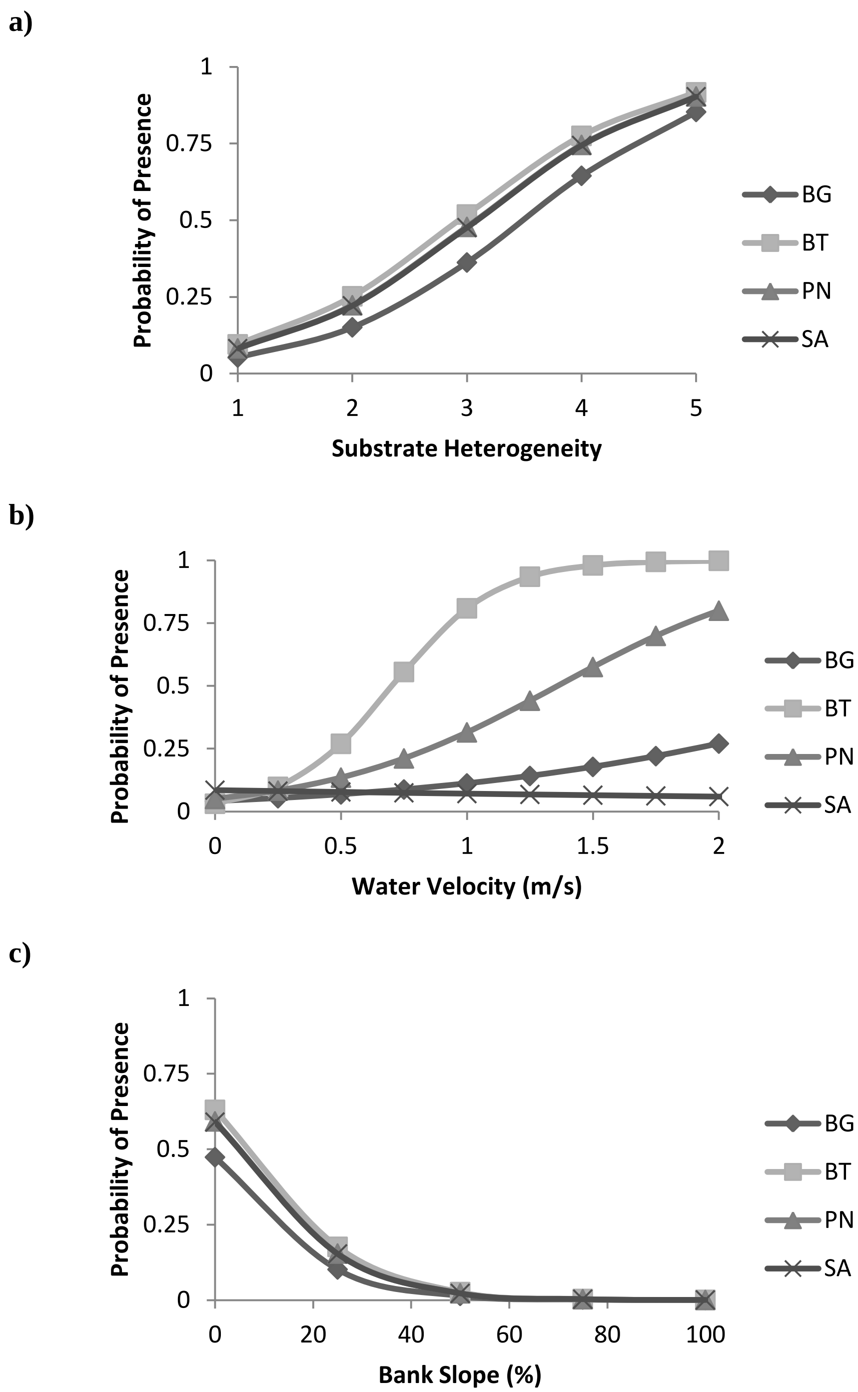


Figure 3. Predicted probability of presence for the Channel Darter (*Percina copelandi*), estimated from the final logistic regression model, as a function of (a) substrate heterogeneity (low (1) to high (5)), (b) water velocity (ms^{-1}) and (c) bank slope (5) for the four tributaries of the Ottawa River: Saumon River (SA), Petite-Nation River (PN), Blanche River (Thurso, BT) and Blanche River (Gatineau, BG).

a)

b)

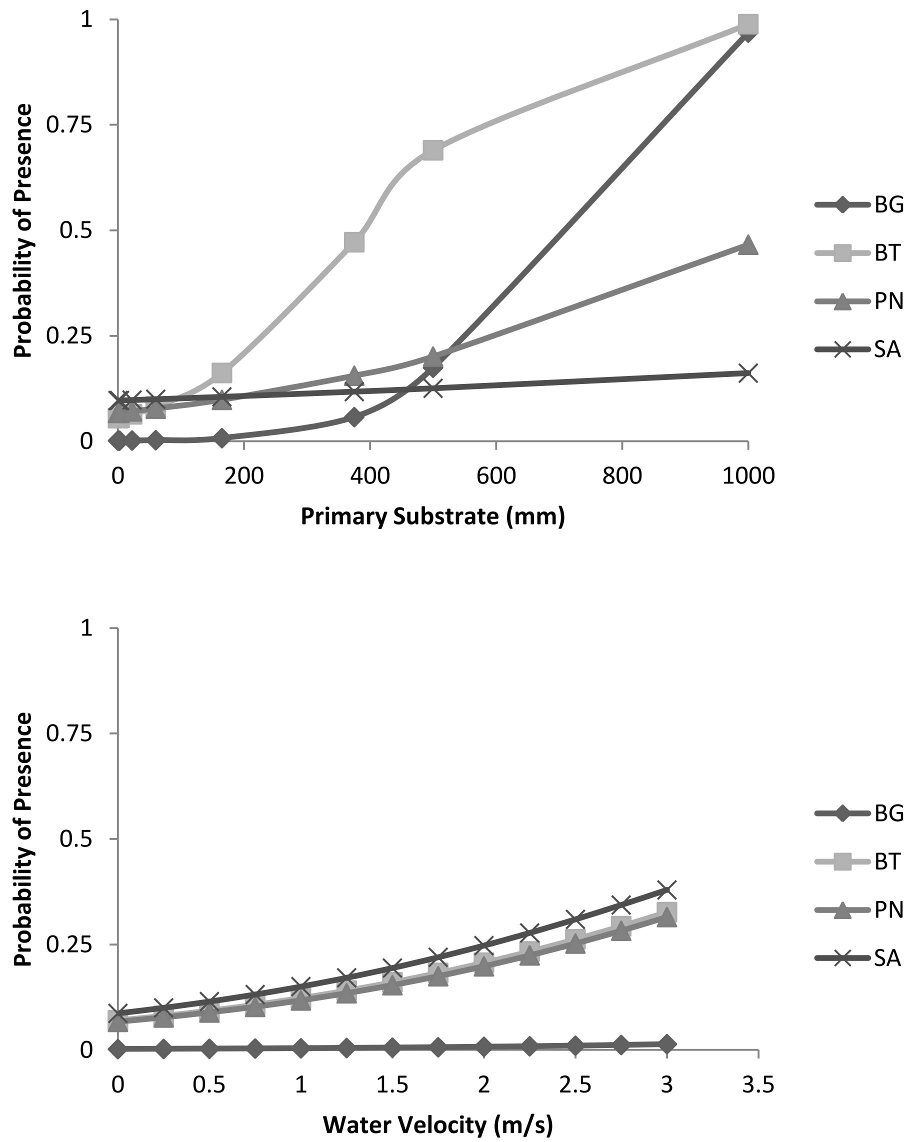


Figure 4. Predicted probability of presence for the Logperch (*Percina caprodes*), estimated from the final logistic regression model, as a function of (a) primary substrate particle size (mm) and (b) water velocity (ms^{-1}) for the four tributaries of the Ottawa River: Saumon River (SA), Petite-Nation River (PN), Blanche River (Thurso, BT) and Blanche River (Gatineau, BG).

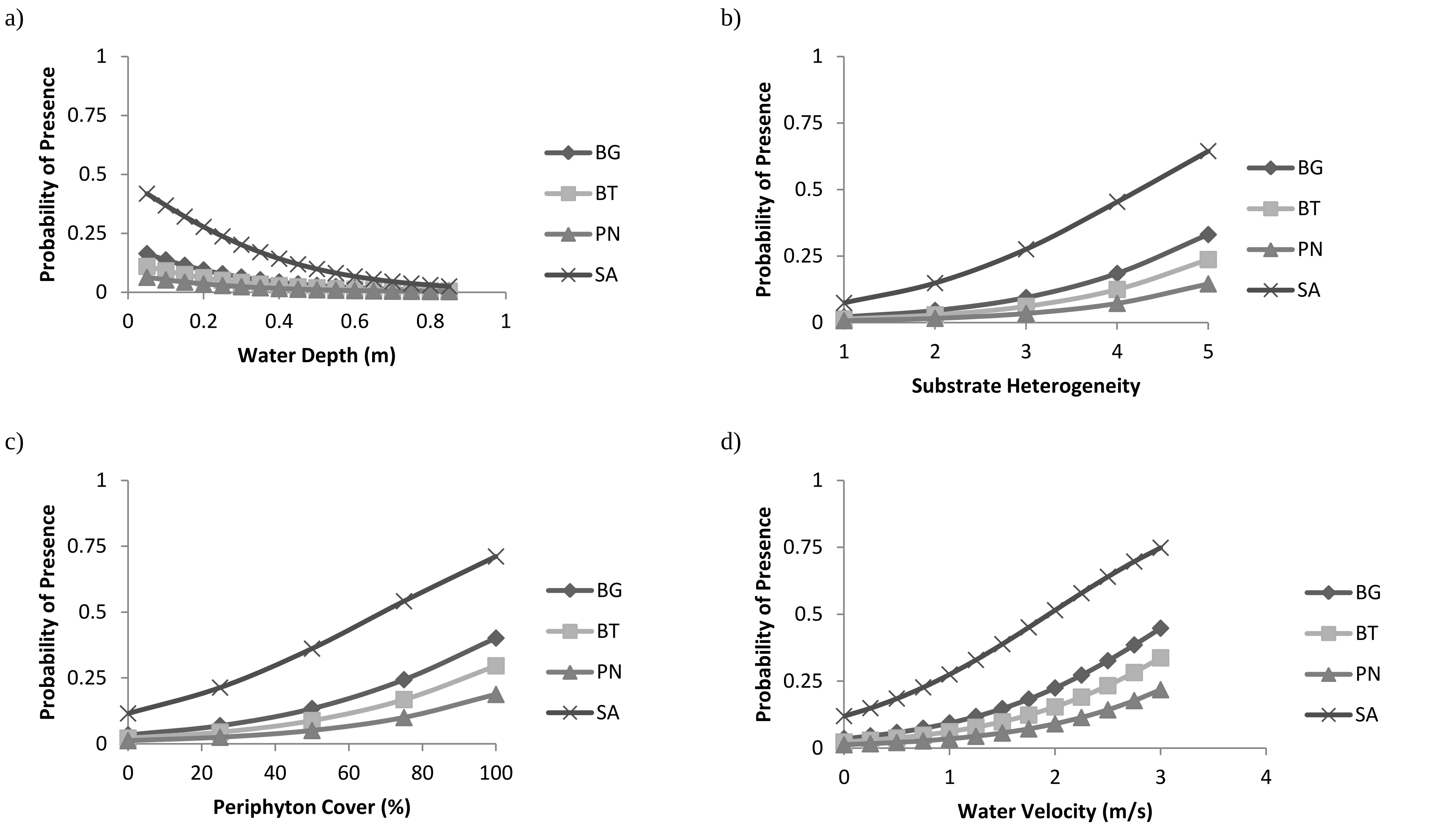


Figure 5. Predicted probability of presence for the Fantail Darter (*Etheostoma flabellare*), estimated from the final logistic regression model, as a function of (a) water depth (m) (b) substrate heterogeneity (low (1) to high (5)), (c) periphyton cover (%) and (d) water velocity (ms^{-1}) for the four tributaries of the Ottawa River: Saumon River (SA), Petite-Nation River (PN), Blanche River (Thurso, BT) and Blanche River (Gatineau, BG).

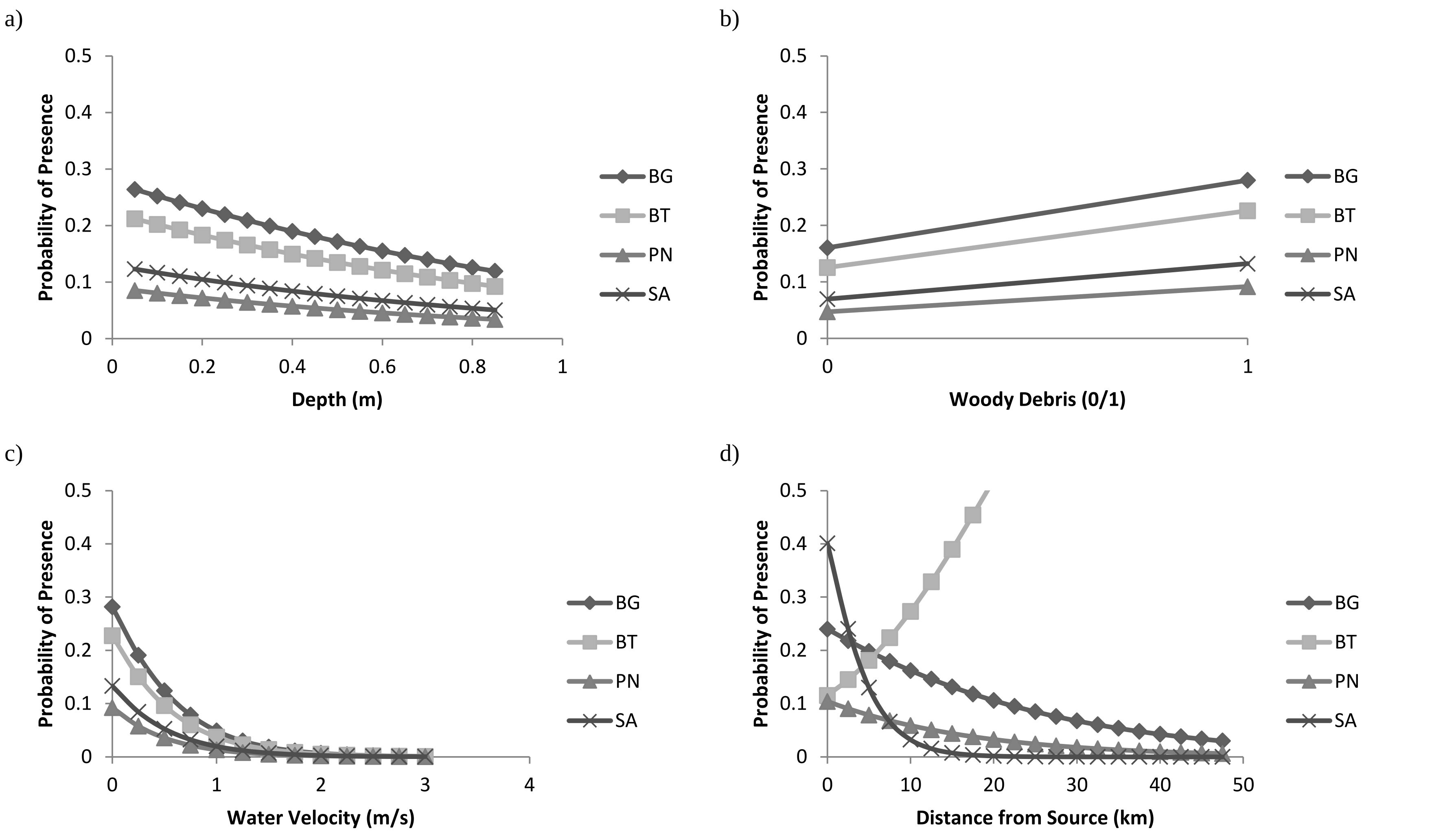


Figure 6. Predicted probability of presence for the Tessellated Darter (*Etheostoma olmstedi*), estimated from the final logistic regression model, as a function of (a) water depth (m) (b) the presence of woody debris, (c) water velocity (ms^{-1}) and (d) distance from Ottawa River (km) for the four tributaries of the Ottawa River: Saumon River (SA), Petite-Nation River (PN), Blanche River (Thurso, BT) and Blanche River (Gatineau, BG).

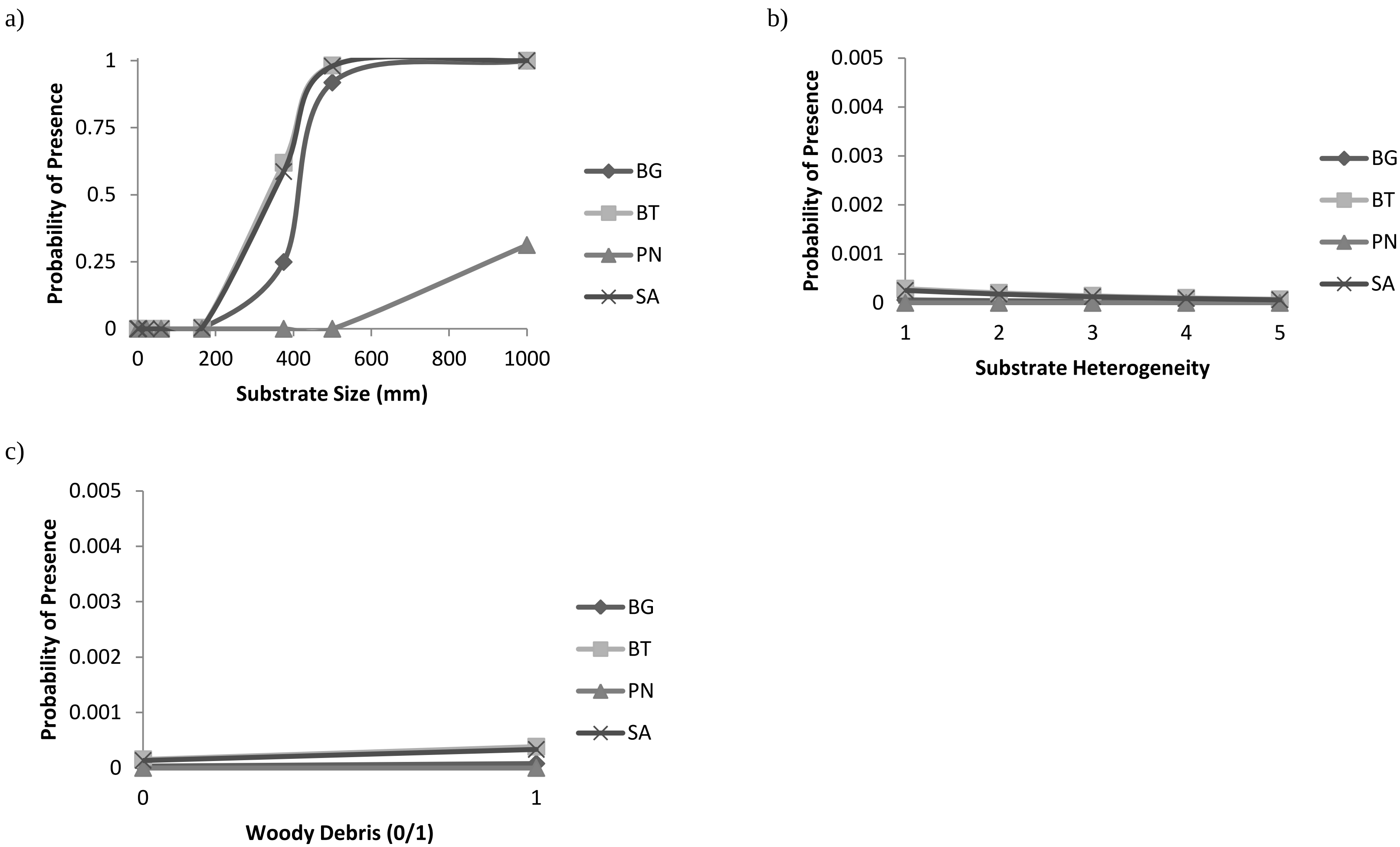


Figure 7. Predicted probability of presence for the Johnny Darter (*Etheostoma nigrum*), estimated from the final logistic regression model, as a function of (a) substrate particle size (mm), (b) substrate heterogeneity (low (1) to high (5)) and (c) the presence of woody debris for the four tributaries of the Ottawa River: Saumon River (SA), Petite-Nation River (PN), Blanche River (Thurso, BT) and Blanche River (Gatineau, BG). Note the difference in y-axis scale.

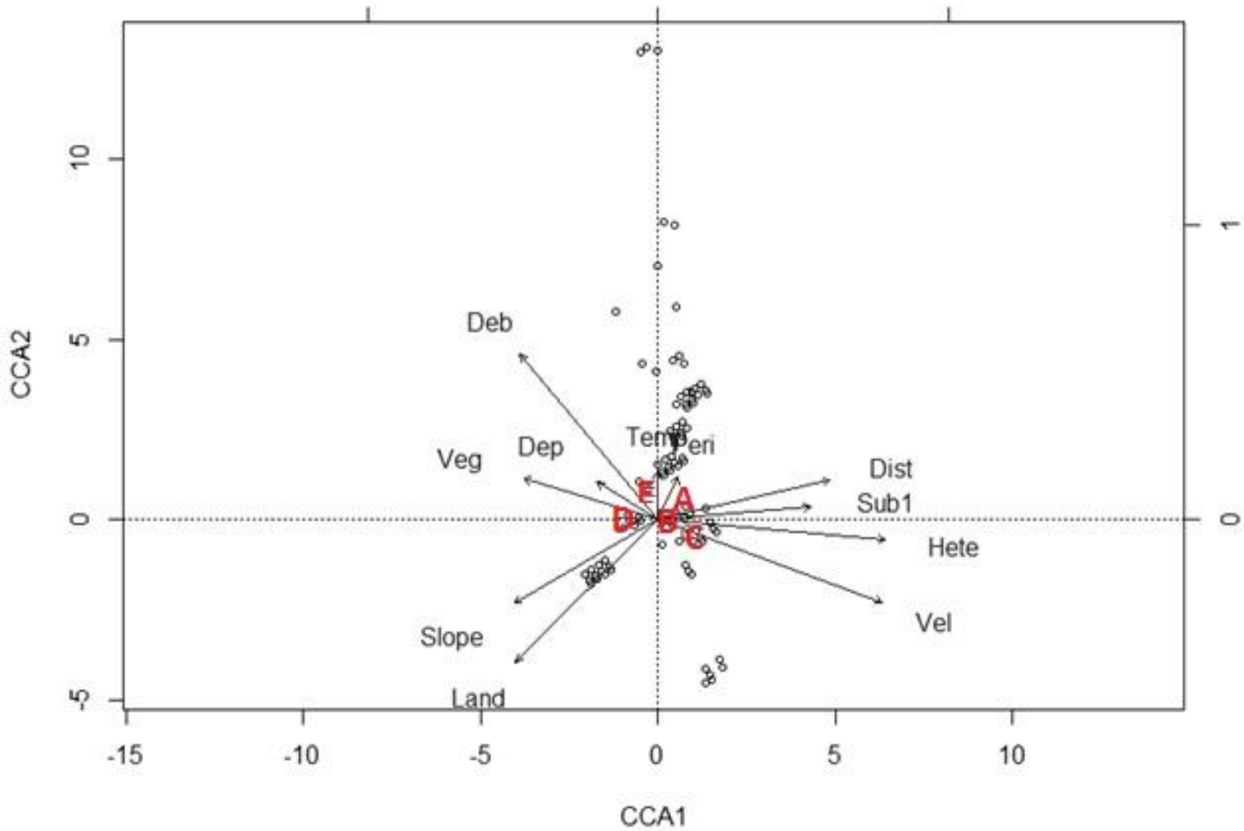
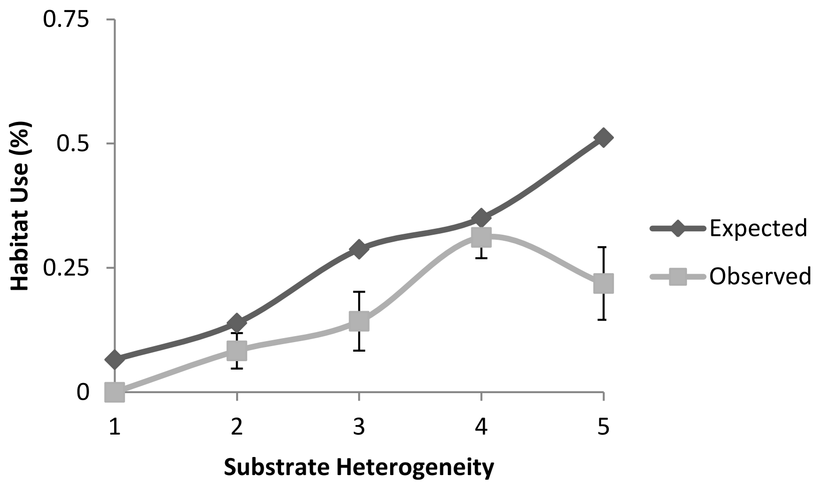


Figure 8. Biplot demonstrating the contribution of environmental variables to the first two axis of the CCA. Species are represented by letters; Channel Darter (A), Logperch (B), Fantail Darter (C), Tessellated Darter (D) and Johnny Darter (E).Environmental variables are represented by vectors; water temperature (Temp), water depth (Dep), primary substrate (Sub1), substrate heterogeneity (Hete), vegetative cover (Veg), periphyton cover (Peri), woody debris (Deb), water velocity (Vel), bank slope (Slope), distance from the Ottawa River (Dist) and land use (Land).

a)



b)

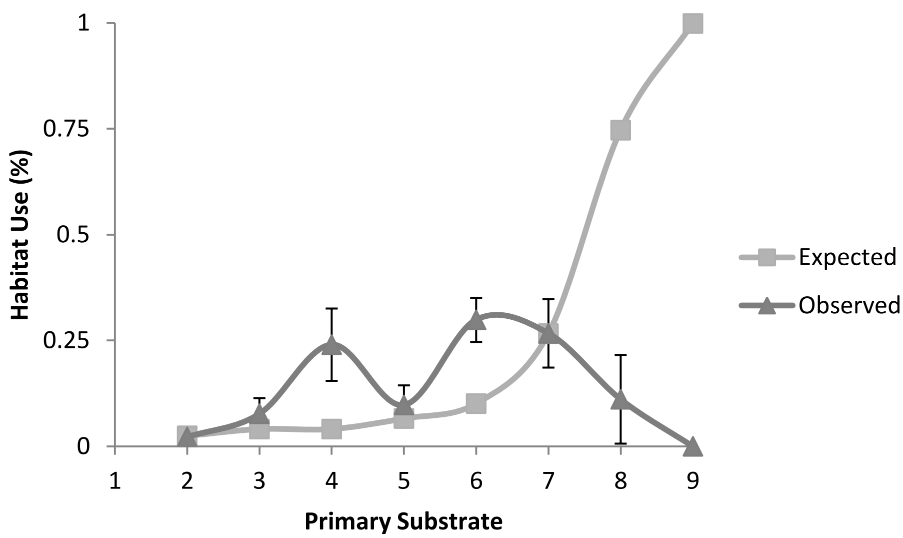
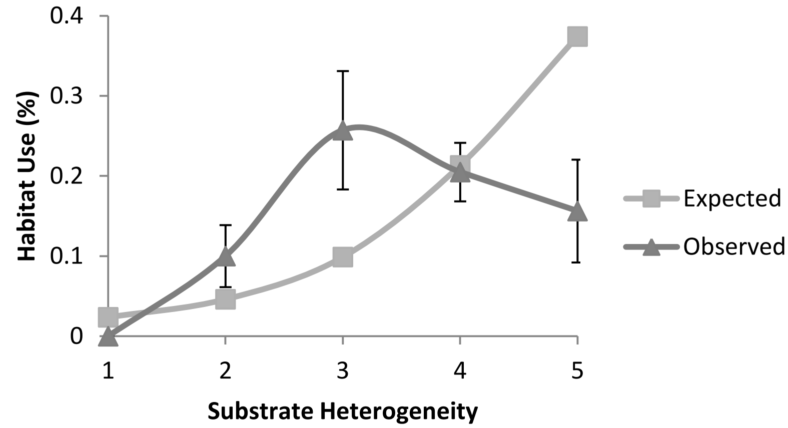
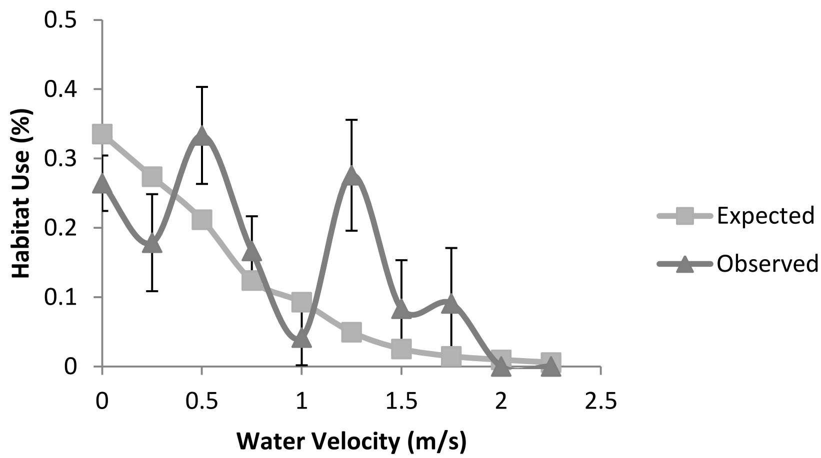


Figure 9. A comparison of the expected and observed (±SE) uses of (a) substrate heterogeneity (low (1) to high (5)) by the Channel Darter and (b) primary substrate (from silt (2) to bedrock (9)) by the Logperch in several tributaries of the Ottawa River sampled in 2013.

a)



b)



c)

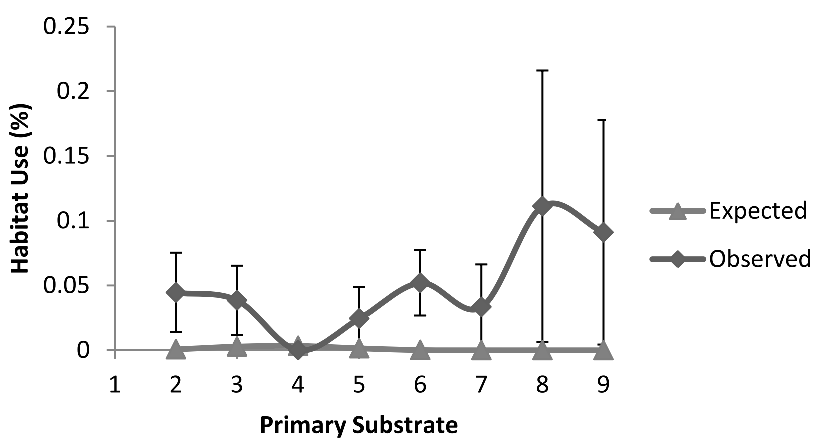


Figure 10. A comparison of the expected and observed (±SE) uses of (a) substrate heterogeneity (low (1) to high (5)) by the Fantail Darter, (b) water velocity by the Tessellated Darter and (c) primary substrate (from silt (2) to bedrock (9)) by the Johnny Darter in several tributaries of the Ottawa River sampled in 2013.

CHAPTER 2: AGE AND GROWTH OF DARTERS (PERCIDAE) FOUND IN FOUR TRIBUTARIES OF THE OTTAWA RIVER (QUÉBEC, CANADA).

ABSTRACT

Age and growth of five species of darters (Channel Darter *Percina copelandi*, Logperch, *Percina caprodes*, Fantail Darter *Etheostoma flabellare*, Tessellated Darter *Etheostoma olmstedi* and Johnny Darter *Etheostoma nigrum*) from four tributaries of the Ottawa River were examined. At each site, darters were captured with a portable electrofishing unit and environmental variables (e.g. primary substrate and heterogeneity, vegetative cover, water velocity) were quantified. Measurements on scales were used to elucidate some of the main features of the life histories of these five species, observed length-at-age increments observed on scales were used as surrogates for growth rates. Back-calculated lengths using the Fraser-Lee method demonstrated that 56 to 80% of observed length at capture was attained during the first year, suggesting that maturity is attained at age 1+ and energy allocation is invested mainly in reproduction instead of somatic growth afterwards. Although growth rates differed among rivers for the Channel Darter, none of the measured environmental variables seemed to be the cause. Growth rates were negatively correlated with the presence of parasites (examined visually) in the Channel Darter and Fantail Darter, non-parasitized individuals growing faster than parasitized individuals. Growth rates also differed among males and females in the Channel Darter, males growing faster than females.

Keywords: Habitat, Life-history, Parasite, Sex, Size

RÉSUMÉ

L’âge et la croissance de cinq espèces de dards (Fouille-roche gris *Percina coplandi*, Fouille-roche zébré *Percina caprodes*, Dard barré *Etheostoma flabellare*, Raseux-de-terre gris *Etheostoma olmstedi* et Raseux-de-terre noir *Etheostoma nigrum*) dans quatre tributaires de la rivière des Outaouais ont été examinés. À chaque site, les dards ont été capturés avec la pêche électrique portative et plusieurs variables environnementales (ex. substrat primaire, hétérogénéité du substrat, couvert végétale, courant) ont été quantifiées. La détermination de l’âge à partir d’écailles a permis d’utiliser la relation entre la longueur totale et l’âge comme indicateur du taux de croissance. Les rétro-calculs de longueurs à des âges antérieurs a démontré que 56 à 80% de la longueur total est atteinte pendant la première année. Ceci suggère que les espèces deviennent matures à l’âge 1+ et qu’après cet âge l’énergie est principalement investie dans la reproduction au lieu de la croissance somatique. Aucunes variables environnementales mesurées ne semblent être la cause des différent taux de croissance du fouille-roche gris dans les rivières. La croissance est affectée par la présence de parasites (examiné visuellement) chez le fouille-roche gris et le dard barré, celle-ci étant plus élevée chez les individus non-parasités. La croissance était aussi différente entre les sexes chez les fouille-roche gris, celle-ci étant plus élevée chez les males que chez les femelles.

Mots clés: Habitat, Histoire évolutive, Parasite, Sexe, Taille

INTRODUCTION

Quantifying components of animal fitness is fundamental in ecology. In animals with indeterminate growth, such as most fish species, researchers can rely on measures likely to be correlated with fitness such as individual growth rates (Pujolar et al, 2006). Fish growth can be influenced by various biotic and abiotic factors allowing for differences in growth patterns among populations. The combination of biotic factors, such as predator density, competition for and availability of resources, infection by parasites (Budy et al, 2011; Hall and Rudstam, 1999; Marcogliese and Compagna, 1999), and abiotic factors, such as water temperature and velocity (Clady, 1976; Drake et al, 2008; Kitchell et al, 1974), can create variations in the size of fish of the same age. Faster growth rates within species can confer many reproductive and survival advantages, and thus higher fitness. Body size has been found to be positively correlated with fish mate selection (Hanson and Smith, 1967; Noonan, 1983), the ability to defend spawning territory (Grant and Colgan, 1983; Roff, 1983) and egg clutch size or fecundity (Roff, 1983; Parrish et al, 1991). In addition, prey foraging ability in many fish is gape-limited (Matthews et al, 1982) and predation rate is typically greater on smaller fish (Jackson et al, 2001). Indeterminate growth thus leads to size-structured populations in which different sized individuals essentially function as different species, the so-called ontogenetic niche (Werner and Gilliam, 1984).

Several calcified structures such as scales, operculas, otoliths and fins produce periodic increments useful for age determination in fish. These structures have commonly been used to estimate individual fish growth of various species of darters (e.g. Drake et al, 2008; Layzer and Reed, 1978; Raney and Lachner, 1943; Reid, 2004). Darters (Percidae: Etheostomatini) are a specious group of small benthic predators inhabiting a variety of freshwater lake or stream habitats in North America (Carlson and Wainwright, 2010). Darters, which comprise predominantly of two genera (*Etheostoma* and *Percina*), have diverse life history traits and reproductive behaviour which are generally associated with body size (Paine, 1990). Larger darter species (i.e. *Percina* vs. *Etheostoma*) have been found to grow faster, mature at larger sizes, undertake more extensive spawning migrations, produce bigger clutches, remain reproductive longer and have longer lifespans than smaller species (Paine, 1990). Darter females exhibit a broad range of egg-deposition behaviour including egg-burying, egg-attaching, egg-clustering, and egg-clumping; the latter two being associated with male parental care (Kelly et al, 2012).

Many species of darters are considered endangered (Jelks et al, 2008), the largest probable threats including the loss and fragmentation of freshwater habitat as well as water pollution (Allan and Flecker, 1993). In Canada however, the lack of information on the biology of numerous species of darters, such as the channel darter (*Percina copelandi*), is a major obstacle to the protection and rehabilitation of endangered species. The channel darter was designed as threatened in 1993 and again in 2002 (COSEWIC, 2002), its decline being attributed to increased siltation and impoundment of rivers which results in the loss of clear-water habitat (Reid and Mandrak, 2008). The channel darter has recently been found in four tributaries of the Ottawa River in the Outaouais (Québec) along with four other species; the logperch (*Percina caprodes*), fantail darter (*Etheostoma flabellare*), tessellated darter (*Etheostoma olmstedi*) and johnny darter (*Etheostoma nigrum*). The populations within this watershed are thought to be in good condition (Boucher and Garceau, 2010), making it an ideal sector of study in order to fill in some gaps in our knowledge of the population's natural history.

The objective of this study is to examine the demographics of five species of darters in four tributaries of the Ottawa River. More specifically the objectives are to (1) determine individual growth rates for each species, (2) compare population-level growth patterns in the different rivers, (3) test for differences between males and females in the case of the Channel Darter and (4) determine whether factors such as the presence of visual parasites affects the growth rate and thus the fitness level of individuals. This study will provide data that could help with the recovery of the endangered channel darter by determining which factor(s) affect individual or population-level fitness and allowing the national and provincial recovery teams to make informed decisions for its management and conservation.

MATERIALS AND METHODS

***Sampling*. –** Darters were captured in four tributaries of the Ottawa River situated in Québec, Canada; Saumon River (previously Kinonge, Montebello), Petite-Nation River (Plaissance), Blanche River (Thurso) and Blanche River (Gatineau). Sites (mean area = 27.68 m^2) within the rivers were targeted based on previous mentions of species presence and preferences for habitat variables. Darters were captured using a portable electrofishing unit (LR-24 F00512 Smith-Root, Inc., Vancouver, WA, USA) and a large dip net. Six to ten scales were removed from each specimen from the left mid-dorsal region, below the lateral line. Individual total length (TL) and standard length (SL) were measured using a graduated ruler to the nearest 0.5 mm. Scales were dry-mounted onto glass slides in the field.

In the case of the channel darter, sex was identified by visual examination of the abdomen; the presence of scales on the midline of the abdomen indicating the individual is a male (Coad, 2012). Spawning readiness was accessed for all darters by visual examination of coloration and the release of eggs or milt under slight pressures of the abdomen (Coad, 2012; Etnier and Starnes, 1993; Winn, 1953). Parasite load was visually examined on all individuals as a measure of health (Adams et al, 1993). Field necropsies were not performed to avoid fish mortality.

To examine growth variability among rivers, eight different habitat characteristics were measured for each sampled site. Primary substrate type was classified as; organic matter (1), silt < 0.125 mm (2), sand 0.125-5 mm (3), gravel 5-40 mm (4), pebble 40-80 mm (5), cobble 80-250 mm (6), boulder 250-500 mm (7), big boulder >500 mm (8), or bedrock (9). Substrate heterogeneity was classified as; one substrate (1), two substrate where one dominates (2), two equally dominant substrates (3), three unequally dominant substrates (4), three equally dominant substrates or more than three substrates (5). Vegetative cover underwater and periphyton cover on substrate or vegetation was classified as either; 0% (1), 0-25% (2), 25-50% (3), 50-70% (4), 75-100% (5). The average water depth (m) and the distance from the bank of each station were measured using a meter stick. The presence of woody debris (absent=0, present=1) was determined visually. Mean current velocity (ms^{-1}) and water temperature (°C) were measured using a Global water Flo Probe (Vel001) and Waterproof Combo PH/EC Tester (HI 98129) respectively. Finally, bank slope was calculated as the ratio of water depth over the distance from the bank at each station.

***Age and growth determination.* –** Slides were examined with a compound microscope (Olympus CX41, U-CTR30-2) and digital pictures of the scales with the best readable marks were taken using a camera (Infinity 2). Scale growth, which begins at the focus, is in direct relationship with body growth demonstrated by a series of concentric circuli, the number of which increases as the fish ages and thus increases with size. The spacing between circuli decreases during periods of slow growth (ie. fall and winter), creating a darker band called an annuli (Raney and Lachner, 1943). Consequently, each year of normal growth is recorded on the scale with two regions of concentric ridges, one light and one dark, each representing summer and winter periods respectively. Fish age was determined by counting the number of clear annuli. A subsample of scales was reviewed by an independent person for validation of age determination. The distances from the center of the focus to each annulus and to the anterior edges of the scale were measured on the longest anterior radius (scale radius, SR). Pearson chi-squares tests were used to determine whether parasitisation was independent of the river sampled, darter age, darter species, or sex in the case of the Channel Darter. Linear regression modelling was used to examine the relationship between TL and SL and the relationship between TL and SR [1].

$$[1] \quad TL = a + (b * SR)$$

Length-at-age back-calculation. – Length-at-age was back-calculated from scales-annuli increments using the Fraser-Lee intercept-corrected formula [2], where L_i is the back-calculated length-at-age i, a is the intercept from the regression of TL on SR, L_c is the total length at capture, S_i is the corresponding scale radius at age i and S_c is the scale radius at capture (Fraser, 1916; Lee, 1920).

$$[2] \quad L_i = a + (L_c - a)(S_i/S_c)$$

Population-level growth patterns were estimated using analyses of covariance (ANCOVA). Differences in growth patterns between rivers, due to the presence of visible parasites and between sexes (in the Channel Darter only) were tested for in the models. Model selection was done by comparing Akaike Information Criterion (AIC). Models were fitted using R 3.0.2 (R Development Core Team, Vienna Austria) and tests were accepted as significant at alpha ≤ 0.05.

RESULTS

Darters (N=365) were captured at 77 sites within the four river from June 12th to October 25th. Channel Darters TL of 85 individuals (57 females, 28 males) ranged from 44.5 to 71.0 mm (38.5 – 61.0 mm SL), Logperch TL of 101 individuals ranged from 47.5 to 117.0 mm (40.0 - 103.0 mm SL), Fantail Darters TL of 126 individuals ranged from 18.5 to 68.5 mm (15.5 – 57.5 mm SL), Tessellated Darters TL of 70 individuals ranged from 24.0 to 72.0 mm (20.0 – 70.5 mm SL) and Johnny Darters TL of 13 individuals ranged from 32.5 to 59.5 mm (28.0 – 50.0 mm SL) (Table 1; Figure 1). The interpreted age of species ranged from 0+ to 4+ for the Channel Darter, 0+ to 3+ for the Logperch and Fantail Darter and 0+ to 2+ for the Tessellated Darter and Johnny Darter. Predominant ages varied; age 0+ dominating for the Tessellated Darter and Johnny Darter, age 1+ dominating for the Logperch and age 2+ dominating for the Channel Darter and Fantail Darter. In all five species, there was considerable overlap in length for most ages.

Channel darters in spawning conditions were collected from all four rivers from the 3rd of July to the 5th of August. Mean TL of ripe females was 53.1 mm at age-1+ (range = 46.5-58.5 mm, N=6), 56.7 mm at age-2+ (range = 56.0-58.0 mm, N=3) and 60.6 mm at age-3+ (range = 59.0-65.0 mm, N=4). Mean TL of spawning males was 53.3 mm at age-1+ (range = 51.0-57.0 mm, N=4), 57.0 mm at age-2+ (range = 55.0-59.0 mm, N=5) and 61.5 mm at age-3+ (range = 59.0-64.0 mm, N=2). Only one logperch in spawning condition was collected from the Petite-Nation River on July 9th; a male aged-2+ measuring 80.0 mm in TL. Two fantail darters in spawning conditions were collected from the Blanche River (Gatineau) on the 3rd of July; a female measuring 57.0 mm in TL and a male measuring 60.0 mm in TL, both aged-2+. Finally, one tessellated darter in spawning condition was captured from the Petite-Nation River on the 9^{th} of July; a female aged-2+ measuring 42.5 mm in TL.

At least three different types of parasites were observed on the fishes. Anchorworms (*Lernaea spp.*) were observed buried under the skin of some individuals with their anchor-shaped head embedded behind fins. Black spots (*Neascus spp.*) were visible just under the skin of individuals and yellow grubs (*Clinostomum spp.*) were also visible just under the skin of individuals, but were concentrated on the ventral side, behind the opercula or within the jaw. Results from the Pearson chi-squared analysis demonstrated that parasitism was not independent of river (χ^2 = 32.07 P-value < 0.001) or species (χ^2 = 25.23 P-value < 0.001) (Table 2). Parasite prevalence (proportion of fish infected, expressed as a percentage) was highest in the Saumon River and Blanche River (Gatineau) and in the Tessellated Darter and Logperch (Appendix B, Figure B1). Parasitism seems to be independent of darter age and of sex in the case of the Channel Darter.

The relationships between TL and SL (Appendix B, Figure B2), TL and SR (Appendix B, Figure B3) as well as SL and SR as determined by the regression analyses were all highly linear (Table 3). The linear models of TL over SR provided a better fit than that of SL over SR and the intercepts (a) from those equations were therefore used for the back-calculations of length at age (Appendix B; Figure B4). All species exhibited high variation in yearly growth; rapid growth occurring within their first year. Weighted mean back-calculated lengths demonstrated that about 58 to 64 percent of TL growth occurred during the first summer for *Percina* species (Table 4) and about 56 to 80 percent for *Etheostoma* species (Table 5).

TL increased linearly with age in all five species (Table 6, Figure 2). The Channel Darter's growth rate differed from one river to the next ($ß_{river:age}$), among parasitized and non-parasitized individuals ($ß_{parasite:age}$) and among females and males ($ß_{sex:age}$). The rate at which total length increased as a function of age was greatest in the Petite-Nation River, followed by the Blanche River (Thurso), Blanche River (Gatineau) and then Saumon River respectively (Figure 3). Although environmental variables could explain the differences in growth among rivers, no correlations with measured site variables were found (Appendix B, Table 1B). There was however a higher abundance of other darters present at the sites from which Channel Darters were captured in the Saumon River and Blanche River (Gatineau). There is a significant negative effect of parasites on total length ($ß_{parasite}$= -1.39, P-value <0.001) and the rate at which total length increased as a function of age was greatest for non-parasitized individuals (Figure 4a,b). Lastly there is a positive effect of sex on total length, males being generally bigger and growing faster than females (Figure 5).

The Fantail Darter's growth rate also differed among parasitized and non parasitized individuals ($ß_{parasite:age}$), non-parasitized individuals growing faster (Figure 4c,d). The intercepts differed among parasitized and non-parasitized individuals ($ß_{parasite}$) for the Channel Darter, Logperch and Fantail Darter. No age 0+ Channel or Fantail Darters were parasitized, but parasitized age 0+ Logperches were generally bigger than non-parasitized age 0+. Although growth rates did not differ among rivers for the Logperch and Tessellated Darter, the intercepts differed among rivers ($ß_{river}$). Similar to the Channel Darter, individuals seem to be initially bigger in the Blanche River (Gatineau). Effect of river or parasites was not significant for the other species. Differences among populations and differences due to the presence of parasites could not be tested for the Johnny Darter as individuals were only collected in the Blanche River (Gatineau) and only one individual was visually parasitized.

DISCUSSION

The observed maximum length achieved by the darter populations of the Ottawa River tributaries is smaller than those observed in other studies conducted on these species, the majority being in the United States; 73 mm TL at age 5 in the Channel Darter, 180 mm TL at age 3 in the Logperch, 110 mm TL, 71 mm TL and 84 mm TL at age 4 in the Fantail Darter, Tessellated Darter and Johnny Darter respectively (Boucher et al, 2009; Holm et al, 1009; Layzer and Reed, 1978; Raney and Lachner, 1943; Reid, 2004; Thomas, 1970; Trautman, 1981). Latitudinal trends, such as this observed decrease in growth with an increase in latitude, are expected due to differences in growing seasons and thermal variations (Davies et al, 2014; Paine, 1990; Yamamoto and Kao, 2012). Similarly, the oldest specimens of darters captured from these populations are younger than the maximum lifespan reported in other populations for all species but the Logperch. The Tessellated and Johnny Darters seem to be short lived species within these tributaries; no specimens older than 2+ were captured indicating that very few individuals might live beyond their second breeding season or that our sampling method is not adequate to capture them.

Young-of-the-year individuals of the Logperch and Fantail Darter were usually found isolated from other age groups, while adult individuals of all ages inhabited the same sites. Tessellated and Johnny Darter individuals of all ages occurred in the same stations. Very few young-of-the-year Channel Darters were captured within the tributaries, an issue observed in other studies (Boucher et al, 2009; Reid, 2004). It is unclear whether juveniles of this species inhabit different habitats than adults or whether the sampling method is not adequate to captured them.

All species grew the fastest during their first year of life, which is to be expected in specimens with lifespans ranging from 3 to 5 years (Drake et al, 2008; Etnier and Starnes, 1993; Karr, 1963; 1993; Reid, 2004; Ross, 2001). Channel Darters were sexually mature during their second summer, at age 1+, indicating that that this decrease in growth is correlated with the onset of maturity (Roff, 1983). In females especially, growth will diminish as more resources are invested in the production of gametes (Ware, 1982). Spawning in temperate regions is thought to occur in early summer (June-July) for both the Channel Darter and Logperch at water temperatures of 20°C and 15°C, respectively (Holm, 2009). For the Fantail Darter, Tessellated Darter and Johnny Darter spawning is thought to occur in late spring (May-June) at water temperatures of 17°C, 12°C, and 10°C, respectively (Holm, 2009). Females lay small eggs measuring about 1.50-2.00 mm, 1.12-1.20 mm and 1.60-1.80 mm in diameter for the Channel Darter, Logperch and *Etheostoma sp.* respectively (Cooper, 1978; Lemieux et al, 2005; Paine and Balon, 1984ab). Female darters display a variety of egg-depositing behaviours including egg burying in the *Percina sp.* and egg attaching in the *Etheostoma sp.* which is accompanied with parental care such as male egg-guarding behaviour (Kelly et al, 2012; Lake, 1936).

Tendencies towards sexual differences in growth rates were exhibited by the Channel Darter, males growing faster than females. This phenomenon has been found in other darter species such as the Johnny Darter, and is thought to be related to territorial behaviour in males (Raney and Lachner, 1943). Larger males will be better able to drive off egg predators, maximizing their parental care (Roff, 1983). Channel Darter males are not associated with male parental care however and it is unclear whether the growth differences between males and females is simply a result of females investing more resources in reproduction or that an advantage is awarded to larger males. Body size for example is sometimes positively correlated with female mate choice in fish (Hanson and Smith, 1967; Noonan, 1983).

Infection by parasites seems to negatively affect the growth rates of the Channel Darters and Fantail Darters. The biological significance of the effect of parasites on darter growth is, however, hard to assess due to the small sample sizes. No young-of-the-year individuals were infected for these two species. This could suggest that infected age 0+ fish are particularly susceptible to parasite-induced mortality (Marcogliese and Compagna, 1999). Alternatively this could suggest that young-of-the-year individuals have not had enough exposure to parasites to get infected. The intensity of parasites has been found to increase with the age and size of fish hosts (Poulin, 2000). The older the fish the longer parasites have to accumulate within them, and the larger the fish the more space the parasites have to get established (Poulin, 2000). Infected age 0+ Logperch were larger than non-infected young, implying that either the fittest individuals survive being parasitized or that larger individuals are easier to colonize by parasites. Parasites of other darter species appear to be commensals and benefit from their host without affecting fish health, growth or survival (Marcogliese and Compagna, 1999).

Individual growth is related to both reproduction and survival. As habitat use is coupled to these measures of fitness, environments which promote larger individuals will also promote increased fecundity, clutch size and egg guarding behaviour. These processes will in turn promote the survival of juveniles and increased growth of individuals within a population. Further research is necessary in order to determine whether factors abiotic (e.g. environmental variables) or biotic factors (e.g. resource availability) can account for the differences in the growth patterns among the rivers. In addition acquiring more information on the distribution of parasites among darters could provide more insight on the susceptibility to infection and the relationship between parasite load and the age or size of fish hosts. Relating patterns of individual growth to more ultimate measures of fitness is crucial when assessing the status of populations and central to making informed decisions about the conservation and management of habitat which will promote the fitness of these species.

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Tables

Table 1. Number of specimens, mean average total and standard observed lengths (TL and SL), range, and percent of parasitized individuals (Pa) for five species of darters captured for growth analyses in four tributaries of the Ottawa River, Québec, Canada; (1) Saumon, (2) Petite-Nation, (3) Blanche (Thurso) and (4) Blanche (Gatineau).

Species	River	Count *	TL Average (SD)	TL Range	SL Average (SD)	SL Range	Pa (%)
Channel Darter	1	13 (6,7)	55.3 (2.7)	51.0-59.0	47.0 (2.2)	44.0-47.0	61.5
	2	15 (10,5)	52.6 (3.9)	45.5-58.0	44.8 (3.5)	38.5-49.5	0.0
	3	23 (18,5)	53.1 (3.7)	46.5-59.0	44.8 (3.4)	39.0-50.0	4.4
	4	34 (23,11)	62.0 (4.6)	44.5-71.0	53.2 (3.7)	40.0-61.0	23.5
	Total	85 (57,28)	56.9 (5.8)	44.5-71.0	48.5 (5.2)	38.5-61.0	20.0
Logperch	1	7	76.2 (9.9)	60.00-90.0	65.4 (9.4)	50.5-78.5	42.9
	2	69	71.9 (9.5)	47.50-97.0	61.4 (8.5)	40.0-83.5	39.1
	3	16	74.6 (9.2)	63.00-94.0	64.3 (8.7)	54.0-85.5	50.0
	4	9	100.4 (10.4)	87.0-117.0	88.3 (9.2)	76.5-103.0	55.6
	Total	101	75.2 (12.4)	47.5-117.0	64.6 (11.4)	40.0-103.0	42.6
Fantail Darter	1	52	44.2 (10.6)	18.5-65.0	37.0 (8.9)	15.5-55.0	36.5
	4	74	47.2 (13.4)	19.0-68.5	40.5 (11.4)	16.5-57.5	4.1
	Total	126	45.9 (12.4)	18.5-68.5	39.1 (10.5)	15.5-57.5	17.5
Tessellated Darter	1	15	55.4 (14.3)	28.5-72.0	46.5 (11.8)	24.5-60.5	66.7
	2	10	55.9 (6.9)	42.5-65.0	47.2 (5.9)	36.0-54.5	80.0
	3	31	42.9 (12.8)	24.0-63.5	36.1 (10.4)	20.0-53.0	0.0
	4	14	47.9 (9.5)	34.5-64.0	39.9 (8.2)	20.0-53.0	64.3
	Total	70	48.4 (13.0)	24.0-72.0	40.7 (10.8)	20.0-60.5	38.6
Johnny Darter	4	12	45.9 (9.9)	32.5-59.5	39.00 (8.18)	28.0-50.0	8.3

*Count also represented by sex in the case of the Channel Darter (female, male)

Table 2. Contingency table and results from the Pearson's chi-square test of independence between parasitism and age, river, species (Channel Darter *Percina copelandi*, Logperch *Percina caprodes*, Fantail Darter *Etheostoma flabellare*, Tessellated Darter *Etheostoma olmstedi* and Johnny Darter *Etheostoma nigrum*) and sex in the case of the Channel Darter.

	Parasitisation					
	0	**1**	**%**	**X^2**	**df**	**p-value**
Age						
0	66	18	21.4	5.47	4	0.2428
1	97	40	29.2			
2	87	43	33.1			
3	31	7	18.4			
4	4	1	20.0			
River				32.07	3	5.051^{-6}
SA	47	40	46.0			
PN	60	34	36.2			
BT	61	9	12.9			
BG	117	26	18.2			
Species				25.23	4	4.517^{-5}
P. copelandi	68	17	20.0			
P. caprodes	59	42	41.6			
E. flabellare	104	22	17.5			
E. olmstedi	43	27	38.6			
E. nigrum	11	1	8.3			
Sex						
Female	48	9	15.8	1.20	1	0.273
Male	20	8	28.6			

Table 3. Linear regression equations of total length (TL) on standard length (SL) for each darter species as well as TL on scale radius (SR) for each of the five darter species captured within four tributaries of the Ottawa River, Québec, Canada.

Species		**Regression Equation**	**R^2**	**N**
Channel Darter	Overall	$TL = 2.51 + 1.12\,SL$	0.985	87
(*Percina copelandi*)		$TL = 18.0 + 32.0\,SR$	0.683	
		$SL = 14.6 + 27.9\,SR$	0.661	
	Female	$TL = 1.09 + 4.23\,SL$	0.986	57
		$TL = 21.6 + 29.0\,SR$	0.647	
		$SL = 16.6 + 26.2\,SR$	0.631	
	Male	$TL = 0.18 + 1.17\,SL$	0.988	28
		$TL = 12.2 + 37.0\,SR$	0.747	
		$SL = 11.4 + 30.8\,SR$	0.714	
Logperch		$TL = 5.41 + 1.08\,SL$	0.996	101
(*Percina caprodes*)		$TL = 20.0 + 46.4\,SR$	0.864	
		$SL = 13.7 + 42.6\,SR$	0.861	
Fantail Darter		$TL = 0.39 + 1.17\,SL$	0.990	126
(*Etheostoma flabellare*)		$TL = 1.08 + 50.4\,SR$	0.881	
		$SL = 1.10 + 42.6\,SR$	0.865	
Tessellated Darter		$TL = 0.70 + 1.20\,SL$	0.996	70
(*Etheostoma olmstedi*)		$TL = 11.4 + 36.1\,SR$	0.919	
		$SL = 10.1 + 29.9SR$	0.916	
Johnny Darter		$TL = 1.24 + 1.21\,SL$	0.999	12
(*Etheostoma nigrum*)		$TL = 11.8 + 29.0\,SR$	0.896	
		$SL = 10.8 + 24.0\,SR$	0.896	

Table 4. Mean total lengths and growth increments of 2 species of darter from the genera *Percina* collected from four tributaries of the Ottawa River, Québec, Canada.

		Mean TL (mm)			
No. Annuli	**N**	**Age 0+**	**Age 1+**	**Age 2+**	**Age 3+**
		Channel Darter (*Percina copelandi*), Females			
1	16	42.0 (0.7)			
2	27	39.2 (0.3)	49.2 (0.5)		
3	10	38.7 (0.6)	48.1 (0.8)	57.3 (0.6)	
4	3	37.6 (1.2)	45.8 (1.8)	55.5 (0.9)	61.8 (1.0)
Weighted Mean		39.8	48.7	56.9	61.8
Average Growth Increment		39.8	8.8	8.2	4.9
Proportion Growth (%)		64.4	14.3	13.3	8.0
		Channel Darter (*Percina copelandi*), Males			
1	12	41.4 (0.6)			
2	8	40.8 (0.5)	50.9 (1.0)		
3	5	40.0 (1.3)	49.4 (1.1)	59.2 (1.3)	
4	2	42.1 (1.0)	54.2 (5.5)	61.4 (3.7)	66.4 (2.2)
Weighted Mean		41.0	50.8	59.8	66.4
Average Growth Increment		41.0	9.8	9.0	6.6
Proportion Growth (%)		61.7	14.8	13.5	10.0
		Logperch (*Percina caprodes*)			
1	50	56.9 (0.7)			
2	22	54.8 (0.7)	72.8 (1.7)		
3	3	55.6 (1.4)	70.1 (0.4)	97.0 (3.5)	
Weighted Mean		56.2	72.5	97.0	
Average Growth Increment		56.2	16.2	24.3	
Proportion Growth (%)		58.0	16.7	25.3	

Table 5. Mean total lengths and growth increments of 3 species of darter from the genera *Etheostoma* collected from four tributaries of the Ottawa River, Québec, Canada.

		Mean TL (mm)		
No. Annuli	**N**	**Age 0+**	**Age 1+**	**Age 2+**
		Fantail Darter (*Etheostoma flabellare*)		
1	40	31.4 (0.5)		
2	49	32.6 (0.6)	44.2 (0.7)	
3	14	34.6 (1.6)	48.5 (1.5)	57.1 (1.2)
Weighted Mean		32.4	45.2	57.1
Average Growth Increment		32.4	12.7	11.9
Proportion Growth (%)		56.8	22.3	20.9
		Tessellated Darter (*Etheostoma olmstedi*)		
1	18	38.5 (0.9)		
2	24	37.4 (1.0)	52.9 (0.9)	
Weighted Mean		37.9	52.9	
Average Growth Increment		37.9	15.0	
Proportion Growth (%)		71.6	28.4	
		Johnny Darter (*Etheostoma nigrum*)		
1	4	35.6 (2.3)		
2	3	37.8 (0.8)	45.7 (2.5)	
Weighted Mean		36.5	45.7	
Average Growth Increment		36.5	9.2	
Proportion Growth (%)		80.0	20.1	

Table 6. General linear models of growth for each darter species demonstrating the estimated coefficients (ß), standard error (SE) and p-values for all significant variables. Darters were captured within four tributaries of the Ottawa River; Saumon River (SA), Petite-Nation River (PN), Blanche River (Thurso, BT) and Blanche River (Gatineau, BG).

	Channel Darter (*P. copelandi*)			**Logperch Darter (*P. caprodes*)**			**Fantail Darter (*E. flabellare*)**			**Tessellated Darter (*E. olmstedi*)**			**Johnny Darter (*E. nigrum*)**		
Variable	**ß**	**SE**	**p-value**	**ß**	**SE**	**p-value**	**ß**	**SE**	**p-value**	**ß**	**SE**	**p-value**	**ß**	**SE**	**p-value**
Intercept	53.63	1.7	<0.001	80.48	3.1	<0.001	27.98	0.9	<0.001	39.37	1.3	<0.001	36.67	1.5	<0.001
Age	2.81	0.6	<0.001	8.94	1.0	<0.001	12.43	0.5	<0.001	13.21	0.7	<0.001	11.14	1.3	<0.001
Sex															
Male	1.14	1.4	0.415												
Sex:Age	1.45	0.6	0.022												
Parasite	-1.39	0.4	<0.001	0.90	0.3	0.005	3.71	1.9	0.065	–	–	–			
Parasite:Age	0.612	0.2	0.002	–	–	–	-1.62	0.8	0.044	–	–	–			
River															
BT	-6.17	2.2	0.006	-15.05	3.1	<0.001	–	–	–	-6.74	1.5	<0.001			
PN	-8.47	2.4	<0.001	-17.71	2.7	<0.001	–	–	–	-3.23	1.9	0.108			
SA	2.01	2.5	0.432	-13.84	3.6	<0.001	–	–	–	-0.70	1.8	0.693			
BT:Age	0.973	1.0	0.351	–	–	–	–	–	–	–	–	–			
PN:Age	2.74	1.3	0.032	–	–	–	–	–	–	–	–	–			
SA:Age	-2.93	1.3	0.022	–	–	–	–	–	–	–	–	–			
R^2	0.833			0.698			0.829			0.876			0.870		

* Dashes (-) are present when a term was tested for and was no significant whereas blank spots represent variables that were not tested for in a particular model.

Figures

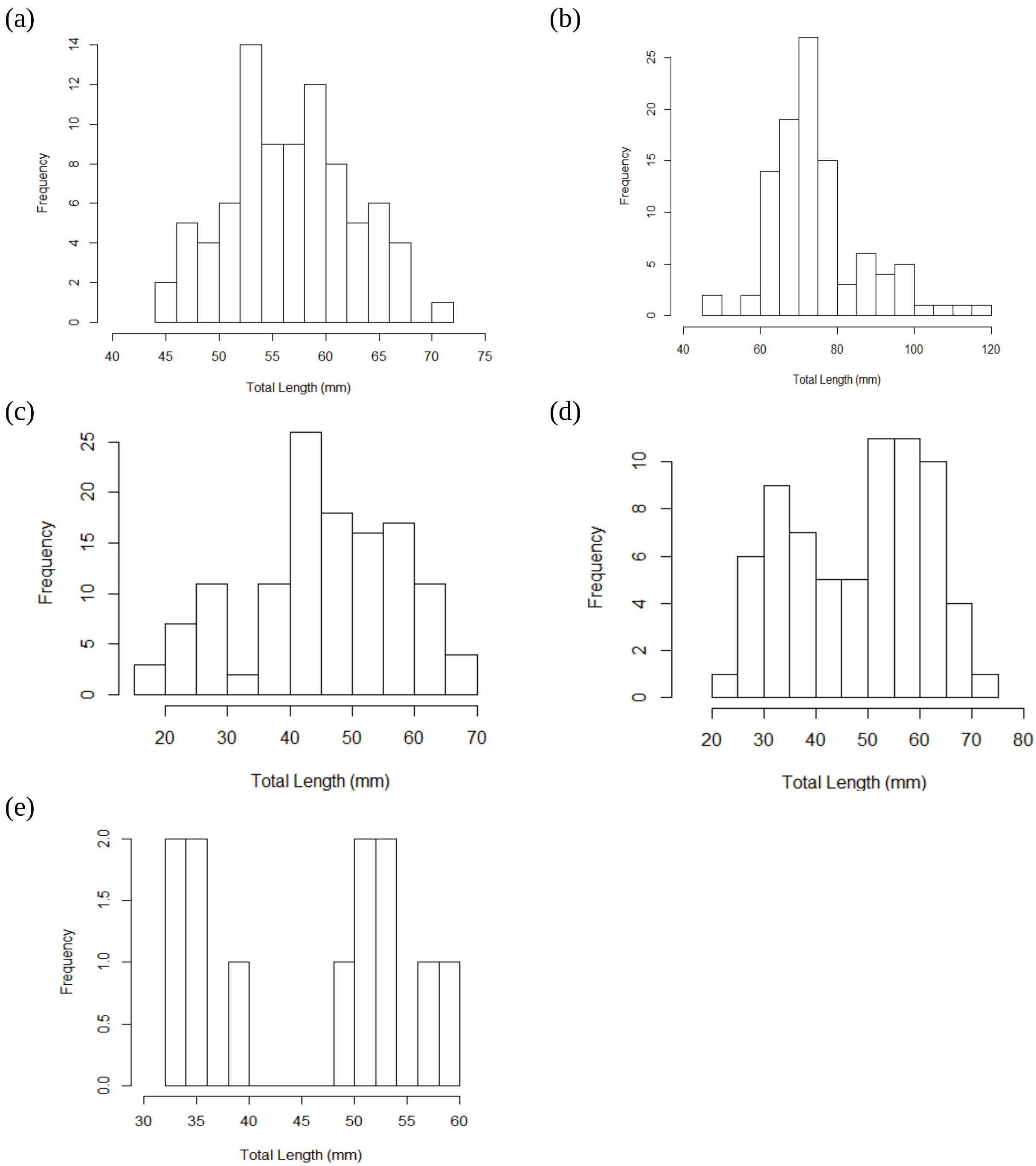


Figure 1. Total length-frequency histograms of (a) Channel Darter (*Percina copelandi*), (b) Logperch (*Percina caprodes*), (c) Fantail Darter (*Etheostoma flabellare*), (d) Tessellated Darter (*Etheostoma olmstedi*) and (e) Johnny Darter (*Etheostoma nigrum*) captured in four tributaries of the Ottawa River (N = 394).

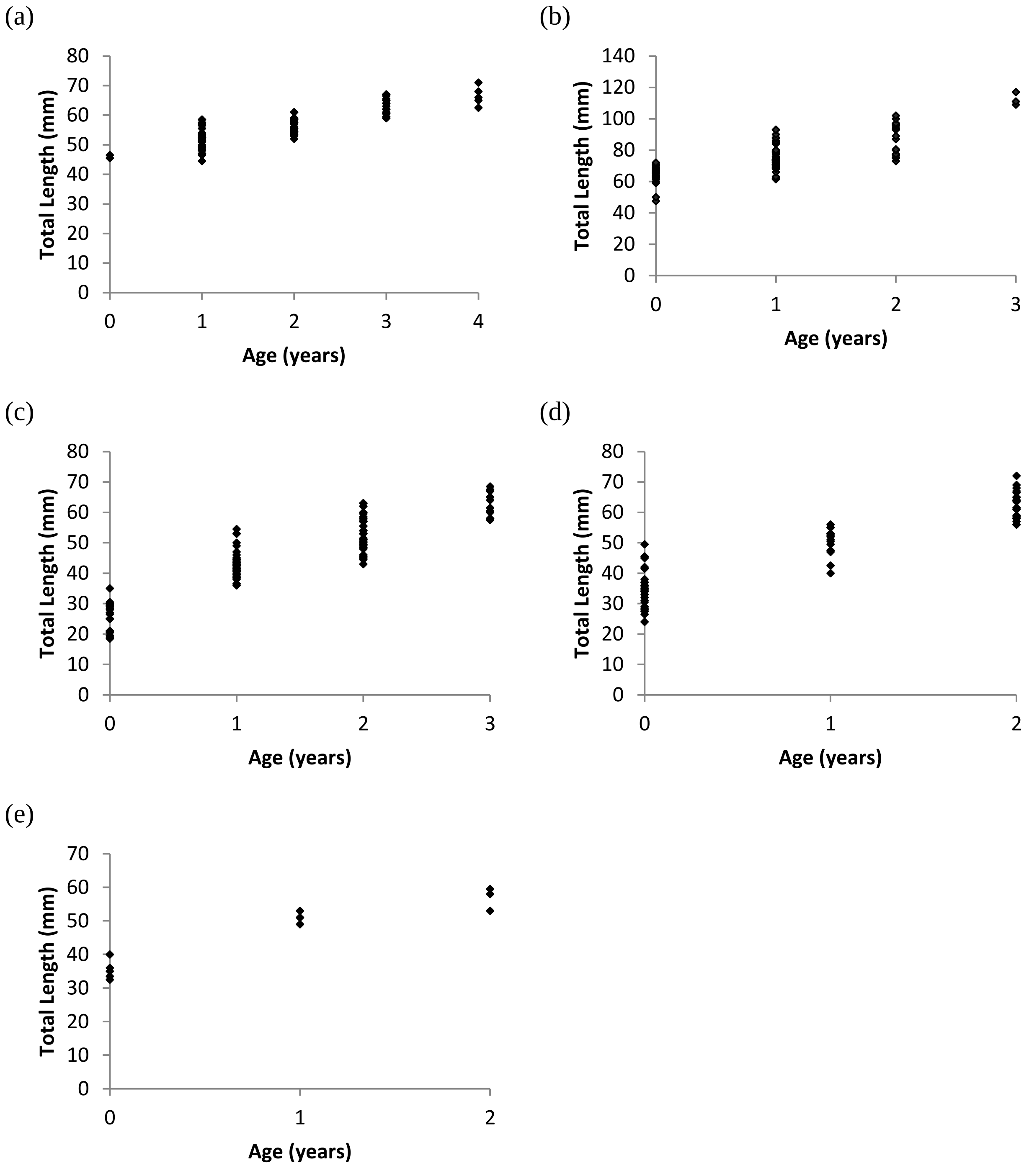


Figure 2. Observed length-at-age relationship for the (a) Channel Darter (*Percina copelandi*), (b) Logperch (*Percina caprodes*), (c) Fantail Darter (*Etheostoma flabellare*), (d) Tessellated Darter (*Etheostoma olmstedi*) and (e) Johnny Darter (*Etheostoma nigrum*) captured in four tributaries of the Ottawa River (N = 394).

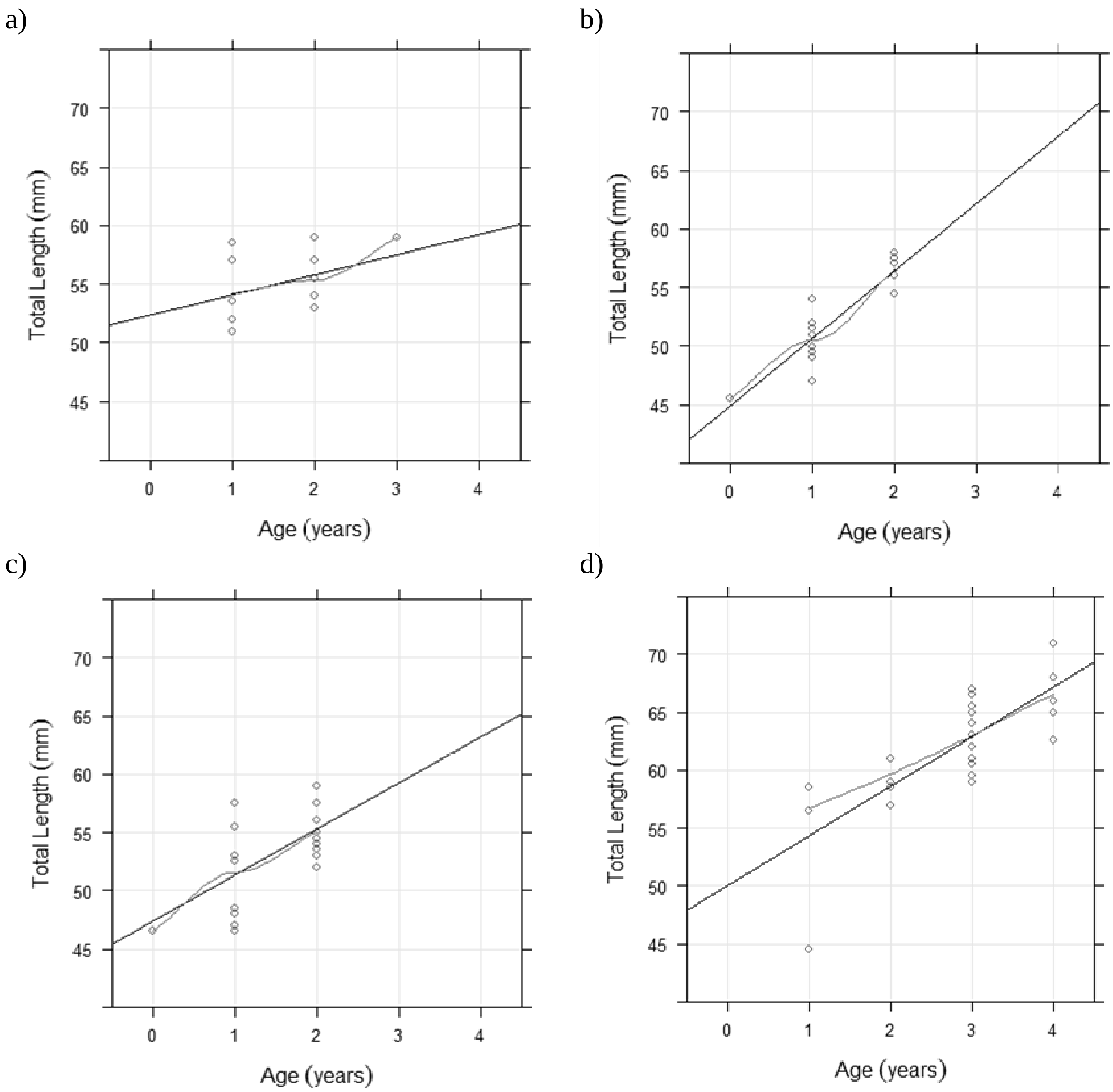


Figure 3. Comparison of the Channel Darter's (*Percina copelandi*) growth rate, demonstrated by the relationship between total length and age, for all four tributaries of the Ottawa River; (a) Saumon River, (b) Petite-Nation River, (c) Blanche River (Thurso) and (d) Blanche River (Gatineau).

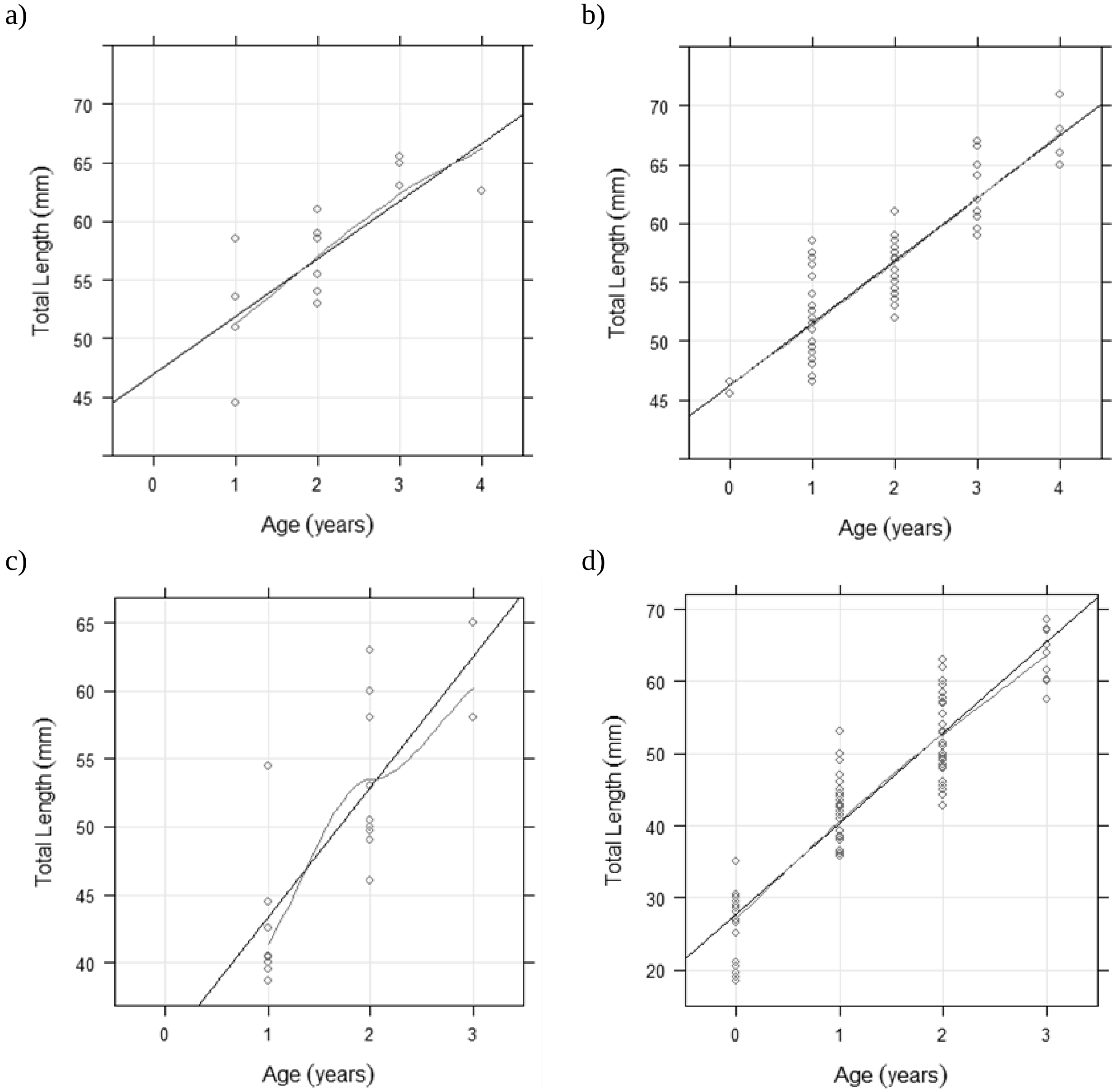
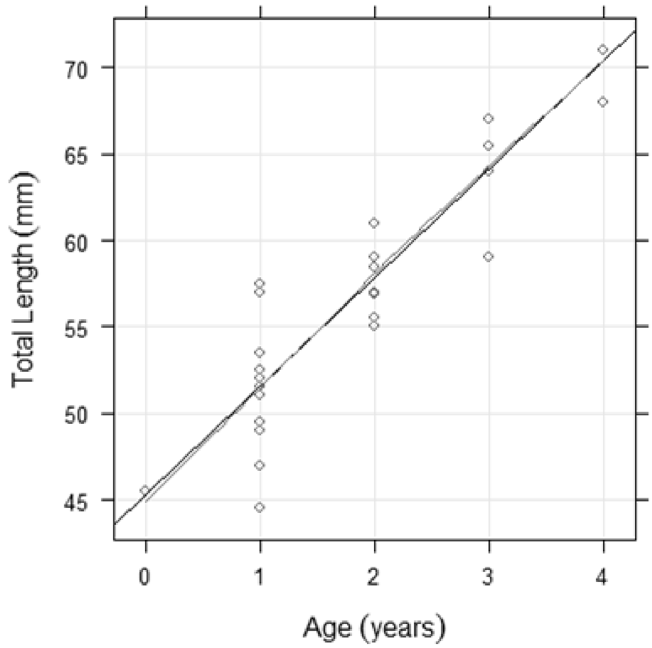


Figure 4. Comparison of the Channel Darter's *Percina copelandi* (a,b) and Fantail Darter's *Etheostoma flabellare* (c,d) growth rates, demonstrated by the relationship between total length and age, for parasitized (a,c) and non-parasitized (b,d) individuals.

a)



b)

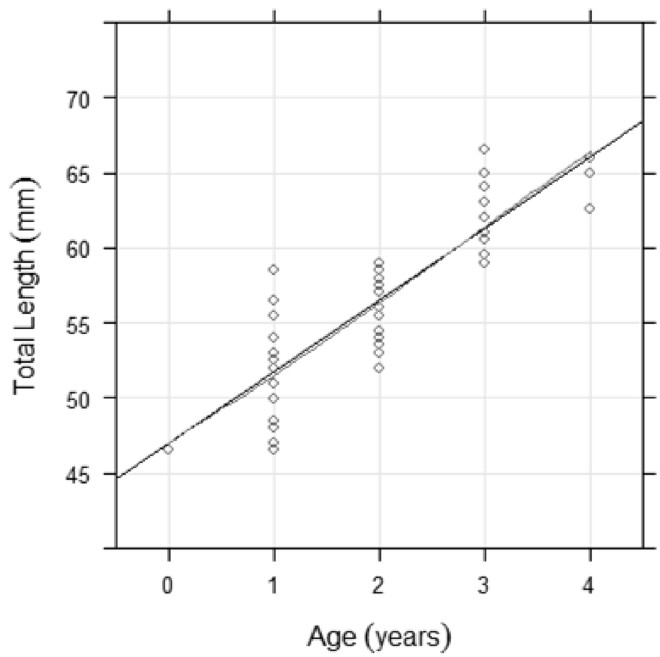


Figure 5. Comparison of the Channel Darter's (*Percina copelandi*) growth rate, demonstrated by the relationship between total length and age, for (a) males and (b) females.

GENERAL DISCUSSION

This study is the first to compare the habitat use, distribution and growth of darter populations present within several rivers in South Western Québec, Canada. This knowledge acquisition is especially important for the Channel Darter, a vulnerable species in Québec and an endangered species in Canada. The Channel Darter`s habitat, in waters less than 0.8 m within the four tributaries of the Ottawa River (Saumon River, Petite-Nation River, Blanche River (Thurso), Blanche River (Gatineau)), can be characterised by coarse and heterogeneous substrate with water velocities greater than 0.25 ms^{-2} in zones with low bank slopes. The distribution of this species seems to only extend to one other tributary of the Ottawa River, the Gatineau River, in which substrate heterogeneity is a good predictor of Channel Darter presence. Physical barriers limit the upstream distribution of the species within all rivers. The Channel Darter matures at age 1+, the majority of its growth in length being attained during its first year. Growth rates differed among rivers, were lower for parasitized individuals and for females.

Substrate size and heterogeneity, water velocity, the distance from the confluence with the Ottawa River and bank slope were important variables in determining the habitat use and partitioning of all darter species within the four tributaries. The Logperch and Fantail Darter`s habitats, in waters less than 0.8m within the four tributaries, can be characterised by coarse and heterogeneous substrate with water velocities greater than 0.25 ms^2 and low banks slopes. The Fantail Darter's habitat can also be characterised by shallow waters. The presence of both species was highly correlated with that of the Channel Darter, all three being present in riffle-like habitats. Thus no clear segregation was found between *Percina* and *Etheostoma*. The Logperch and Fantail Darter were however present upstream of the first physical barriers in the Saumon River and Blanche River (Gatineau) suggesting that the timing of the species post-glacial colonization may differ. The Tessellated Darter was spatially partitioned from the other darter species within the four tributaries. Although the species seems to prefer shallow and slow moving waters over small substrate, it was often found in silt dominated habitats. The Johnny Darter was the least abundance darter present within three of the four tributaries, limiting the habitat characterisation of this species. It seems to prefer coarse and heterogeneous substrate. Further investigation of the suitability of habitats upstream of natural barriers and in other tributaries of the Ottawa River should be conducted to determine whether the local distribution of the Channel Darter could be expanded through introductions. In addition, the juvenile (age 0+) habitat of this species remains unknown and should be subject to further studies. Lastly the fitness consequences of habitat associations in darters remains unclear, as well as the role that parasitism plays in the growth of these species.

APPENDIX A

TABLES

Table A1. Tetrachoric correlation matrix for the occurrence of the five darter species (Channel Darter *Percina copelandi*, Logperch *Percina caprodes*, Fantail Darter *Etheostoma flabellare*, Tessellated Darter *Etheostoma olmstedi* and Johnny Darter *Etheostoma nigrum*) in four tributaries of the Ottawa River (Québec, Canada) sampled in 2011 and 2012 (N=1133).

			Saumon		
	P. copelandi	***P. caprodes***	***E. flabellare***	***E. olmstedi***	***E. nigrum***
P. copelandi	1.00	-	-	-	-
P. caprodes	**0.60**	1.00	-	-	-
E. flabellare	**0.49**	0.18	1.00	-	-
E. olmstedi	-0.19	-0.17	**-0.50**	1.00	-
E. nigrum	-0.04	0.11	0.09	-0.02	1.00
			Petite-Nation		
	P. copelandi	***P. caprodes***	***E. flabellare***	***E. olmstedi***	***E. nigrum***
P. copelandi	1.00	-	-	-	-
P. caprodes	**0.83**	1.00	-	-	-
E. flabellare	**0.70**	0.38	1.00	-	-
E. olmstedi	-0.21	-0.27	0.03	1.00	-
E. nigrum	NA	NA	NA	NA	NA
			Blanche (Thurso)		
	P. copelandi	***P. caprodes***	***E. flabellare***	***E. olmstedi***	***E. nigrum***
P. copelandi	1.00	-	-	-	-
P. caprodes	**0.59**	1.00	-	-	-
E. flabellare	0.35	0.33	1.00	-	-
E. olmstedi	-0.15	0.30	0.09	1.00	-
E. nigrum	**0.55**	**0.53**	**0.89**	0.10	1.00
			Blanche (Gatineau)		
	P. copelandi	***P. caprodes***	***E. flabellare***	***E. olmstedi***	***E. nigrum***
P. copelandi	1.00	-	-	-	-
P. caprodes	**0.58**	1.00	-	-	-
E. flabellare	**0.87**	**0.53**	1.00	-	-
E. olmstedi	-0.39	-0.19	**-0.44**	1.00	-
E. nigrum	0.40	**0.69**	0.35	-0.13	1.00

Table A2. Among-station variations in habitat variables of sampled tributaries of the Ottawa River, Québec, Canada (N=1133).

Means for the habitat variables between all four tributaries were compared using a Bonferroni adjusted pairwise t-test.

	Saumon (N=349)		Petite-Nation (N=304)		Blanche (Thurso, N=267)		Blanche (Gatineau, N=213)	
Habitat variable	**Mean (SE)***	**Range**	**Mean (SE)***	**Range**	**Mean (SE)***	**Range**	**Mean (SE)***	**Range**
Water depth (m)	0.36 (7.6^{-3})^{A}	0.09 – 0.75	0.37 (9.4^{-3})^{A}	0.09 – 0.75	0.43 (1.0^{-2})^{B}	0.10 – 0.79	0.39 (1.1^{-2})^{AB}	0.11 – 0.89
Distance to bank (m)	2.44 (0.1)^{A}	0.25 – 10	1.68 (0.1)^{B}	0.25 – 10	2.28 (0.2)^{A}	0.25 – 20	2.11 (0.1)^{AB}	0.25 - 15
Primary substrate (mm)	95.86 (7.1)^{A}	0.125 – 1000	55.93 (9.1)^{B}	0.125 – 1000	9.14 (3.2)^{C}	0.125 – 375	53.9 (8.7)^{B}	0.125 – 1000
Substrate heterogeneity	2.61 (0.1)^{A}	1 – 5	1.91 (0.1)^{B}	1 – 5	1.28 (3.9^{-2})^{C}	1 – 5	2.02 (0.1)^{B}	1 – 5
Vegetative cover (%)	18.70 (1.5)^{A}	0 – 87.5	12.92 (1.2)^{B}	0 – 87.5	31.51 (1.7)^{C}	0 – 87.5	17.7 (1.8)^{AB}	0 – 87.5
Periphyton cover (%)	6.25 (0.9)^{A}	0 – 87.5	1.64 (0.4)^{B}	0 – 87.5	16.65 (1.1)^{C}	0 – 87.5	19.2 (1.5)^{C}	0 – 87.5
Water velocity (ms^{-1})	0.49 (3.5^{-2})^{A}	0 – 2.743	0.12 (1.3^{-2})^{B}	0 – 1.402	0.09 (1.3^{-2})^{B}	0 - 1.036	0.20 (3.1^{-2})^{B}	0 – 3.079
Water temperature (°C)	17.66 (0.4)^{A}	5.0 – 23.0	19.40 (0.4)^{B}	7.3 – 24.4	20.40 (0.4)^{B}	9.45 – 24.1	19.0 (0.5)^{AB}	9.4 – 24.3
Bank slope (%)	26.16 (1.3)	1.67 – 188	43.31 (2.7)	2.05 – 340	33.76 (1.4)	1 – 204	31.38 (1.7)	1.23 - 180
Distance from Ottawa River (km)	5.73 (0.2)^{A}	0 – 13.8	3.48 (0.1)^{B}	0 – 6.8	3.24 (0.1)^{B}	0 – 6.4	11.60 (0.9)^{C}	0 – 46

*Different letters represent means that varied significantly (p-value<0.05

Table A3. Comparison of the Channel Darter`s (*Percina copelandi*) use and the availability of eight habitat variables measured within four tributaries of the Ottawa River, Québec, Canada. The Channel Darter was observed in 99 stations.

Parameter		**Usage (%)**	**Availability (%)**	**Usage Rank**	**Availability Rank**	**Rank Difference**	**Conclusion**
Depth	[0-20[	19.19	12.97	3	3	0	Null
	[20-40[	53.54	46.87	1	1	0	Null
	[40-60[	25.25	29.83	2	2	0	Null
	≥60	2.02	10.33	4	4	0	Null
Substrate	2	6.06	62.93	5	1	4	Avoided
	3	15.15	12.36	2	3	-1	Preferred
	4	5.05	0.97	6	7	-1	Preferred
	5	8.08	3.44	4	5	-1	Preferred
	6	53.54	12.89	1	2	-1	Preferred
	7	10.10	5.47	3	4	-1	Preferred
	8	1.01	1.41	7.5	6	1.5	NA
	9	1.01	0.53	7.5	8	-0.5	NA
Heterogeneity	1	5.05	46.87	5	1	4	Avoided
	2	23.23	27.63	3	2	1	Avoided
	3	29.29	9.62	1	4	-3	Preferred
	4	24.24	10.41	2	3	-1	Preferred
	5	18.18	5.47	4	5	-1	Preferred
Vegetation	1	72.73	44.22	1	1	0	Null
	2	20.20	26.48	2	2	0	Null
	3	4.04	12.89	3	3	0	Null
	4	3.03	8.83	4	4	0	Null
	5	0	7.59	5	5	0	Null
Periphyton	1	46.46	56.49	1	1	0	Null
	2	33.33	32.04	2	2	0	Null
	3	17.17	6.62	3	3	0	Null
	4	2.02	2.65	4	4	0	NA
	5	1.01	2.21	5	5	0	NA
Woody Debris	0	75.76	68.58	1	1	0	Null
	1	24.24	31.42	2	2	0	Null
Current Velocity	0	2.02	58.52	6	1	5	Avoided
	]0-0.25[	14.14	14.12	4.5	2	2.5	Avoided
	[0.25-0.50[	29.29	11.30	1	3	-2	Preferred
	[0.50-0.75[	21.21	4.85	2	5	-3	Preferred
	[0.75-1.0[	14.14	4.06	4.5	6	-1.5	Preferred
	≥1.0	19.19	7.15	3	4	-1	Preferred
Bank Slope	[0-10[	62.62	14.74	1	4	-3	Preferred
	[10-20[	25.25	22.68	2	1	1	Avoided
	[20-30[	8.08	21.89	3	2	1	Avoided
	[30-40[	1.01	16.86	5.5	3	2.5	Avoided
	[40-50[	1.01	9.53	5.5	6	-0.5	Preferred
	[50-60[	1.01	3.44	5.5	7	-1.5	NA
	≥60	1.01	10.86	5.5	5	0.5	Avoided

Table A4. Comparison of the Logperch`s (*Percina caprodes*) use and the availability of eight habitat variables measured within four tributaries of the Ottawa River, Québec, Canada. The Logperch was observed in 101 stations.

Parameter		Usage (%)	Availability (%)	Usage Rank	Availability Rank	Rank Difference	Conclusion
Depth	[0-20[	8.91	12.97	3	3	0	Null
	[20-40[	48.51	45.87	1	1	0	Null
	[40-60[	34.65	29.83	2	2	0	Null
	≥60	7.92	10.33	4	4	0	Null
Substrate	2	19.80	62.93	2	1	1	Avoided
	3	12.87	12.36	4	3	1	Avoided
	4	0	0.97	8	7	1	NA
	5	4.95	3.44	5	5	0	Null
	6	44.55	12.89	1	2	-1	Preferred
	7	14.85	5.47	3	4	-1	Preferred
	8	1.98	1.41	6	6	0	NA
	9	0.99	0.53	7	8	-1	NA
Heterogeneity	1	11.88	46.87	5	1	4	Avoided
	2	30.69	27.63	1	2	-1	Preferred
	3	24.75	9.62	2	4	-2	Preferred
	4	15.84	10.42	4	3	1	Avoided
	5	16.83	5.47	3	5	-2	Preferred
Vegetation	1	64.36	44.22	1	1	0	Null
	2	21.78	26.78	2	2	0	Null
	3	10.89	12.89	3	3	0	Null
	4	2.97	8.83	4	4	0	Null
	5	0	7.59	5	5	0	Null
Periphyton	1	63.37	56.49	1	1	0	Null
	2	21.78	32.04	2	2	0	Null
	3	13.86	6.62	3	3	0	Null
	4	0.99	2.65	4	4	0	NA
	5	0	2.21	5	5	0	NA
Woody Debris	0	79.21	68.58	1	1	0	Null
	1	20.79	31.42	2	2	0	Null
Current Velocity	0	15.84	59.52	3.5	1	2.5	Avoided
	]0-0.25[	17.82	14.12	2	2	0	Null
	[0.25-0.50[	23.76	11.30	1	3	-2	Preferred
	[0.50-0.75[	15.84	4.85	3.5	5	-1.5	Preferred
	[0.75-1.0[	12.87	4.06	6	6	0	Null
	≥1.0	13.86	7.15	5	4	1	Avoided
Bank Slope	[0-10[	35.64	14.74	1	4	-3	Preferred
	[10-20[	28.71	22.68	2	1	1	Avoided
	[20-30[	12.87	21.89	3	2	1	Avoided
	[30-40[	9.90	16.86	4	3	1	Avoided
	[40-50[	4.95	9.53	5.5	6	-0.5	Preferred
	[50-60[	2.97	3.44	7	7	0	NA
	≥60	4.95	10.86	5.5	5	0.5	Avoided

Table A5. Comparison of the Fantail Darter`s (*Etheostoma flabellare*) use and the availability of eight habitat variables measured within four tributaries of the Ottawa River, Québec, Canada. The Channel Darter was observed in 118 stations.

Parameter		**Usage (%)**	**Availability (%)**	**Usage Rank**	**Availability Rank**	**Rank Difference**	**Conclusion**
Depth	[0-20[	21.19	12.97	2	3	-1	Preferred
	[20-40[	61.86	46.87	1	1	0	Null
	[40-60[	16.10	29.83	3	2	1	Avoided
	≥60	0.85	10.33	4	4	0	Null
Substrate	2	3.39	62.93	4	1	3	Avoided
	3	1.69	12.36	6	3	3	Avoided
	4	2.54	0.97	5	7	-2	Preferred
	5	18.64	3.44	2	5	-3	Preferred
	6	61.86	12.89	1	2	-1	Preferred
	7	11.02	5.47	3	4	-1	Preferred
	8	0	1.41	8	6	2	NA
	9	0.85	0.53	7	8	-1	NA
Heterogeneity	1	0	46.87	5	1	4	Avoided
	2	9.32	27.63	4	2	2	Avoided
	3	39.83	9.62	1	4	-3	Preferred
	4	25.42	10.41	2.5	3	-0.5	Preferred
	5	25.42	5.47	2.5	5	-2.5	Preferred
Vegetation	1	83.89	44.22	1	1	0	Null
	2	9.32	26.48	2	2	0	Null
	3	3.39	12.89	3	3	0	Null
	4	2.54	8.83	4	4	0	Null
	5	0.85	7.59	5	5	0	Null
Periphyton	1	51.69	56.49	1	1	0	Null
	2	29.66	32.04	2	2	0	Null
	3	11.86	6.62	3	3	0	Null
	4	5.08	2.65	4	4	0	Null
	5	1.69	2.21	5	5	0	NA
Woody Debris	0	97.46	68.58	1	1	0	Null
	1	2.54	31.42	2	2	0	Null
Current Velocity	0	2.54	58.52	6	1	5	Avoided
	]0-0.25[	8.47	14.12	5	2	3	Avoided
	[0.25-0.50[	20.34	11.30	2	3	-1	Preferred
	[0.50-0.75[	16.95	4.85	4	5	-1	Preferred
	[0.75-1.0[	17.80	4.06	3	6	-3	Preferred
	≥1.0	33.90	7.15	1	4	-3	Preferred
Bank Slope	[0-10[	56.78	14.74	1	4	-3	Preferred
	[10-20[	23.83	22.68	2	1	1	Avoided
	[20-30[	11.86	21.89	3	2	1	Avoided
	[30-40[	3.40	16.86	4	3	1	Avoided
	[40-50[	1.69	9.53	5.5	6	-0.5	Preferred
	[50-60[	0.85	3.44	7	7	0	NA
	≥60	1.69	10.86	5.5	5	0.5	Avoided

Table A6. Comparison of the Tessellated Darter`s (*Etheostoma olmstedi*) use and the availability of eight habitat variables measured within four tributaries of the Ottawa River, Québec, Canada. The Tessellated Darter was observed in 178 stations.

Parameter		Usage (%)	Availability (%)	Usage Rank	Availability Rank	Rank Difference	Conclusion
Depth	[0-20[	7.30	12.97	3	3	0	Null
	[20-40[	58.43	46.87	1	1	0	Null
	[40-60[	229.21	29.83	2	2	0	Null
	≥60	5.06	10.33	4	4	0	Null
Substrate	2	71.35	62.93	1	1	0	Null
	3	16.85	12.36	2	3	-1	Preferred
	4	1.69	0.97	5	7	-2	Preferred
	5	1.12	3.44	6	5	1	NA
	6	4.49	12.89	3	2	1	Avoided
	7	3.93	5.47	4	4	0	Null
	8	0.56	1.41	7	6	1	NA
	9	0	0.53	8	8	0	NA
Heterogeneity	1	52.81	46.87	1	1	0	Null
	2	34.27	27.63	2	2	0	Null
	3	6.18	9.62	3.5	4	-0.5	Preferred
	4	6.18	10.41	3.5	3	0.5	Avoided
	5	0.56	5.47	5	5	0	Null
Vegetation	1	29.21	44.22	2	1	1	Avoided
	2	37.08	26.48	1	2	-1	Preferred
	3	16.29	12.89	3	3	0	Null
	4	10.11	8.83	4	4	0	Null
	5	7.30	7.59	5	5	0	Null
Periphyton	1	50.56	56.49	1	1	0	Null
	2	33.71	32.04	2	2	0	Null
	3	10.67	6.62	3	3	0	Null
	4	2.25	2.65	5	4	1	NA
	5	2.81	2.21	4	5	-1	NA
Woody Debris	0	50.56	68.58	1	1	0	Null
	1	49.44	31.42	2	2	0	Null
Current Velocity	0	75.84	58.52	1	1	0	Null
	]0-0.25[	13.48	14.12	2	2	0	Null
	[0.25-0.50[	9.55	11.30	3	3	0	Null
	[0.50-0.75[	1.12	4.85	4	5	-1	NA
	[0.75-1.0[	0	4.06	5.5	6	-0.5	NA
	≥1.0	0	7.15	5.5	4	1.5	Avoided
Bank Slope	[0-10[	7.30	14.74	6	4	2	Avoided
	[10-20[	19.10	22.68	3	1	2	Avoided
	[20-30[	24.16	21.89	1	2	-1	Preferred
	[30-40[	21.35	16.86	2	3	-1	Preferred
	[40-50[	11.24	9.53	5	6	-1	Preferred
	[50-60[	4.49	3.44	7	7	0	NA
	≥60	12.36	10.86	4	5	-1	Preferred

Table A7. Comparison of the Johnny Darter`s (*Etheostoma nigrum*) use and the availability of eight habitat variables measured within four tributaries of the Ottawa River, Québec, Canada. The Tessellated Darter was observed in 178 stations.

Parameter		**Usage (%)**	**Availability (%)**	**Usage Rank**	**Availability Rank**	**Rank Difference**	**Conclusion**
Depth	[0-20[	5.00	12.97	3.5	3	0.5	Avoided
	[20-40[	80.00	46.87	1	1	0	Null
	[40-60[	10.00	29.83	2	2	0	Null
	≥60	5.00	10.33	3.5	4	-0.5	Preferred
Substrate	2	45.00	62.93	1	1	0	Null
	3	40.00	12.36	2	3	-1	Preferred
	4	0	0.97	6.5	7	-0.5	NA
	5	0	3.44	6.5	5	1.5	NA
	6	10.0	12.89	3	2	1	Avoided
	7	0	5.47	6.5	4	2.5	NA
	8	0	1.41	6.5	6	0.5	NA
	9	5.00	0.53	4	8	-4	NA
Heterogeneity	1	20	46.87	2	1	1	Avoided
	2	50	27.63	1	2	-1	Preferred
	3	5	9.62	5	4	1	Avoided
	4	15	10.41	3	3	0	Null
	5	10	5.47	4	5	-1	Preferred
Vegetation	1	30	44.22	2	1	1	Avoided
	2	35	26.48	1	2	-1	Preferred
	3	15	12.89	3	3	0	Null
	4	10	8.83	4.5	4	0.5	Avoided
	5	10	7.59	4.5	5	-0.5	Preferred
Periphyton	1	20	56.49	2.5	1	1.5	Avoided
	2	55	32.04	1	2	-1	Preferred
	3	20	6.62	2.5	3	-0.5	Preferred
	4	0	2.65	5	4	1	NA
	5	5	2.21	4	5	-1	NA
Woody Debris	0	40	68.58	2	1	1	Avoided
	1	60	31.42	1	2	-1	Preferred
Current Velocity	0	30.0	58.5	2	1	1	Avoided
	]0-0.25[	15.0	14.1	3	2	1	Avoided
	[0.25-0.50[	40.0	11.3	1	3	-2	Preferred
	[0.50-0.75[	5.0	4.9	5	5	0	Null
	[0.75-1.0[	10.0	4.1	4	6	-2	Preferred
	≥1.0	0.0	7.15	6	4	2	Avoided
Bank Slope	[0-10[	30	14.74	1	4	-3	Preferred
	[10-20[	25	22.68	2	1	1	Avoided
	[20-30[	20	21.89	3	2	1	Avoided
	[30-40[	15	16.86	4	3	1	Avoided
	[40-50[	2	9.53	5.5	6	-0.5	Preferred
	[50-60[	0	3.44	7	7	0	NA
	≥60	5	10.86	5.5	5	0.5	Avoided

Table A8. Results of the final logistic regression model predicting the presence of the Channel Darter (*Percina copelandi*), for which the McFadden's pseudo R^2 is 0.399.

Variable	**Estimated Coefficients**	**SE**	**p-value**	**Chi-square**	**DF**	**p-value (>Chisq)**
Intercept ($ß_0$)	-3.95	0.68	6.27^{-9}			
Heterogeneity	0.42	0.13	9.89^{-4}	18.01	1	2.20^{-5}
Velocity	0.71	0.48	0.138			
Bank Slope	-0.06	0.01	1.53^{-5}	41.04	1	1.49^{-10}
Sampled Area	0.18	0.03	6.05^{-8}	47.80	1	4.72^{-12}
River				3.17	3	0.367
Blanche (T)	-0.33	0.73	0.653			
Petite-Nation	0.09	0.61	0.881			
Saumon	0.63	0.52	0.233			
River: Velocity				18.36	3	3.71^{-4}
Blanche (T)	3.12	1.31	0.017			
Petite-Nation	1.50	0.96	0.119			
Saumon	-0.86	0.53	0.108			

Table A9. Results of the final logistic regression model predicting the presence of the Logperch (*Percina caprodes*), for which the McFadden's pseudo R^2 is 0.199.

Variable	Estimated Coefficients	SE	p-value	Chi-square	DF	p-value (>Chisq)
Intercept ($ß_0$)	-7.63	1.21	2.76^{-10}			
Substrate	0.01	3.4^{-3}	0.004	12.92	1	3.24^{-4}
Velocity	0.62	0.22	0.005	7.35	1	0.007
Sampled Area	0.18	0.03	2.64^{-11}	46.07		1.14^{-11}
River				36.39	3	0.007
BT	3.68	1.17	0.002			
PN	3.90	1.19	0.001			
SA	4.29	1.16	2.23^{-4}			
River: Substrate				12.12	3	6.19^{-8}
BT	-2.7^{-3}	4.2^{-3}	0.530			
PN	-0.01	3.6^{-3}	0.038			
SA	-0.01	3.7^{-3}	0.011			

Table A10. Results of the final logistic regression model predicting the presence of the Fantail Darter (*Etheostoma flabellare*), for which the McFadden's pseudo R^2 is 0.462.

Variable	Estimated Coefficients	SE	p-value	Chi-square	DF	p-value (>Chisq)
Intercept	-4.81	0.66	3.92^{-13}			
Depth	-3.96	1.02	1.05^{-4}	16.46	1	4.97^{-5}
Heterogeneity	0.68	0.12	2.64^{-8}	32.33	1	1.30^{-8}
Periphyton	0.03	0.01	3.47^{-5}	16.07	1	6.12^{-5}
Velocity	1.03	0.22	3.75^{-6}	22.88	1	1.73^{-6}
Sampled Area	0.12	0.03	1.58^{-4}	15.49	1	8.31^{-5}
River				40.06	3	2.675^{-8}
Blanche (T)	-0.53	0.63	0.40			
Petite-Nation	-1.02	0.70	0.15			
Saumon	1.39	0.38	2.13^{-4}			

Table A11. Results of the final logistic regression model predicting the presence of the Tessellated Darter (*Etheostoma olmstedi*), for which the McFadden's pseudo R^2 is 0.133.

Variable	**Estimated Coefficients**	**SE**	**p-value**	**Chi-square**	**DF**	**p-value (>Chisq)**
Intercept	-0.337	0.619	0.1601			
Depth	-1.216	0.558	0.0293	4.870	1	0.0027
Woody D	0.710	0.181	8.630^{-5}	15.361	1	8.897^{-5}
Velocity	-2.036	0.566	0.0003	19.855	1	8.356^{-6}
Dist	-0.049	0.025	0.0539	4.709	1	0.0300
Land U	-0.037	0.113	0.7398	0.111	1	0.7393
River				26.178	3	8.756^{-6}
BT	-1.279	0.663	0.0536			
PN	-1.752	0.667	0.0087			
SA	2.061	0.760	0.0067			
River:LandU				25.508	3	1.209^{-5}
BT	0.183	0.167	0.2736			
PN	0.348	0.166	0.0359			
SA	-0.605	0.193	0.0017			
River:Dist				13.977	3	0.0029
BT	0.106	0.100	0.2886			
PN	-0.062	0.115	0.5934			
SA	-0.300	0.100	0.0017			

Table A12. Results of the final logistic regression model predicting the presence of the Johnny Darter (*Etheostoma nigrum*), for which the McFadden's pseudo R^2 is 0.267.

Variable	Estimated Coefficients	SE	p-value	Chi-square	DF	p-value (>Chisq)
Intercept	-6.558	1.203	4.970^{-8}			
Substrate	-0.020	0.009	0.0294	8.934	1	0.0028
Hetero	0.982	0.314	0.0018	8.912	1	0.0028
WoodyD	0.902	0.763	0.2370	1.367	1	0.2424
River				20.398	3	0.0001
BT	1.590	0.829	0.0554			
PN	-17.310	142.20	0.9903			
SA	1.452	0.801	0.0697			
Period				1.945	2	0.3782
2	-1.394	1.916	0.4670			
3	-3.319	2.898	0.2522			
Period:Substrate				15.741	2	0.0004
2	0.030	0.010	0.0032			
3	0.018	0.013	0.1474			
Periode:Hetero				4.677	2	0.0965
2	-1.382	0.707	0.0505			
3	0.005	0.645	0.9323			
Periode:Woody				6.259	2	0.0437
2	3.663	1.972	0.0632			
3	2.337	2.135	0.2738			

Table A13 . Correlation matrix demonstrating the Pearson moment correlation coefficients (*r*) for the ordinal and quantitative environmental variables measured within four tributaries of the Ottawa River ; water temperature (Te), water depth (De), primary substrate (Su), substrate heterogeneity (He), vegetative cover (Ve), periphyton cover (Pe), woody debris (Wo), water velocity (Wa), bank slope (Sl) and the distance from the Ottawa River (Di).

	Te	De	Su	He	Ve	Pe	Wo	Wa	Sl	Di
Te	1.00	-	-	-	-	-	-	-	-	-
De	-0.02	1.00	-	-	-	-	-	-	-	-
Su	-0.05	-0.06	1.00	-	-	-	-	-	-	-
He	-0.1	-0.14	0.55	1.00	-	-	-	-	-	-
Ve	0.16	0.08	-0.26	-0.30	1.00	-	-	-	-	-
Pe	0.21	0.10	-0.05	-0.07	0.37	1.00	-	-	-	-
Wo	-0.09	-0.01	-0.24	-0.24	-0.11	0.01	1.00	-	-	-
Wa	-0.24	-0.08	0.46	0.59	-0.28	-0.09	-0.21	1.00	-	-
Sl	0.07	0.20	-0.07	-0.15	-0.05	-0.07	0.06	-0.22	1.00	-
Di	-0.06	-0.10	0.30	0.41	-0.25	0.07	-0.13	0.41	-0.10	1.00

APPENDIX B

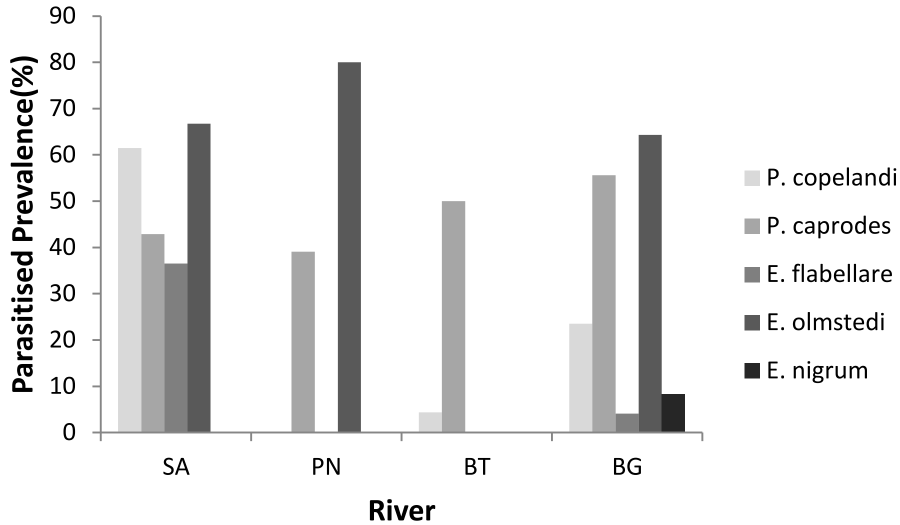
Tables

Table B1. Mean values of the environmental variables measured in stations where scale samples were collected from five species of darters from four tributaries of the Ottawa River: Saumon River (SA), Petite-Nation River (PN), Blanche River (Thurso, BT) and Blanche River (Gatineau, BG). Eight ordinal and quantitative variables were measured; water temperature (Te), primary substrate (Su), substrate heterogeneity (He), vegetative cover (Ve), periphyton cover (Pe), woody debris (Wo), water velocity (Wa) and bank slope (Sl). The number of stations in which fish scales were collected (N), the number of individuals captured in the station (#) and the average number of other darters also present in that station (Da) are also shown.

River	**N**	**#**	**Da**	**Te(°C)**	**Su**	**He**	**Ve**	**Pe**	**Wo**	**Wa(m/s)**	**Sl(%)**
Channel Darter (*Percina copelandi*)											
SA	4	10	12.0	20.5	5.5	3.3	1.8	2.5	0.5	1.4	7.2
PN	6	11	4.2	20.8	4.8	2.8	2.0	1.8	0.3	1.3	20.4
BT	6	23	3.5	22.5	3.0	2.0	1.8	2.3	1.0	0.9	4.4
BG	9	26	12.0	17.3	4.8	3.3	1.9	2.3	0.4	1.5	14.4
Logperch (*Percina caprodes*)											
SA	3	5	13.0	17.0	5.7	3.3	2.7	2.7	1.0	0.8	15.4
PN	14	57	1.3	19.2	5.7	3.6	2.4	2.4	0.4	0.8	17.5
BT	6	16	5.5	22.5	3.0	2.0	2.2	2.3	1.0	0.8	9.3
BG	11	3	16.0	17.3	5.3	3.3	2.3	2.3	1.0	0.6	17.8
Fantail Darter (*Etheostoma flabellare*)											
SA	8	70	3.3	18.9	5.3	3.4	1.9	2	0.6	1.3	11.5
BG	10	128	4.3	18.0	5.1	3.5	1.9	2.2	0.4	1.6	12.3
Tessellated Darter (*Etheostoma olmstedi*)											
SA	2	11	14.5	16.8	6.0	3.0	2.0	3.5	1.0	0.8	15.6
PN	3	10	2.3	19.7	2.7	1.3	2.3	1.3	0.7	0.5	16.2
BT	11	32	2.9	20.7	2.5	1.6	2.1	1.8	0.9	0.5	30.3
BG	2	3	24.0	15.9	6.5	4.0	2.5	2.5	1.0	0.7	20.0
Johnny Darter (*Etheostoma nigrum*)											
BG	5	12	14.0	16.7	4.6	3.2	2.2	2.2	0.8	0.7	17.3

Figures

a)



b)

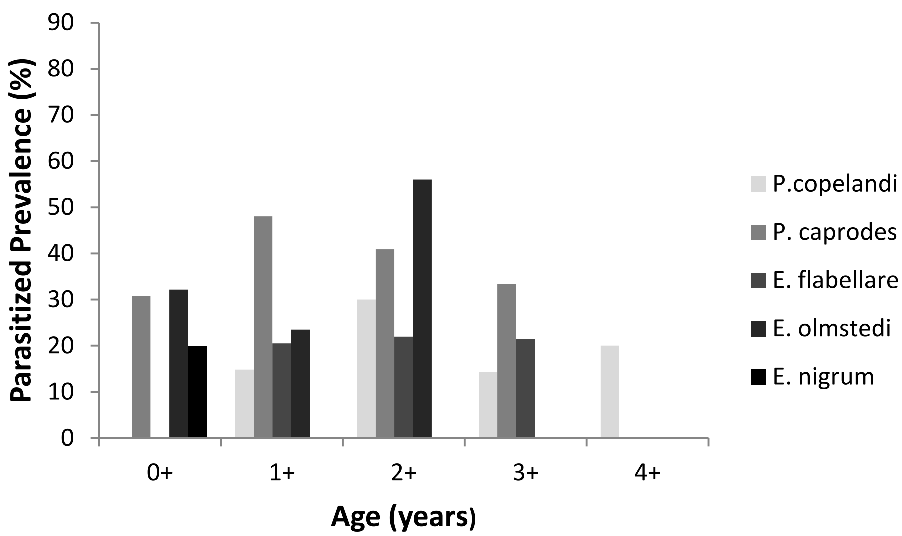


Figure B1 – Parasite prevalence, expressed as a percentage, for each (a) river and (b) age group of five species of darters; Channel Darter (*Percina copelandi*), Logperch (*Percina caprodes*), Fantail Darter (*Etheostoma flabellare*), Tessellated Darter (*Etheostoma olmstedi*) and Johnny Darter (*Etheostoma nigrum*). Rivers sampled are four tributaries of the Ottawa River: Saumon (SA), Petite-Nation (PN), Blanche Thurso (BT) and Blanche Gatineau (BG).

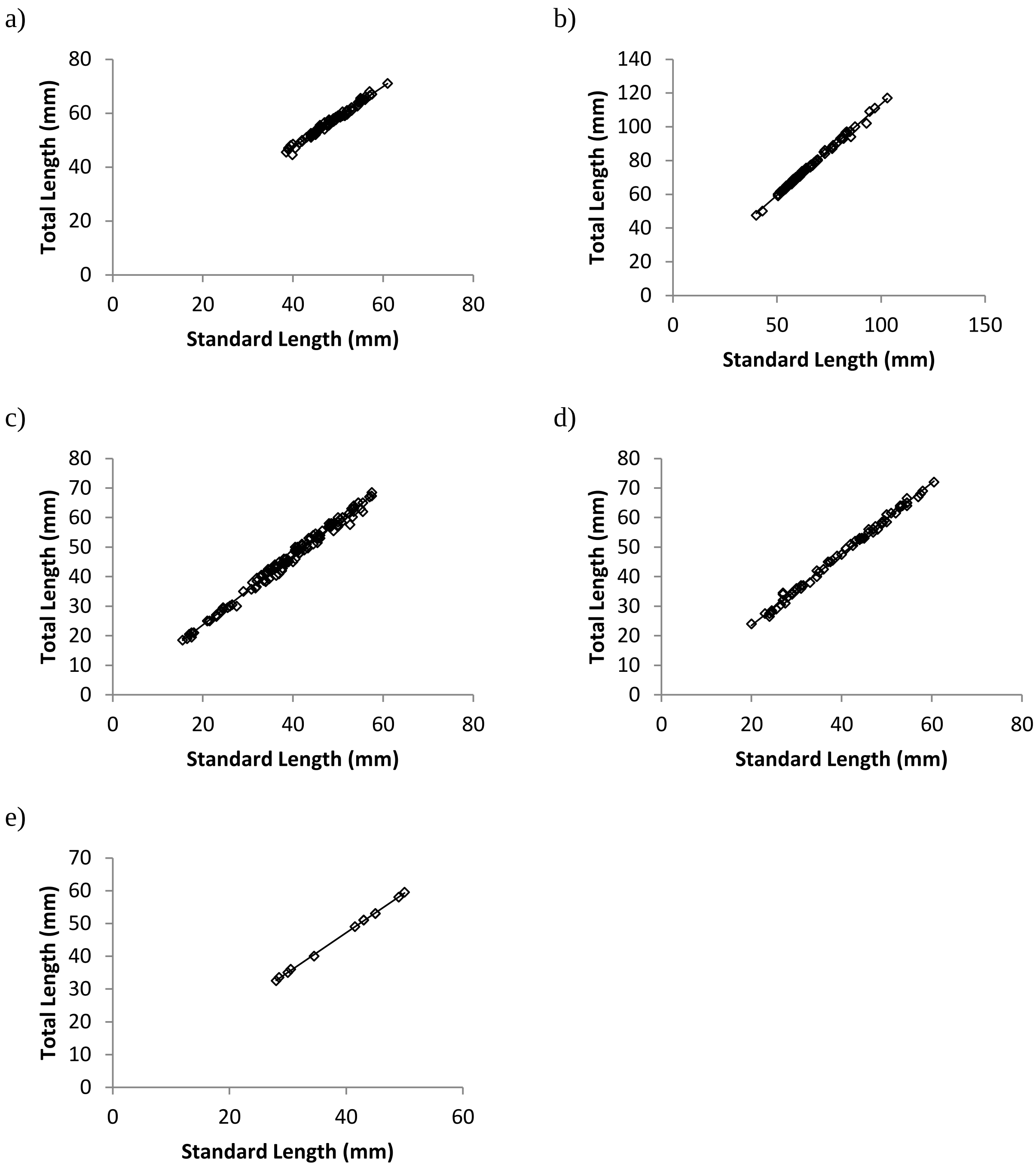


Figure B2. Relationship between total length (TL) and standard length (SL) in the (a) Channel Darter (*Percina copelandi*), (b) Logperch (*Percina caprodes*), (c) Fantail Darter (*Etheostoma flabellare*), (d) Tessellated Darter (*Etheostoma olmstedi*) and (e) Johnny Darter (*Etheostoma nigrum*) captured in four tributaries of the Ottawa River (N = 394).

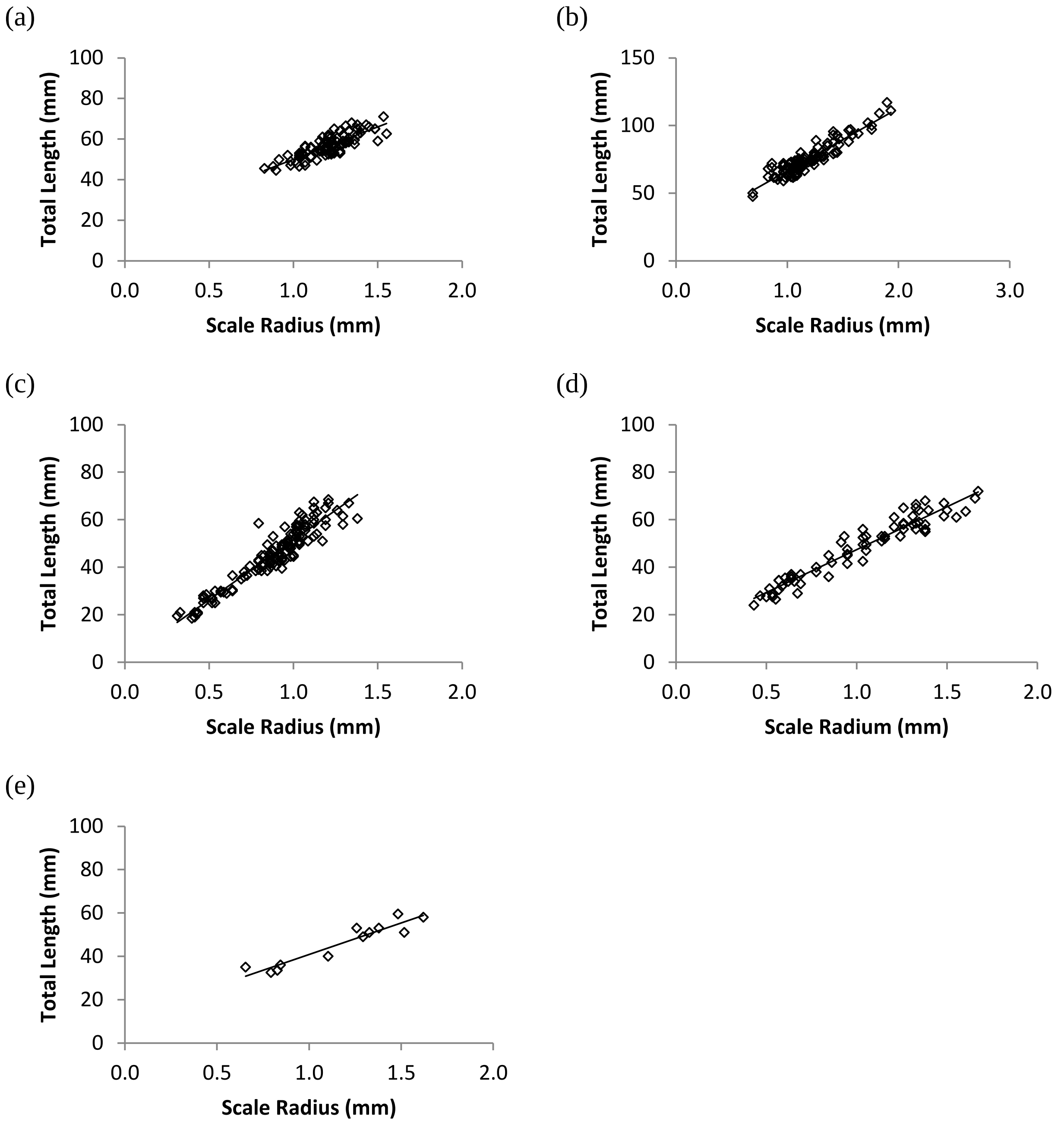


Figure B3. Relationship between total length (TL, mm) and scale radius (SR) in the (a) Channel Darter (*Percina copelandi*), (b) Logperch (*Percina caprodes*), (c) Fantail Darter (*Etheostoma flabellare*), (d) Tessellated Darter (*Etheostoma olmstedi*) and (e) Johnny Darter (*Etheostoma nigrum*) captured in four tributaries of the Ottawa River (N = 394).

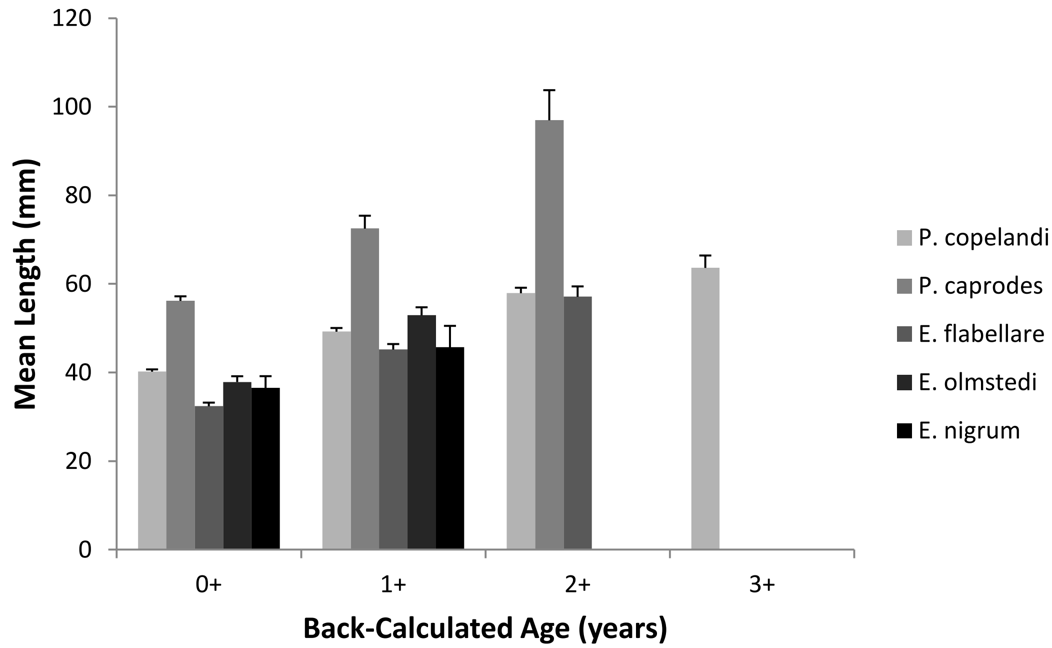


Figure B4. Mean back-calculated length increments (mm) of the five species of darters captured in four tributaries of the Ottawa River (N = 394). Error bars represent positive 95% confidence intervals.