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Habitat losses and anthropogenic barriers as a cause of population decline for American eel (*Anguilla rostrata*) in the St. Lawrence watershed, Canada

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Abstract

American eel (*Anguilla rostrata*) experienced a major decline over past decades. Although fisheries-related mortality could be accurately estimated, there is no global assessment of non-exploitation anthropogenic impacts. Within the St. Lawrence watershed, which contributes about 19% of the freshwater runoff in the species' range, we found that more than 8411 dams were erected whose 151 are equipped with hydroelectricity facilities. These obstacles prevent free access to an estimated 12 140 km^2 of freshwater habitat. Data analysis from three tributaries in the St. Lawrence watershed allowed evaluating annual productivity and production for female from freshwater habitats. Calculation leads to an estimated escapement of 87.1 kg/km^2/year. The extension of this value to the area above barriers in the historic distribution range, suggests that the annual productivity losses could have been as much as 836 500 eels, mostly large fecund females. In comparison, the estuarine fishery at the outlet of the St. Lawrence watershed, with an historical annual peak capture of 340,000 silver eels (1920-2004) represented a loss for the population equivalent to only 40% of the potential production above dams. By preventing upstream passage, dams are clearly a major cause of abundance decline. Thus, re-opening access should be a priority. Simulations of re-opening some access could potentially contribute for 737 000 spawners per year. This net contribution could however only be obtained with the addition of efficient protection devices against mortalities caused by turbines. These actions appear as being among the most efficient to stop the decline of the species.

Introduction

The St. Lawrence River watershed is a large drainage basin inhabited by American eel (*Anguilla rostrata*) from Lake Ontario to the marine waters of the Gulf of St. Lawrence (Fig. 1). With a freshwater runoff averaging 10 100 m³/s on annual basis, it represents approximately 19% of the total freshwater runoff in the species range (Castonguay *et al*. 1994). After entering the Gulf, juvenile eels invade the River itself and all accessible tributaries to complete the freshwater part of their life cycle. They settle in lakes and rivers for relatively long time, up to 20 and even 30 years, until the onset of maturity when they migrate back to the Sargasso Sea to spawn. Annual escapement from freshwater habitat in a given watershed could be seen as an evaluation of productivity for eel.

Commercial fisheries in this water catchment are directed towards juvenile (so-called yellow) and out-migrating (so-called silver) eels and landings are located primarily in the main stem fluvial lakes and in the brackish estuary (Verreault and Dumont 2003). Annual harvest data from commercial fisheries are published by government agencies since 1920. Based on fishermen declaration, these time series have inherent limitations to biological interpretation but provide historical information on eel abundance (Robitaille *et al.* 2003). Among these landing statistics, those concerning silver eel fisheries in the Richelieu River and the St. Lawrence Estuary are the most interesting. Catches from these fisheries are composed exclusively of large out-migrating female from lakes and rivers located upstream (Verdon *et al* 2003; Verreault *et al.* 2003). Under relatively constant fishing effort, annual landings could be seen as annual escapement index for these stocks and they showed dramatic declines since early eighties. From 72.9 tons in 1981, the Richelieu River fishery collapsed in 1997 with a total catch of only 4.7 tons and has been closed the year after (Dumont *et al.* 1997; Verdon *et al.* 2003). Further downstream, the estuarine fishery experienced a significant sharp decrease from 426.2 tons in 1980 to 69.9 in 2003. In the Richelieu River, the decline has been mainly related to the rebuilding of two old cribwork dams in the 1960s (Verdon *et al.* 2003) impeding young up-migrating eels to access Lake Champlain to complete their growth and freshwater cycle. Decreasing silver eels catches in this watershed could likely be linked with recruitment failure in response to blockage by dams. In the estuarine fishery, potential causes of the decline are not so clear. Recruitment index of juvenile eels ascending the eel ladder in Cornwall, at the Lake Ontario outlet, showed drastic decrease from a mean daily number of 27 489 in 1982 to less than 700 in 1995 (Casselman et al. 1997) and this downward trend is continuing (Casselman 2003). Since the contribution of the Upper St. Lawrence and Lake Ontario to the overall downstream migrating eels represented up to 50% to the fishery in recent years (Verreault and Dumont 2003), recruitment failure was likely involved in harvest decline. In their review of the causes of recruitment declining in the St. Lawrence River and Gulf, Castonguay *et al.* (1994) addressed four potential causes: anthropogenic chemical contamination, oceanic changes, commercial fishing, and anthropogenic habitat modification. The authors noted that the strikingly different life histories of catadromous populations are likely to respond more slowly to anthropogenic perturbations compared with anadromous stocks.

The objective of this study is to critically review evidence of loss of accessibility in the eel historic distribution range within the St. Lawrence catchment in order to assess their impact on the species demography. Role and importance of habitat losses and anthropogenic barriers are discussed in a population perspective and compared with other known causes of mortality, namely the fisheries.

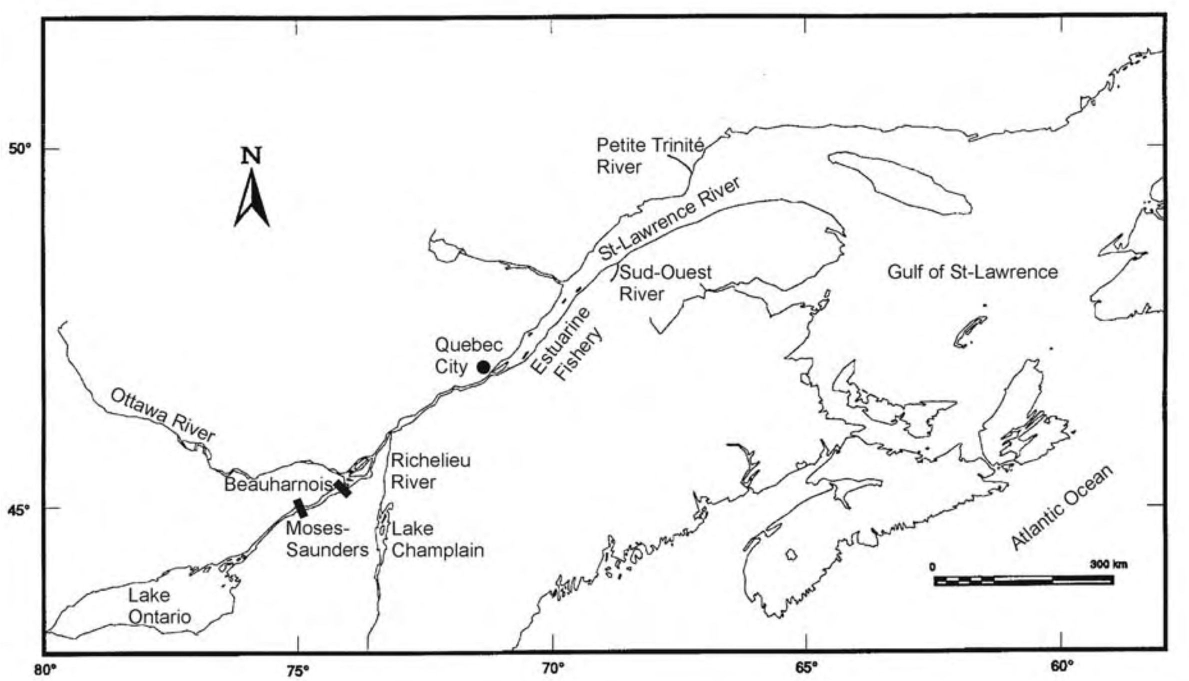

Figure 1. Study area

Methods

Historical distribution range for American eel was primarily inferred from archaeological research on aboriginal fisheries and from documents written by early European Missionaries, traders and explorers. Most data on dams and locks location and description in this study have been taken from databases maintained by government agencies from Québec, Ontario and the US Army Corps of Engineers'.
Eel habitat surface estimation was restricted to water depth 10 m and less. Despite eel could be found in deeper water, higher density is found in shoals habitats (ASMFC 2000).
Annual potential escapement estimates for American eel were restricted to the St. Lawrence catchment and originated from three tributaries: the Richelieu River, The Sud-Ouest River and the Petite Trinité River.
In the Richelieu River, a significant commercial fishery targeting specifically emigrating silver eel from Lake Champlain (Dutil *et al*. 1985) was operating for at least 150 years before its closure in 1998 (Eales 1968; Verdon *et al*. 2003). This single fishery on that river was made of four V-shaped traps covering two-thirds of the river width and remained unchanged at the same location throughout the season that extended from the end of May up to mid-October (Dumont *et al.* 1997). Moving average (three years, 1920 to 1980) annual harvest (kg) was corrected for a weir capture efficiency estimate of 60% to provide annual evaluation of biomass escapement. Finally, total biomass was divided by the mean weight of sampled silver eels in this fishery.
In the Sud-Ouest and the Petite Trinité rivers, annual escapement estimates were obtained from out-migrating silver eel counts. In the Sud-Ouest River, a non-selective trap was operated during the downstream migration between 1996 and 2003. Located at the river mouth, annual catch was the net output of this water system and represented the total escapement. Sampling operations enabled to know the exact mean weight and number of individuals (Verreault 2002). In the Petite Trinité River, mark-recapture experiments were conducted during downstream migration between 1999 and 2001 with non-selective trapnets settled at the river mouth (Fournier and Caron 2003).
Escapement biomass was computed in accordance with water surface in each watershed by using weighted mean. Population abundance estimates and weight sampling allowed evaluating annual biomass production and escapement. Maximum values in these rivers are a realistic evaluation of escapement from these water systems and we assume it represents its maximum annual potential production for eel.

Results

Historical distribution range

When European settlers arrived on the shore of the St. Lawrence River in early 1600s, eel fishing during the fall was an important activity for aboriginal people (Sagard 1636) and they targeted especially emigrating silver eels. Rich in fat, with 19.4 % lipids content (Tremblay, *in press*.), this species was particularly important for native people as food source and currency (Robitaille and Tremblay 1994; Courtemanche 2003). The very early fisheries, 3000 years ago, consisted of stone weirs constructed on rivers and important sites were found around Morrison Island on the Ottawa River, at Pointe-du-Buisson and Thousand Island area on the St. Lawrence River and on the Oswego River-Lake Oneida area, south of Lake Ontario (M. Courtemanche, Montreal University pers.comm. Junker-Andersen 1988; Pilon 1999). To these archaeological sites, we added all historical fisheries records from early settlements in the St. Lawrence watershed to the mid-1900s. This review allowed to identify fishing sites scattered from southern Lake Ontario (Lary and Busch 1997) to Upper Ottawa valley (Haxton and Chubbuck 2002) and in numerous tributaries connected with the St. Lawrence River (Eales 1968; LaBar and Facey 1983; Vladykov 1966). Eel sampling in recent field works were added to historical data to complete known locations for eel. Then, we took the uppermost locations in each tributary and we assumed that eel could colonize all freshwater habitats extending above until a natural obstacle was present. This procedure allowed the delimitation of what we think was the original distribution range for American eel in the St. Lawrence watershed before anthropogenic modifications (Figure 2). The three largest subwatershed identified were 1- the Upper St. Lawrence-Lake Ontario, 2- the Ottawa River and, 3- The Richelieu River.

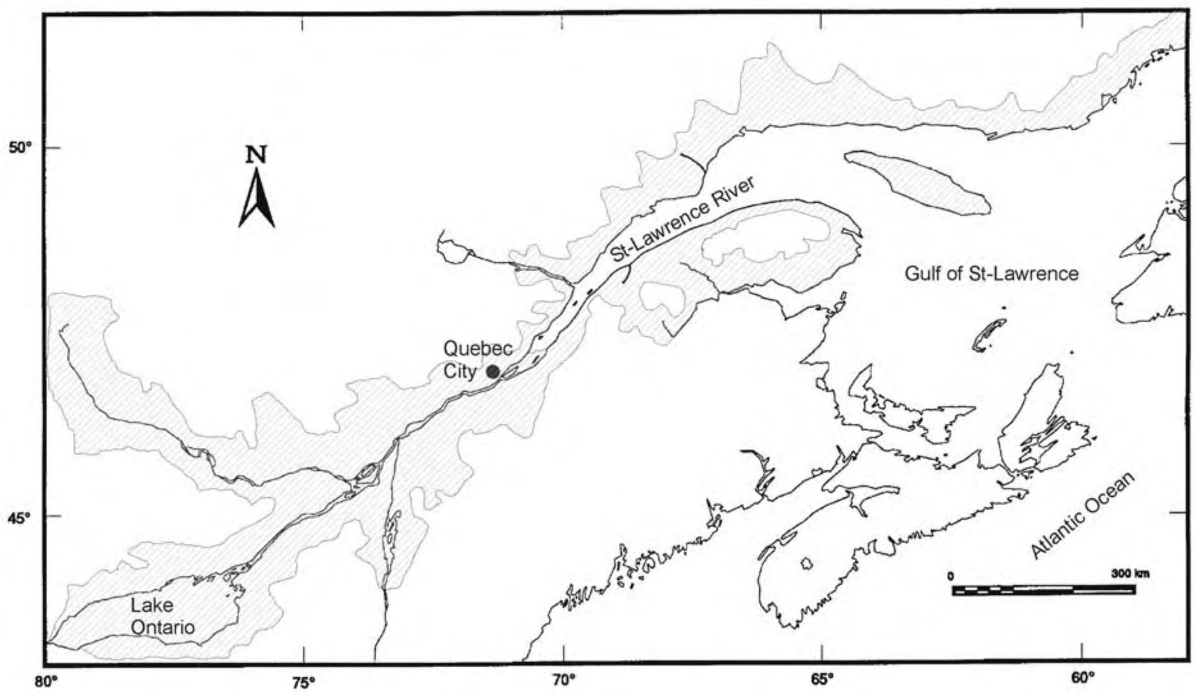

Figure 2. Historical distribution range for American eel in the St. Lawrence watershed

Anthropogenic barriers

Based on historical distribution, we gathered information on dams erected in all accessible tributaries. For practical purpose, we restricted our search for dams which height was higher than 2.5 meters. Dams were classified in two categories: hydrodams equipped with or without turbines. Given the exceptional ability of eels to colonize watersheds with many obstacles (Feunteun et al. 1998; McCleave 2001) we did not intend to classify these barriers as total or partial obstruction. We assumed that these anthropogenic obstacles always generate negative impacts on upstream movements by impeding, altering or delaying elver migration (Couillard et al. 1992; White and Knights 1997; Solomon and Beach 2004). Based on available data, we identified 151 hydrodams equipped with turbines in the eel historical distribution range. These hydrodams varied in size and importance with the largest being the Beauharnois dam (7 500 m^3/s) and the smallest being the St. Raphael dam (5 m^3/s). Hydrodams were present on every major tributary with the exception of the Richelieu River. On the largest subwatershed, the St. Lawrence-Lake Ontario, we found the two largest hydrodams and on the second largest

subwatershed, the Ottawa River, 18 hydrodams are installed. Those hydroelectric projects used almost completely water flow for electricity production, only a small proportion (< 1.0%) was diverted for navigation purposes to locks and canals (Verreault and Dumont 2003).
Dams without turbines are numerous and used mainly for flood control, drinking water supply or recreation in lakes during summer months. We found 8260 of these structures throughout the historical distribution range and characteristics varied from low head earthen dams to large concrete dams. These obstacles prevent free access to an estimated 12 140 km² of freshwater habitat suitable for eel growth (Table 1).

Table 1. Surface area for eel growth habitat impacted by dams in the St. Lawrence watershwed

Subwatershed	Estimated growth habitat (0-10m) above dams (km²)
Upper St. Lawrence River – Lake Ontario	5800
Ottawa River	3700
Richelieu River – Lake Champlain	1200
Others	1440
All	12140

Escapement estimates

Escapement as silver eel reflects the final production of a given habitat after up to 20-30 years of growth and natural mortality. Annual migration represents the output of maturing individuals and total biomass is the expression of annual escapement. Annual escapement estimates are scarce for American eel and often limited to small lakes (Smith and Saunders 1955; Smith 1966). Three annual escapement estimates are available for tributaries in the St. Lawrence River watershed.
For the Richelieu River, moving average maximum was estimated at 104,500 kg/year for total surface of 1200 km² (freshwater habitat less than 10 m depth) upstream the fishery site. This measurement leads to a maximum annual escapement of 87.1 kg/year/km².
In the Sud-Ouest river, a small unexploited watershed (200 km²) with freshwater habitat surface of 870 ha, the maximum escapement estimates was 86.8 kg/year/km².
On the north shore of the Gulf of St. Lawrence, the annual escapement in the Petite Trinité River was estimated to 1479 kg/year. With eel habitat surface of 1430 ha, this estimate represents a mean value of 103.4 kg/year/km².
Weighted mean was performed with these three estimates and escapement value for calculations of productivity in the historic distribution range averaged 87.1 kg/year/km².

Discussion

Among the four potential causes reviewed by Castonguay *et al*. (1994) for eel population decline, habitat modifications were not considered as a primary cause. Without apparent correspondence, the 20- to 30-yr delay between major anthropogenic environmental perturbations and eel recruitment decline in the St. Lawrence was the main argument against this hypothesis. However, they concluded that their impact may have been significant but delayed through compensatory population process. The complex life history complicated the analysis of this panmictic species. Unlike other anthropogenic causes, barriers on migration routes do not lead to direct mortality and their impact are considered indirect, synergic and cumulative. Because all streams, rivers and lakes throughout the historical distribution range constituted potential habitat for eels, hydroelectric projects and dams represents a potential source of impact to American eel (Richkus and Whalen 1999).

In the St. Lawrence watershed, according to our findings, free access to growth habitat in the historical distribution range could have shrank by 12 140 km² with the erection of dams and others obstacles (Table 1). This is the first attempt of which we are aware to estimate habitat loss in such a large scale. In spite of uncertainties and inaccuracies which arise with historic and prehistoric data during our search, we believe that our range delimitation is realistic.

Every time a dam is erected on a river does not mean that habitats located upstream are not accessible. Upstream migration could still be possible if alternative passages (e.g. locks) are available for migrant elvers. However, it seems that the number of successive dams on a river could be more detrimental. In their study, White and Knights (1997) found that barriers on the rivers Severn and Avon had a greater effect on European eel (*Anguilla anguilla*) densities than distance from the ocean, upstream habitats being practically deserted. For American eel, significant differences in age and size were observed in river reaches segmented by dams (Levesque and Whitworth 1987). In that study, age at the first and second dam were estimated at 2.1-yr and 2.8-yr and suddenly rose to 6.2-yr above the third dam. This difference could reflect the decreasing ability to climb when size is increasing (Legault 1988).

Even if eel abundance naturally decreases with distance upriver of the ocean (Tesch 1977; Smogor *et al.* 1995; Chaput *et al*. 1997), it seems realistic to extend our annual escapement estimates to the total surface area above dams. In Lake Ontario, the largest growth habitat for eel in the distribution range, a re-examination of data presented by Verreault and Dumont (2003) allows new interpretation of annual escapement estimates. In that study, escapement estimates from Lake Ontario for 1996 and 1997 was respectively 525 281 and 423 717 fecund females. With a mean weight of 2.118 kg (McGrath *et al.* 2003), total biomass was estimated to average 1,004,989 kg. Relatively scarce in deep cold-water lakes, eel is most abundant in shallow embayment and riverine habitats. In Lake Champlain, most radio-tagged eels used primarily habitats within water depth to 10 m whereas some moved into deeper water (LaBar and Facey 1983). Located more than 1000 km upstream from the ocean and with a maximum depth of 244 m, Lake Ontario is not suitable for eel production on all its surface area of 18 960 km² (Mills *et al.* 2003). We assume that prime habitat for eel is restricted to the 0-10 m depth for a surface area estimated at 2103 km². Although historically abundant in major tributaries (Oswego and Salmon rivers), eel is virtually absent from these waters and production is assumed to be exclusively from the Lake Ontario itself. Calculations on escapement biomass and habitat surface area give an estimated 478 kg/ km²/year. This estimated production was calculated for years of decreasing abundance in that system and historical maximum should have been higher during previous decades. Average value of 87.1 kg/ km²/year for escapement estimates from three tributaries is consistent among these subwatersheds with large difference in water surface area. The estimate for the Richelieu River represents the maximum production for this watershed although the Sud-Ouest River escapement was the higher value recorded during a period of abundance decline in this water catchment. Compared with the escapement on the Petite Trinité River, a less productive watershed, the annual production should be different but surprisingly appears closely similar. This could be the expression of productivity variability within the study area .Our annual escapement estimate (87.1 kg/ km²/year) does not seem too optimistic and we feel comfortable with it.

The loss of free access to 12 140 km² of habitat above dams represents a potential annual escapement estimated at 1 057 394 kg/ year, or 836 545 large fecund females (harvested eel mean weight in the estuarine fishery: 1.264 kg). This large number represents an important loss for the species. In comparison, the important estuarine fishery peaked at 340 000 silver eels during the last 80 years and although fishing is often seen as an important source of additive mortality, it represents only 41% of potential annual production lost above dams. It seems appropriate to state that anthropogenic barriers could act as a significant cause of population decline and among all, mitigating their impact should be a priority.

Given the long history of upstream passage with various equipments, and the immediate observable success (Solomon and Beach 2004), providing upstream passage above dams is probably the most effective way to restore eel abundance. Eel ladders are already installed on two hydrodams (Moses-Saunders and Beauharnois) in the upper St. Lawrence-Lake Ontario subwatershed and the same equipment is also found on two dams in the Richelieu River subwatershed. These mitigation measures give access to two of the three largest subwatershed for eel production in the historic distribution range. The third one is the Ottawa River and this subwatershed encompasses 3 700 km² of eel habitat. Twelve hydrodams are located on this river itself and six on connected tributaries (Couillard et al. 1992; Haxton and Chubbuck 2002). None of these are equipped with eel ladder and re-opening access could potentially generate nearly 255 000 female silver eels per year.

Upstream passage facilities for eel should be implemented by dam operators throughout historical distribution range and systematically required by regulatory agencies as an appropriate action to help this major resource species. However, this could only be obtained with addition of efficient protection devices against turbine mortality during downstream migration. With a mean length of 85.3 cm (SD=9.3), eels in the St. Lawrence watershed are much larger than reported anywhere in North America (Verreault *et al* 2003). Because turbine mortality is positively related to eel length (Mitchell and Boubée 1992), and turbine size (Larinier and Dartiguelongue 1989), they are more vulnerable than anywhere in the species range. Survival rates were estimated at Moses-Saunders and Beauharnois hydrodams for fixed-blade propeller and Francis turbines (Desrochers 1995; Normandeau Associates Inc and Skalski 1998). Francis turbines are less detrimental with survival rates of 84.2% (CI= 76.7%-91.7%) than fixed-blade propeller turbines with survival rates of 76.1% (CI= 68.3%-83.9%) and 73.5% (CI= 67.9%-79.1%). For these two large hydroelectric complex in the St. Lawrence River (Moses-Saunders and Beauharnois) turbine entrainment mortality was estimated to 207 490 silver eels in 1996 (Verreault and Dumont 2003).

Information on turbine type and runner diameter were not available for all the 151 hydrodams located in the historic distribution range but we assume that survival rates was not greater than those from Moses-Saunders and Beauharnois, and likely lower since survival increases according to the size of the turbine (Larinier and Dartiguelongue 1989). In rivers with successive hydroelectric projects, even a little reduction in survival rates leads to important escapement decrease (McCleave 2001).

Development of downstream passage facilities or diversion mitigation measures would contribute to increase escapement from re-opened eel habitats above dams and may be another key to restore population in the St. Lawrence watershed. There is no evidence that relationship between the size of the spawning stock and the level of recruitment does not exist (Russell and Potter 2003). Such relationship for determining a spawning escapement target on a watershed scale is not available but, unless it can be scientifically demonstrated to the contrary, the application of the precautionary approach should prevail for conserving productive capacity of this species (FAO 1996). The widespread concern about population decline and weak recruitment on a large portion of the St. Lawrence watershed (Castonguay *et al.* 1994; Casselman 2003) urge the need for providing access to more growth habitat and safe downstream facilities for rising escapement and eventually increasing recruitment. We believe that among all mitigation measures, a strong involvement in habitat restoration is one of the key action to restore American eel abundance in large portion of the St. Lawrence watershed.

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The American eel (Anguilla rostrat) is a catadromous panmictic species that has long provided important fisheries (Eales 1968). These resources have been heavily utilized across its North American...Â Indeed, the earliest and best documented index comes from the number of juvenile eels ascending the eel ladder in the St. Lawrence River (Fig. 1) at the Moses Saunders Hydroelectric Dam (Fig. 2) (Castonguay et al. 1994a; Casselman et al. 1997b). As the ladder is an index of recruitment at the extremity of the population range of this panmictic species, Casselman and Marcogliese (2000) and others have contended that it provides evidence of general species decline, reflecting inadequate juvenile recruitment to maintain distant stocks. The American Eel (Anguilla rostrata) is a catadromous species that spawns in the Sargasso Sea and is distributed by ocean currents to North America, the Caribbean and the northern drainages of South America [1]. This species can use one of several life strategies and live in saltwater, brackish estuarine water and freshwater [2, 3]. Catadromous eels are found in more diverse habitats than.Â American Eels can adapt to a variety of habitats through local adaptation and phenotype plasticity.Â Habitat loss from barriers is considered a historical effect and its population level effects have likely already been realized [23]. Abstract Populations of American eel Anguilla rostrata along the eastern coast of North America have declined drastically for largely unknown reasons. We examined the population dynamics of American eels in six tributaries of the Hudson River, New York, to quantify their distribution and the impacts of anthropogenic stressors.Â However, upstream of natural and artificial barriers, American eel densities were reduced by at least a factor of 10 and condition, as measured by mass, was significantly lower. Significantly lower American eel condition was also found with increasing riparian urbanization. Density-dependent growth limita...Â Habitat use of American eel (Anguilla rostrata) in a tributary of the Hudson River, New York. James H. Johnson, Christopher C. Nack. Biology.