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Sackville, Canada

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Executive summary

The ICES Study Group on Anguillid Eels in Saline Waters (SGAESAW) met on 16–18 March 2009 in Sackville, Canada, and on 3–5 September in Gothenburg, Sweden. The chair was David Cairns (Canada). Thirty-two participants representing 12 nations attended one or both of the meetings.

Saline (i.e. salt or brackish) waters are important growth habitats for eels, but receive little attention in most assessments. To address this, SGAESAW was asked to review knowledge of saline-fresh differences in ecological parameters and stock assessment methods, and recommend approaches that embrace salinity-based differences in management models.

The approach taken at the meetings was to hear presentations on topics pertinent to the SGAESAW mandate, to discuss reported findings, and to formulate recommendations for research and management. This report contains an introduction, chapters that summarize reported findings, and annexes that present agendas, participant lists, and recommendations.

Measurements of otolith strontium:calcium (Sr:Ca) ratios have revealed that eel populations typically contain a mix of freshwater residents, saline water residents, and inter-habitat migrants.

Eel growth increases with temperature, and eels generally grow faster in saline water than in fresh. European eels produced in saline waters have lower loads of the swim-bladder nematode *Anguillicoloides crassus* than those grown in fresh water, which may improve their chances of reaching the spawning grounds. An estimated 11 million yellow eels occupy saline waters of the southern Gulf of St. Lawrence, Canada. Yellow American eels appear to be rare or absent in exposed marine waters. In Europe, eels are found in exposed waters of the southern North Sea close to the Dutch, German, and Swedish coasts. Most silver eels exiting the Baltic Sea have grown in brackish water. In other regions, there is little information from which to infer the ratio of saline to fresh origin in eel production.

Given limits to understanding, it is not currently possible to formulate management recommendations that are specific to salinity zones. Future progress towards properly treating eel conservation in saline waters will require broad-scale efforts which draw advantage from novel approaches, including the loading of multiple investigations on a single field sampling campaign, measurements of stable isotopes and fatty acid composition in conjunction with strontium:calcium studies, mapping and measurement of saline-water eel habitat on a continental scale, and measurements of yellow eel abundance by open-bottom metal drop traps, by night time glass bottom boat surveys, and by large corral nets.

It is recommended that data be collated on the quantity, demographic characteristics, distribution, potential habitat, and quality of eels in saline waters of Europe and North America, that analyses be undertaken of eel demographic processes in relation to habitat characteristics, that the precautionary approach be applied to European and American eels at all locations where they occur, that work be undertaken to calibrate and validate sampling methods, and that an ICES Study Group on Anguillid Eel Stock Assessment Methodology in Saline Waters be formed.

Introduction

At its meeting in September 2008 in Halifax, Canada, the ICES Diadromous Fish Committee struck a **Study Group on Anguillid Eels in Saline Waters** (SGAESAW) (Chair: D. Cairns, Canada). Formation of this Study Group was set against the backdrop of international concerns about declining indicators of eel abundance. It is now well known that eels produced in brackish and salt water are significant components of anguillid eel populations. However, in many regions eel conservation and management programs are largely oriented towards freshwater issues. Anthropogenic impacts on eel populations are geographically heterogeneous. Dams and pollution affect eels in fresh water, but eels in saline waters are less affected by these impacts. Fisheries affect eel populations, but eel populations are not affected where there is no fishery. Because temperate anguillid eels have little or no spatial genetic structure, effective conservation requires measures that produce benefits, and mitigate harm, at the scale of the entire species. It is possible to evaluate impacts of dams, pollution, fishing, and other human influences on eels at a local scale, but it is not currently possible to scale up these impacts to the species level, because the proportion of the stock that is in fresh vs. saline water is not known, nor is the proportion of the stock that is fished vs. unfished.

The SGAESAW Terms of Reference (ToR) call for the Study Group to review knowledge on the ecology and production of eels from saline waters in comparison with those in fresh water, to review knowledge about factors which influence eel choice of habitat salinity, to recommend conservation approaches that embrace salinity-based differences, and to define approaches that will advance progress towards robust stockwide management models (Annex 1). The SGAESAW mandate includes generating a better understanding of eels in saline waters vis-à-vis those in fresh water in terms of the population size and production potential. Temperate-zone eels in saline waters tend to grow more rapidly than those of fresh waters. Salinity-specific growth rates are also an important theme because growth rates affect time to maturity and other vital parameters used in stock assessment models.

To facilitate participation of both North American and European scientists, it was decided that SGAESAW would hold two meetings, the first in Canada and the second in Europe. The first meeting of SGAESAW took place on 16–18 March 2009, in Sackville, New Brunswick, Canada, and the second took place on 3–5 September 2009, in Gothenburg, Sweden. Thirty-two participants representing 12 nations attended one or both of the meetings. Agendas of the meeting are given in Annex 2, a list of participants is given in Annex 3, and photographs of participants are given in Annex 4. Recommendations put forward by the Study Group are listed in the Report to the ICES Steering Group on Ecosystem Function (Annexes 5 and 6). The Resolution for the SGAESAW meeting in 2010 is available in Annex 7.

1 Overview

Anguillid eel habitat use in saline and fresh water

Reviews of temperate-zone eel life history investigations that measured strontium:calcium (Sr:Ca) ratios in otolith transects have shown that anguillid eel populations contain three main migratory contingents: freshwater residents, saline water residents, and inter-habitat migrants. The co-existence of these groups is termed facultative catadromy. The Sr:Ca technique is a powerful tool but nevertheless has limitations.

Choice of analytic instrument influences the results that can be obtained from Sr:Ca analysis. Instruments vary in their spatial resolution, ability to measure concentrations of a variety of trace elements, and whether or not they sample destructively or non-destructively. The Sr:Ca technique relies on the fact that Sr:Ca ratios are higher in sea water than in fresh water, but natural concentrations of elements can vary in both environments. Sr:Ca can generally distinguish between fresh and saline water, but may not be able to distinguish between salt water and brackish water. There are unresolved questions around interpretation of Sr:Ca ratios at the otolith edge, significance of outlying points, and temporal resolution of habitat occupancy.

Eel movements between fresh and salt water were investigated in Fundy National Park, New Brunswick, Canada, using both stable isotopes and Sr:Ca. Organisms collected in fresh and salt water had distinct N and C isotopic signatures. Isotopic data suggested that >70% of sampled eels leave freshwater in spring, feed in salt water over summer, and return in fall to freshwater overwintering grounds. These movements to salt water were not detected by otolith Sr:Ca measurements, presumably because eels grow slowly in winter and winter accretion of elements was too small to be detected. Knowledge of seasonal movements to freshwater is essential for effective conservation because dams and other obstacles may impede access to wintering grounds.

Sr:Ca analysis can be used to help assess the effect of migratory contingent on reproductive potential. Among silver eels collected near the mouth of the Baltic Sea, eels identified as catadromous had the highest potential to reach the spawning grounds, while those which had not entered fresh water were judged to have insufficient energy stores to reach the spawning grounds.

Investigations in tributaries of the Hudson River indicate very high abundance of eels, up to the point of the first barrier to upstream migration. Eel densities were much lower above barriers, particularly artificial barriers. Eel condition was inversely associated with the intensity of barriers on a system, but eel growth was positively associated with barrier intensity. The rate of dam building in the Hudson system was highest in the second half of the 20th century. Construction of eel ladders at dams allows eels to reach upstream waters, but in the case of hydroelectric dams, this may or may not result in net conservation benefit because of the risk of turbine mortality during downstream migration.

In the southern Gulf of St. Lawrence, eels caught by electrofishing and rotary screw trap in streams are smaller (modes 27–31 cm) than those recorded in ponds, estuaries, and bays, using fyke nets (modes 50–65 cm). The paucity of large eels in streams cannot be explained by a male-balanced sex ratio, because all differentiated eels sexed from southern Gulf rivers are female. The paucity of small eels recorded in ponds, estuaries, and bays cannot be explained by gear selectivity, because small eels are not detected in glass bottom boat surveys in which the observer can typically detect pencil-sized objects or smaller. In ponds, estuaries, and bays, small eels may avoid larger eels in space or in time in order to reduce risk of cannibalism. There are no clear answers as to where stream eels go when they get larger, or where pond, estuary, and bay eels were when they were smaller.

Members of the SGAESAW are preparing an atlas of American eel habitat and fisheries on the east coast of North America. The atlas will map and measure potential eel habitat in saline waters on the basis of depth, degree of exposure from the open sea, and possibly temperature. A methodology for classifying saline waters as Sheltered, Semi-exposed, and Exposed has been developed. Application of this method to the

Estuary and the Gulf of St. Lawrence indicates that Sheltered and Semi-exposed habitats totalled 3742 and 11 615 km² (1.6 and 4.8% of total study area, respectively).

Data on locations of eel fishing in eastern North America were obtained from fisher logbook programs and from government biologists responsible for eel science. In eastern Canada, fishing occurs in both saline and fresh sites, but in the eastern U.S. most fisheries occur in saline waters. In both countries there are substantial areas of coastline which are not fished for eels.

In Delaware, eel fishing is permitted only in tidal waters and nearly all landings come from saline waters as tidal fresh fishing areas are limited. In the upper, less saline, part of Delaware Bay, fishing effort occurs in the tidal tributaries and the nearshore part of the Bay. In the lower, more saline, part of Delaware Bay, nearly all effort occurs in the tidal tributaries with little occurring in the Bay. Waters of low and mid salinities have the highest landings and CPUE.

The Virginia eel fishery targets yellow eels which are caught in pots, primarily in spring and fall. Fishing tends to be mobile, with a fisher fishing an area intensively for a period, and then moving on. Fishing effort, based on log reports, occurs throughout the tidal waters of Virginia. Over half of state landings comes from three tidal tributaries.

The use by eels of estuaries and sheltered bays is well known, but the extent to which eels may also use open marine waters for growth habitat is poorly known. Scattered anecdotal reports suggest that eels may use exposed marine waters in the Gulf of St. Lawrence. A list of surveys which may shed light on the distribution of eels in saline waters of eastern North America was compiled. The list includes trawl surveys and surveys using lobster traps without escape vents. In the Gulf of St. Lawrence, bottom trawl surveys conducted since the 1970s reported no American eels. Similar surveys in the St. Lawrence estuary rarely caught eels. Trawl surveys in Chesapeake Bay regularly catch eels. These surveys can be used to analyse depth-abundance relations in eels, although there are potential biases related to time of day and to gear avoidance.

The Delaware Division of Fish and Wildlife has two ongoing trawl surveys of Delaware Bay and River and a completed trawl survey of tidal tributaries of Delaware Bay and River. American eel CPUE in the juvenile finfish trawl survey was highest in oligohaline and mesohaline waters of Delaware River and Bay but decreased with increasing salinity. American eels were rarely caught in the adult finfish trawl survey but those that were captured were in deep mesohaline to polyhaline waters. American eels were captured in all tidal tributaries sampled in the tidal tributary trawl survey. American eel CPUE was low at the lowest and highest salinity sites and highest in waters ranging from oligohaline to mesohaline. Trawl survey results suggested that eel distribution is influenced by salinity in systems with steep salinity gradients.

Eel ecology and movements were investigated in the St. Jones River, a tidal tributary of Delaware Bay, using research and commercial captures and large-scale PIT tagging. Relative abundance as indicated by CPUE was positively correlated with salinity although mean eel size decreased with distance from the river mouth. Growth rates increased significantly with eel size and salinity. Recapture probabilities of American eel increased significantly with distance from the river mouth. Apparent survival rates of American eel in non-harvest months varied little with eel size class or location strata although they were lowest in the middle portions of the river and greatest in upper river locations. Increased downstream transition probabilities for

marked American eel in winter months coupled with increased catches of American eel at supplemental sampling locations in Delaware Bay in October and November may indicate winter residency of American eel in relatively higher saline/warmer bay waters.

There is no established or widely used method of monitoring small yellow eels in saline waters. Eels at this stage have been monitored in Sweden by a drop-trap consisting of a bottomless aluminium box. The box is dropped on the substrate, and animals removed. Traps of this type can be small and deployed by hand, or larger and deployed from a boat equipped with crane and winch. Investigations using these devices indicate that small yellow eels are found primarily in shallow water, and are generally associated with vegetation. The amphipod *Corophium voluator* was the major dietary component.

Physical tags and otolith strontium:calcium analysis were used to assess movements of Japanese eels in a Taiwanese lagoon-estuary system. About 80% of recaptures occurred within 1 km of release sites. There were three migratory types: freshwater residents, seawater residents, and estuarine residents. Estuarine resident eels dominated catches in both the bay and the river.

Silver eels were collected in a canal which is the sole freshwater passageway between the Rhone River, France, and its delta. Migratory histories were reconstructed by linear discriminant analysis of otolith strontium:calcium ratios. Most (67%) eels entered the canal directly; the remainder entered after 1 or 2 years in brackish water. Most of the eels sampled in the canal had stayed in fresh water after their original entry to fresh water, but others moved once to several times between brackish water and fresh.

Stable isotope and fatty acid analysis were used to elucidate movement patterns of eels captured by fyke net in fresh, estuarine, and marine portions of a catchment in western Ireland. Eels captured in different salinity zones differed significantly in isotopic carbon and nitrogen signatures. Eels in freshwater were the most ^{13}C -depleted and eels in salt water the most ^{13}C -enriched, but there was overlap in depletion levels between adjacent zones. Ratios of n3:n6 fatty acids declined significantly with increasing salinity. A discriminant analysis based on isotopic depletion values, C:N values, and fatty acid results achieved an almost 90% classification success in a jack-knife test.

Anguillid eel demographic characteristics in saline and fresh water

Eels were sampled along a salinity gradient of 30 to 7 ppt from the Swedish coast of the North Sea, to the Swedish east coast on the Baltic Sea proper. On average, sampled yellow eels were longer in the central Baltic Sea than in the North Sea, and sampled yellow eels were older in the central Baltic proper than in the southern Baltic. Yellow eels showed the greatest length-at-age in the central Baltic proper, and the best condition factor in the central and southern Baltic. Length and age of silver eels increased with further penetration into the Baltic Sea. Prevalence of the swim bladder parasite *Anguillicola crassus* was lower in the Skagerrak and the Kattegat (<20%) than in the Baltic Sea (>40%). The minimum legal size is 40 cm in part of the study area, but few eels are below the legal size, which suggests that a greater minimum size is needed to protect a larger part of the population.

Otolith strontium:calcium ratios were used to investigate the growth and migration patterns of eels sampled in Latvia. Eels which naturally recruited to this area were identified by a brackish water signal laid down when the animal migrated across the

Baltic Sea. Eels which had been artificially stocked in the area lacked this signal. Naturally colonized eels showed faster growth than stocked ones in two of three locations, which might be due to stocked eels having occupied areas of low productivity before they reached the sites where they were captured.

The life history and ecology of 370 eels sampled in the North Sea, the Baltic Sea, and freshwater sites in northern Germany, were investigated by measuring otolith strontium:calcium ratios, growth rates, and parasite and viral infestations. Habitat shifts occurred in all directions. No eels sampled near the offshore island of Helgoland had purely marine otolith strontium:calcium ratios. Preliminary analysis suggests that <20% of eels in the western Baltic are of stocked origin. Prevalence of the HVA virus in northern Germany was only 2%. Prevalence of *Anguillicola crassus* and *Pseudodactylogyrus* spp. was high in freshwater and brackish sampling sites. Eels that remain in a purely marine environment have a lower risk of acquiring pathological parasites and may have a better chance of reaching the spawning grounds in good condition.

Growth and sex ratio were compared between eels caught in freshwater and estuarine areas of the Severn River, England. Growth in the estuary was approximately 40% higher than growth in fresh water. The higher estuarine growth is presumed to reflect higher productivity and higher summer temperatures in that habitat. In the estuary, 79.1% of eels which could be sexed were female. In fresh water, 74.2% of eels were undifferentiated, and males were 63.2% of eels which could be sexed.

A population model was developed that accounts for density-dependent survival, sexually dimorphic and individually variable growth, sexual differentiation, maturation, and natural mortality related to size, fishing mortality dependent on maturation stage, body size, and gear selectivity, and severe fluctuations in glass eel recruitment. The model was calibrated on the eel population in the Camargue lagoons in southern France, using data for 1993–2006. Model results indicated that yellow eel settlement is density-dependent, with the number of eels successfully colonizing the lagoons never exceeding 1000 individuals/ha. Eels <300 mm dominated the population, which was estimated to vary between 1 million and 18 million. Estimated biomass varied between 50 and 250 t, with yellow males and females accounting for 68% of the total. Annual fisheries harvest varied between 55 t and 96 t.

Eels were sampled in three saline lagoons and in the freshwater Tiber River, Italy. Length structure was similar between two saline lagoons, but females in the other saline lagoon were significantly larger. Eels in the Tiber showed a narrow size range. Most eels in the three saline lagoons were female (62.5–100%), while only 13% of Tiber eels were female. A comparison of growth performance of eels at various Mediterranean sites indicates that growth rate declines with increasing salinity. *Anguillicola crassus* prevalence was 45.9% on one saline lagoon, 0% in two other lagoons, and 76.5% in the Tiber River.

Anguillid eel densities, populations, and relative abundance in saline and fresh water

Eel movements and abundance have been investigated in the Saint-Jean River system in eastern Quebec since 2001. Eel densities were estimated at 145–177 eels/ha in a lake, 0–150 eels/ha in the river, and 645 eels/ha in the brackish estuary. Large numbers of eels migrate from fresh water to the estuary in spring. Eels growing in the estuary grew faster than those in fresh water. Some eels in the Saint-Jean system are freshwater residents, some are brackish residents, and some move between habitats.

A preliminary compilation of American eel landings indicates that Canadian landings come from a mix of fresh and saline waters while U.S. landings are nearly all

from saline waters. FAO data suggest that landings from Mexico are from saline waters while those from the Dominican Republic are from fresh waters. Estimated densities of American eels from literature and unpublished sources are compiled. Estimated eel densities in saline waters of the southern Gulf of St. Lawrence had modal values between 0 and 100 eels/ha. Densities from stream electrofishing surveys are higher, with most between 0 and 3000 eels/ha.

The total amount of saline habitat (lagoons, transitional habitats, coastal waters) in England and Wales is about 14 times greater than the amount of habitat in rivers and lakes. However, data on eels in saline habitats are sparse. Eel demography was investigated in Poole Harbour, a large coastal lagoon in southern England. In 1996, eels >450 mm comprised 31% of catches, and in 2004, eels >450 mm were 43% of catches. Mean ages were greatest in 2004, and growth rate in 2004 was 40.4 mm/year as opposed to 72.8 mm/year in 1996. Growth rates in inflowing rivers were much lower (20.2 and 19.3 mm/year). Acoustic tracking of eels in and around the mouths of rivers draining into Poole Harbour indicates movements less than 150 m during October to January. Eels move greater distances, up to 3.5 km within a few days, during summer.

American eel densities were estimated at 27 sites in the southern Gulf of St. Lawrence by surveys conducted with a glass bottom boat (GBB) equipped with underwater lights. Eels were counted at night during zigzag transects that ran across bays and estuaries. Visibility conditions typically limited survey depth to 2 to 2.5 m depth. Mean densities (and 95% confidence limits), estimated from a bootstrap routine, were 34.1 (23.0–45.5) eels/ha for Gulf New Brunswick, 40.9 (24.8–57.3) eels/ha for Gulf Nova Scotia, and 155.7 (86.3–235.9) eels/ha for Prince Edward Island. Area occupied by eels was taken as the Sheltered category as defined in a scheme that classifies habitat by degree of exposure to the open sea. On Prince Edward Island, 65.9% of water in the Sheltered category is ≤ 2 m in depth. On the basis of GBB density estimates and Sheltered habitat measurements, standing stocks of yellow eels in saline waters of the southern Gulf of St. Lawrence are 1 579 504 eels in Gulf New Brunswick, 920 833 eels in Gulf Nova Scotia, and 8 898 766 eels in Prince Edward Island, for a regional total of 11 399 103 eels. Uncertainties in these standing stock estimates arise from sampling error in density estimates as analysed by the bootstrap procedure, and limited knowledge regarding eel densities in waters deeper than 2.5 m and in the proportion of eels that remain buried in the substrate during the night.

Fyke nets were used to capture eels in western Ireland. The proportion of eels which were recaptured in fyke nets was nil at 30–35 cm but 0.2 at length 60–65 cm. Based on data from >20 000 net-nights, the standard deviation of CPUE increased linearly with CPUE. Doubling the number of fyke nets did not decrease standard deviation of CPUE. More locations or more fishing nights may be more helpful in providing accurate estimates than increasing the number of nets.

A planned investigation will characterise the ecological status of eels along salinity gradients from estuarine to full salinity in Northern Ireland. Migratory contingents will be identified by use of carbon and nitrogen stable isotope analysis, fatty acid analysis, and otolith strontium:calcium ratios. Eel abundance will be assessed by mark-recapture, using PIT tags as markers. Preliminary field work indicates much higher CPUEs in a saline habitat of western Ireland than in saline habitats of eastern Ireland.

Eels in Portuguese brackish water systems face stronger anthropogenic impacts (fishing, contaminant loads), predation, and competition than eels in fresh waters. Brack-

ish water fisheries are directed at yellow eels and the minimum size is 22 cm in most locations. Fishing is permitted year-round, and coastal lagoons are important fishing sites. Contrary to freshwater, eel activity in brackish waters is not reduced during summer months, which contributes to better condition in brackish water systems. Additionally, the infection by the parasite *A. crassus* seems to decrease with salinity, which implies the lower part of estuaries should be classified as protected areas. Portuguese estuaries are free from obstacles to migration, in opposition to freshwater where these obstacles increase density and competition, and lead to an artificial manipulation of sex, favouring male production, which can have negative effects on a declining population.

Coastal fish communities have been monitored on the Swedish west and east coasts since the 1960s in programs that were primarily triggered by the need to monitor effects of nuclear power plants. Fyke nets are the standard fishing gear in these programs on the west coast. Marine yellow eel CPUE is higher in shallow coastal habitats on the Swedish west coast than in similar habitats of the Baltic Proper. Off-shore shallow banks are also inhabited by yellow eel. A preference by yellow eel for habitats with vegetation is indicated. A recruitment index from the Kattegat indicates declining trends, but relative abundance of yellow eels at a nearby reference area increased during the period 1976–2008.

Stocked eels are common in Swedish fresh waters and dominate populations in many lakes which have low natural recruitment. Eels are also commonly stocked in brackish waters. Silver eels were sampled at the outlet to the Baltic Sea, and subject to otolith strontium and calcium measurements to determine their migratory histories. Most (>65%) of these eels were brackish water residents, and 8% were freshwater residents. The remaining eels showed a mix of brackish and freshwater growth areas. An estimated 21% of sampled silver eels were of stocked origin. Eels of stocked origin had used both fresh and brackish growth areas. Silver eels of stocked origin in a lake on the Swedish east coast tended to roam about the lake, without being able to find the exit to the sea.

A commercial trawl fishery for European eels operated in the southeast North Sea (German Bight) from 1964 to the 1980s. Annual catches were as high as 300 t. Fishing occurred primarily at depths of 10–50 m, and during May to November. Scientific trawl surveys indicated higher numbers of small eels at 11–18 m depth than at 20–24 m depth. The population was dominated by yellow eels, but silver eels reached 25% of the catch in November. The population was estimated at 1.85 million eels with a biomass of 323 t. A large-scale tagging program provided information on eel movements. Eels living upstream of the tidal limit did not migrate to coastal waters. Eels summering near the coast tended to winter in rivers, but eels summering in offshore waters tended to winter in deep areas near Helgoland.

Data from ICES-coordinated beam trawl surveys were used to evaluate historic and current distribution and abundance of eels in coastal waters of the southern North Sea. Data were analysed from 1970 to 2008, as provided by Dutch and German survey operations. Abundance peaked in 1980–1985, and thereafter declined to an all-time low in 2008. Abundance declined steeply with distance from the coast, and eels are present only in a coastal fringe that is less than 20 km wide. If the trawl is 100% efficient, calculations based on swept area indicate abundances of 222 t in 1982 and 3 t in 2008. If the trawl is only 15% efficient, abundance would be >3250 t in 1982 and >44 t in 2008. The time trend in the beam-trawl data corresponds reasonably well to the trend in European eel glass eel abundance, taking into account that the eels sam-

pled in the trawl survey are several years older. At present eels inhabiting these marine waters are only a minor fraction of the total stock around the southern North Sea.

A new type of eel sampling device was developed to monitor eel populations on the northeast German coast. The device consists of a square netted corral, 100 m on each side, with fyke net chambers at each corner. The area inside the corral is 1 ha. Six chains of fyke nets are deployed inside the corral to increase the likelihood of capturing eels present within the corral. The system was tested in 48 hour deployments at 43 stations in 2008. Eels caught had a mean length of 45.7 cm, and 3.2 eels were caught per ha fished. This method was judged to provide a suitable approach for monitoring eel populations in different habitat types.

The distribution of riverine eels in relation to distance from the river mouth has been described, but little is known about eel distribution in tidal vs. non-tidal water. Data on catches of yellow and silver eels in France were used to infer the relative abundance of eels in relation to salinity and tidal zones. The average reported annual catch in France since 1999 is 1127 t, of which 12% is taken from fresh water, 1% is from tidal fresh water, 36% from brackish water, and 51% from marine water. Angling catches of eel in freshwater are not covered by official statistics, but such catches are probably very substantial. Overall, fresh and saline waters probably contribute roughly equally to total French eel landings.

A national eel stocking program has been ongoing in Denmark since 1987, covering both inland and marine waters. About 75% of stocked eels are released in saline waters. Examination of eels commercially fished in Roskilde Fjord for coded wire tags resulted in a recapture rate of 1.8% of stocked fish. Eels generally stayed in or near the stocking site. Otolith strontium:calcium ratios indicated that stocked eels did not enter fresh water. Stocked eels grew between 30 and 75 mm per year. Silver eels of stocked origin migrated toward the outlet of the fjord, as did wild eels. It is conservatively estimated that 10.3% of eels released at 3 g and 6.8% of eels released at 9 g were recaptured by professional fishermen. This does not include captures by recreational fishermen. At least 18% of a cohort of eels stocked at 3 g are captured or escape as silver eels.

Choice of salinity zone in growth-phase anguillid eels

Partial migration in animals is due to early developmental switchpoints. The storage effect refers to a long segment of a life cycle which has relatively low variation in survival, in contrast to a short segment which has high variability. In eels, the storage stage is the yellow stage due to its larger size and attributes that adapt to seasonal and spatial environmental changes. The storage effect applies to eels because reproduction involves multiple, rather than single, year classes. The portfolio effect (derived from stock market terminology) refers to the dampening of variance caused by use of a diversity of habitats or resources. Eel use of both fresh and saline growth habitats can be viewed as a portfolio effect. A modelling exercise shows that the degree of dampening arising from facultative catadromy depends on the type of relation between performance in the two habitats (negative, positive, random), and on the difference in size of the contingent using each habitat (equal sizes, one contingent larger than the other). Facultative catadromy in temperate eels may have evolved to support population colonization, growth and stability where past populations were exposed to periodic variations in climate and oceanic regimes. From a precautionary perspective, we should focus on the consequences of partial migration as it relates to population dynamics and stability. To this end, due to their likely independence in

habitat production rates in comparison to saltwater, freshwater habitats play a key role in enhancing population stability and persistence through the storage (diverse age structure) and portfolio (independent growth habitats) effects.

Behavioural experiments have been conducted on glass eels since about 1930, and recent research has focussed on swimming capacity, perception ability, and migratory behaviour. Glass eels are capable of swimming 1–2 body lengths/sec. This speed is insufficient to overcome ebb tidal currents in estuaries, so glass eels use selective tidal transport to ascend estuaries. Glass eels are able to detect small differences in salinity and temperature, and also water-borne chemicals at low concentrations. They are also sensitive to the presence of light and conspecifics. Glass eels can be sorted into fish with (M+) and without (M-) a high propensity to migrate, on the basis of preference for fresh water, for swimming against the current, and activity at dusk. M+ eels generally have a high level of thyroid hormone T₄, a high body weight and condition factor, and a high energetic status as indicated by percent of dry weight. Studies have reported conflicting results regarding which group has higher growth rates. Migration and settlement behaviour of glass eels is a consequence of energetic state, internal clock state, and social and density cues. Further research is required to integrate these factors into an individual-based model.

The superorder Elopomorpha possesses a unique planktonic leptocephalus larval stage. Anguillid eels are the only member of this group which show facultative catadromy. Their euryhaline abilities may have evolved to take advantage of high productivity and low osmoregulatory costs in brackish waters. Tropical fresh waters are advantageous to growth-phase eels because of their high productivity, but the freshwater advantage is lost in the temperate zone where freshwater eel growth tends to be lower than that of saline waters. Anguillids have long generation times and high fecundity which compensate for potentially high mortality during the planktonic larval stage, whose variability is exacerbated by fluctuations in ocean climate. Facultative catadromy in anguillid eels can be interpreted as a bet-hedging strategy in that growth rate penalties in fresh water are offset by extensions of habitat utilisation and smoothing of stock-recruitment relations. Colonization of fresh water may depend on threshold densities being exceeded in saline habitats. Because of their dispersal and mobility powers, eels can rapidly colonize or re-colonize disturbed or defaunated habitats.

Catadromous migrations by anguillid eels in the temperate zone are paradoxical, because eels tend to grow faster in saline waters, and rapid fish growth is generally associated with higher fitness. Gross et al. (Science 239:1291-1293, 1988) proposed that high ratios of anadromous:catadromous species richness at temperate latitudes, and low ratios at tropical latitudes, are explained by latitudinal clines in marine:fresh productivity ratios. This model is widely cited to explain why many eels at temperate latitudes are exclusive marine residents. However, the model is principally based on productivities estimated for deep oceanic waters, which have little relevance to the habitat choices made by growth-phase eels. The notion that latitudinal shifts in food availability ratios explain migratory patterns of anguillid eels is further undermined by the findings that glass and early yellow eels fed ad lib in tanks grow more rapidly in salt water than in fresh, that the ratio of saline to freshwater growth in eels does not consistently increase with latitude, and by the lack of evidence that food availability influences species richness. The adaptive nature of facultative eel catadromy can be approached from the viewpoints of arithmetic mean fitness, geometric mean fitness, and non-adaptiveness. Low fitness variability improves geometric mean fitness, and it is possible that use of both saline and brackish habitats may reduce fit-

ness variability and hence be adaptive. Eel life histories show features that are oriented towards slow growth and low mortality. This suggests that eel choice of habitat during the growth phase may be guided by minimization of predation and other mortality risk, more than by maximization of feeding opportunities.

Recommendations

SGAESAW recommends that data on demographic and other features of Atlantic eels in saline waters be assembled in an overview report, that eel demographic processes be analysed in relation to habitat characteristics in saline environments, that the precautionary approach be applied to European and American eels at all locations where they occur, that sampling methods be calibrated and validated to facilitate robust assessments of eel production, that results of these exercises be reported to appropriate subgroups of the ICES/EIFAC Eel Working Group, and that an ICES Study Group on Anguillid Eel Stock Assessment Methodology in Saline Waters be struck.

2 Anguillid eel habitat use in saline and fresh water

2.1 Inter-habitat movements in eels - an introduction

Otoliths of anguillid eels and other teleost fishes grow throughout the life of the fish. The elemental composition of accreting layers on the otolith reflects the chemistry of ambient waters. In particular, ratios of strontium (Sr) to calcium (Ca), which are high in marine waters and low in fresh waters, are reflected in otoliths. Hence the Sr:Ca ratio, measured along a centre-edge transect on the otolith, can be used to reconstruct the salinity history of individual fish (Kraus and Secor 2003, Fablet *et al.* 2007).

Reviews of Sr:Ca studies show that anguillid eels show three main migratory patterns or contingents during their growth phase (Daverat *et al.* 2006, Lamson *et al.* 2006, Jessop *et al.* 2008). Some eels are freshwater residents, some are brackish and marine water residents, and some shift between habitats once or several times during their continental phase. The coexistence of eels which enter freshwater with those that don't is termed facultative catadromy. A review of Sr:Ca studies in six eel species at 39 locations found that all species contained animals that had shifted habitat salinity during their continental lives (Lamson *et al.* 2006). Otolith Sr:Ca ratios are a powerful tool for understanding eel movements, but like all tools have their limitations and pitfalls. The following sections deal with some of these limitations and pitfalls.

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2.2 Cautions on the use of otolith microchemistry to infer anguillid eel migration patterns

Fish otolith Sr:Ca data are widely used to assess and interpret the salinity of habitat occupancy and inter-habitat movements (Daverat *et al.* 2006, Elsdon *et al.* 2008, Jessop *et al.* 2008). The accretion of new material on the otolith surface includes trace elements such as Sr, Ba, Mg that may be used to provide a chemical chronology of a fish's life. The use of chemical profiles across a sectioned otolith assumes that the changes in the fish's environment are temporally matched by changes in the concentration of elements incorporated into the otolith.

Instrument choice determines the resolution of the chemical data, both in concentration and temporally, as determined by the size of the analytic target. Typically, a small area ("spot") is analyzed at one time; arrays of spots may be analyzed to form a 2-D map. Electron probe micro-analysis (EPMA) uses X-ray fluorescence (XRF) to quantify minor elements; EPMA in wavelength-dispersive mode is quantitative (Gunn *et al.* 1992, Zimmerman and Nielsen 2003). More powerful XRF methods, e.g., nuclear microscopy combined with particle-induced X-ray emission (micro-PIXE, Malmqvist *et al.* 2000) or synchrotron-based XRF (SXRF, Limburg *et al.* 2007) can probe trace elements. These methods do not destroy the otolith material, so that the samples can be re-analyzed.

Mass spectrometric methods destroy otolith material, but may be preferred in terms of the material analyzed (e.g., stable isotopes), relative availability, and cost. Inductively coupled plasma mass spectrometry, coupled to a laser ablation unit (LA-ICPMS) is becoming a preferred tool due to its ability to analyze trace elements of interest (e.g., Sr, Ca, Zn, Ba, Mn, Mg), relatively low cost, and customer support.

Comparing these methods, wavelength-dispersive EPMA is adequate for Sr:Ca and may utilize smaller spot sizes than is typical for other methods, but has far lower sensitivity. Relatively high concentrations of otolith Sr make EPMA useful, but trace elements found at much lower concentrations such as Ba and Mg require more sensitive instrumentation for accurate measurement. Results for a given element that can be compared by different analytical methods are expected to be broadly comparable and lead to similar conclusions.

Water chemistry may vary in space and time due to mixing of water masses in response to factors such as currents and tidal action, precipitation and underlying watershed geology that will influence the Sr:Ca freshwater value. Long-term stability in environmental parameters should not be assumed, particularly in dynamic environments such as estuaries. Knowledge of both site-specific and temporal variation in water chemistry is important in the interpretation of otolith data because predictive relations between element concentrations and salinity, with the concentration of Sr increasing and Ba decreasing with salinity, may not be constant. Some freshwater locations may have unusually high Sr concentrations (or very low Ca concentrations), with Sr:Ca ratio values exceeding that of seawater while Ba concentrations in seawater may be affected by sediment load. Otolith Sr:Ca ratios are determined by Sr:Ca ratios in the ambient water, not salinity per se, although seawater has about 100 times the concentration of Sr in most fresh waters. The mixing curve between freshwater and marine Sr:Ca is typically nonlinear, with greatest discrimination between freshwater and brackish water and a lower amplitude difference between brackish and marine water (Kraus and Secor 2004).

Measures of water chemistry should take into consideration the importance of the freshwater Sr value in defining the Sr:Ca mixing curve. Across the salinity gradient

of estuaries, water chemistry sampling designs should be matched with expected habitat variability. Recommended approaches include stratified, nested or hierarchical sampling designs rather than fixed or simple random designs.

Fish must reside in an area sufficiently long for a detectable signal to be incorporated into the otolith. This time period varies with fish growth rate and tends to increase with fish age as growth rate decreases with age. This affects the minimum detectable period for residency in a habitat and the potential detectable frequency of inter-habitat movement. Decreased water temperature also reduces growth rate and, during winter, may lead to a sufficiently reduced rate of element incorporation that wintering in freshwater may be undetectable in eels migrating seasonally between estuary and river at northern latitudes (Thibault *et al.* 2007, Clement *et al.* 2009, see also Section 2.3). For recent migrants between habitats, Sr:Ca ratio values at the otolith edge may not reflect the environment at the time of capture.

Otolith Sr:Ca ratio data can be used to simply identify and perhaps quantify the variability in habitat residence into groups or contingents such as freshwater, estuarine/marine, and inter-habitat migrants. Potential problems with ontogenetic changes in otolith Sr:Ca ratio values can be avoided by considering only the transect section between the elver check and otolith edge. Estimates of proportion assume that unbiased and sufficiently large samples have been obtained. More detailed analyses may quantify the proportion of time spent in a given habitat and the frequency of inter-habitat migration but there are no standard methods for doing so. A sharply defined critical level for habitat transition is analytically convenient but moving band limits, such as mean \pm SD, also have problems in application. The possibility that changes in an otolith Sr:Ca ratio profile may result from changing environmental conditions around a stationary fish must be considered, particularly for dynamically changing environments such as estuaries. Laboratory studies can productively investigate the lags between short-term environmental changes and corresponding changes in otolith microchemistry (e.g. Secor *et al.* 1995). Another promising research approach is linking otolith microchemical studies to telemetry research (see Section 4.1).

Otolith chemical profile data are autocorrelated because they represent a time series. Repeated measures Multivariate Analysis of Variance has been used to deal with this issue, treating each fish as the experimental unit. More recently, mixed effects models have been used to specifically account for the covariance structure of the data and can introduce higher degrees of freedom into analyses. Outliers to the local trend in profile or to that expected for a given habitat norm will affect the interpretation of frequency of inter-habitat movement. These outliers can occur at small percentages in profiles, but their interpretation and criteria for their inclusion/exclusion remain unresolved (Jessop *et al.* 2008). Smoothing of a data series down-weights a single or a short series of anomalous data points and could obscure true habitat transitions.

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2.3 Do strontium-calcium measurements fail to detect wintering migrations to freshwater of eels that summer in saline waters?

Otolith microchemistry analysis has brought new insights into the migration patterns of eels. This led to challenging the paradigm of obligate catadromy in European (*Anguilla anguilla*) and Japanese (*Anguilla japonica*) eels by Tsukamoto *et al.* (1998) and in American eels (*Anguilla rostrata*) by Lamson *et al.* (2006). These recent studies have reported that migration into freshwater is not necessary for the completion of the eel life cycle. However, otolith microchemistry analysis is presently under scrutiny (Tzeng *et al.* 2007, Jessop *et al.* 2008, Elsdon *et al.* 2008, Clement *et al.* 2009).

We compared migration patterns of American eels in the Upper Salmon River and Point Wolfe River (Fundy National Park, New Brunswick, Canada) inferred by fin tissue stable isotope analysis (nitrogen ($^{15}\text{N}/^{14}\text{N}$) and carbon ($^{13}\text{C}/^{12}\text{C}$) ratios) and otolith microchemistry analysis (Sr:Ca ratios; laser ablation-inductively coupled plasma-mass spectrometry). During the summer (2005 - 2007), freshwater and saltwater organisms were collected to determine the isotopic signature from both environments (Figs. 2.3.1 and 2.3.2). Freshwater organisms had mean $\delta^{13}\text{C} < -20\text{‰}$ and $\delta^{15}\text{N} < 6.00\text{‰}$ while saltwater organisms were enriched in ^{13}C and ^{15}N (Figs. 2.3.1 and 2.3.2). Eels captured during the summer in both rivers showed isotopic signatures indicative of feeding on freshwater organisms (mean $\delta^{13}\text{C} < -20\text{‰}$ and $\delta^{15}\text{N} < 8.00\text{‰}$; Figs. 2.3.3 and 2.3.4). In contrast, eels captured in freshwater during the spring and fall showed a saltwater signature, with mean $\delta^{13}\text{C} > -15\text{‰}$ and $\delta^{15}\text{N}$ near or above 10‰ (Figs. 2.3.3 and 2.3.4). These results suggest that a large proportion of eels (> 70% of the samples) undertake spring downstream migration to forage in the

saltwater environment during the summer and migrate back into freshwater during the fall for overwintering. Otolith microchemistry analysis resulted in similar conclusions regarding recent habitat use. However, no freshwater signature, indicative of seasonal migration into freshwater during the winter months was detected based on Sr:Ca ratios.

Downstream spring migration and upstream fall migration of yellow eels have been observed in other rivers in Nova Scotia (Jessop 1987). Our results suggest that fall upstream migration to overwintering in freshwater is a frequently used tactic by eels in the rivers of Fundy National Park. Furthermore, our results support the hypothesis put forward by Thibault *et al.* (2007). Indeed, otolith microchemistry analysis of eels undertaking seasonal migration to overwintering in freshwater may not reveal an actual period of freshwater residency because of slow growth rate during the winter months. However, further studies are necessary to eliminate the possible bias induced by inferring habitat utilization from Sr:Ca ratios near the edge of the otolith (recent life history). Telemetry would be adequate to verify the accuracy of the otolith microchemistry analysis in detecting seasonal migrations between saltwater and freshwater habitats. Scientific knowledge on the importance of freshwater winter habitat utilization is essential for the conservation of the species, particularly if obstacles to fish movement (e.g. dams) impede juvenile eel (yellow stage) migration from saltwater to freshwater.

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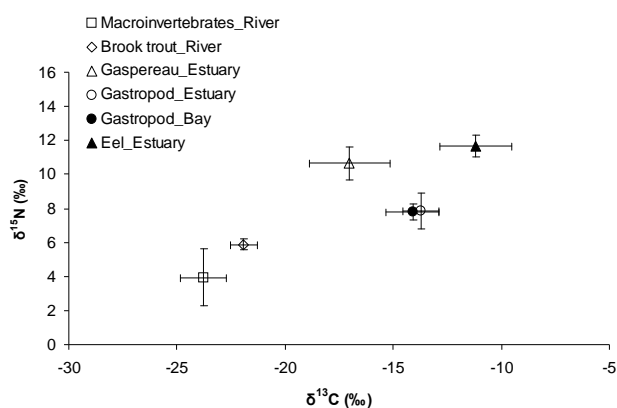


Figure 2.3.1. Mean (\pm SD) $\delta^{15}\text{N}$ versus $\delta^{13}\text{C}$ of the different organisms collected in freshwater and saltwater (estuary and bay) in the Upper Salmon River (Fundy National Park, New Brunswick, Canada).

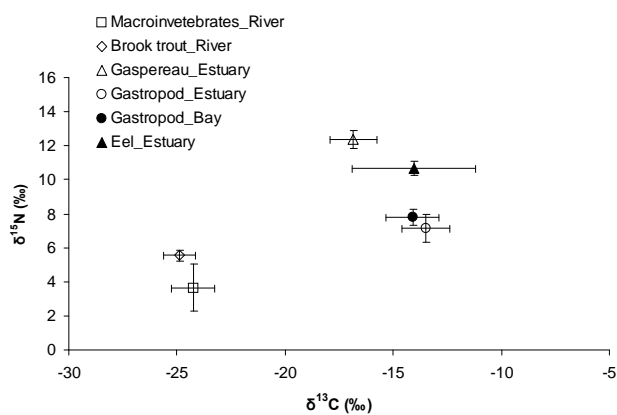


Figure 2.3.2. Mean (\pm SD) $\delta^{15}\text{N}$ versus $\delta^{13}\text{C}$ of different organisms collected in freshwater and saltwater (estuary and bay) in the Point Wolfe River (Fundy National Park, New Brunswick, Canada).

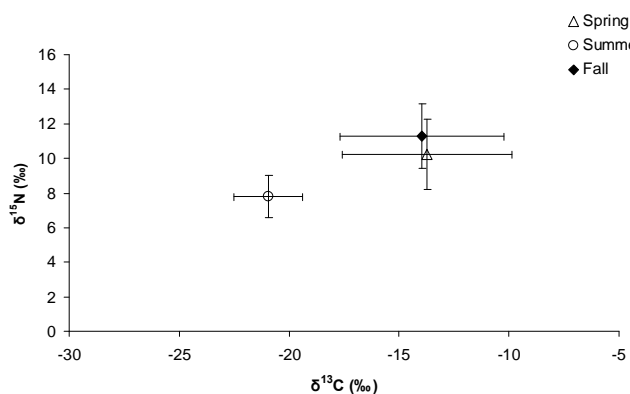


Figure 2.3.3. Mean (\pm SD) $\delta^{15}\text{N}$ versus $\delta^{13}\text{C}$ for eels captured in the Upper Salmon River at different time periods (Fundy National Park, New Brunswick, Canada).

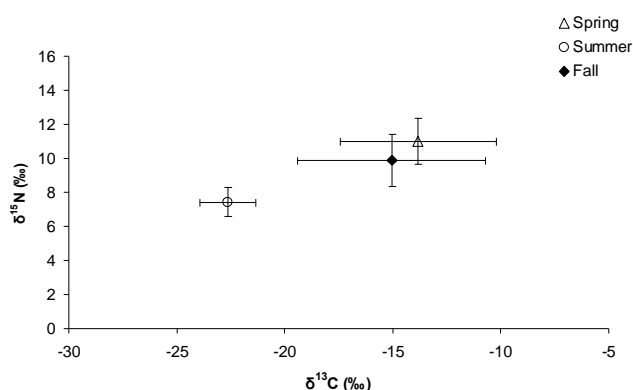


Figure 2.3.4. Mean (\pm SD) $\delta^{15}\text{N}$ versus $\delta^{13}\text{C}$ for eels captured in the Point Wolfe River at different time periods (Fundy National Park, New Brunswick, Canada).

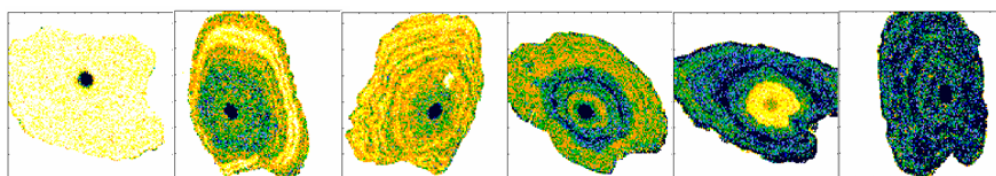
2.4 Diversity of life histories and movement patterns within anguillid eels

This section covers two topics that have received attention in eel ecology. Recent advances in otolith chemistry permit researchers to assess retrospectively the life histories of eels. This has been done primarily by means of quantifying strontium relative to calcium in otoliths. An enormous diversity of individual lifestyles was discovered, and a challenge is to reduce these to a few generic types.

For eels that enter inland waters, dams have become a widespread hindrance to continental penetration. Whereas Section 5 explores the ecological/evolutionary significance of maintaining catadromous eels, the present section uses tributaries in the Hudson River estuary, USA, to describe effects of barriers on eel demography, describe the spread of dams in northeastern North America, and discuss the potential benefits of eel passage, and gaps/limitations in our understanding of the role of artificial impoundments on catadromous eels.

Diversity of life histories and movement patterns within anguillid eels

Life histories of anguillid eels can be interpreted through the use of strontium:calcium (Sr:Ca) ratios measured throughout otoliths. Bearing in mind the caveats raised in Sections 2.2 and 2.3, nevertheless a broad diversity of migratory patterns can be found. Consider the following set of Sr:Ca maps, made using nuclear microscopy combined with particle-induced X-ray emission (micro-PIXE) analysis:



(Limburg, unpublished data)

Each Sr:Ca map represents the movements and periods of residency within or between different waters; paler colours indicate fresh water and darker ones indicate marine water (the dark spots in the otolith cores are due to the high levels of Sr incorporated in early life). It is clear that, at least at annual time scales, individual eels display a great diversity of movements.

In some systems, water movements due to tidal action can produce drastic changes in salinity. Given the stable salinity regime of the Baltic, it is unlikely that drastically changing salinities around the eels would create the patterns observed in emigrating silver eels. It is also unlikely that this method would pick up fine-scale shifts in salinity, e.g., diurnal tidal changes in salinities in meso- and macro-tidal estuaries. Rather, physiology would likely “average out” such short term changes.

The broad diversity of eel life history types contribute to silver eel escapement, but their ultimate success in reaching spawning grounds likely varies as function of nutrition, distance to the spawning grounds, etc. Among silver eels studied exiting the Baltic Sea or “lost” amongst the Danish islands, Limburg *et al.* (2003) categorized eels into five wild life history types, and three putatively stocked types. Lipid contents were analyzed and potential migration distances (km) were measured, allowing for sufficient lipids to fuel the journey to the spawning ground. Eels identified as catadromous (i.e., having had at least some natural ingress into fresh waters, e.g., second from left image above) had highest migration potentials; those identified as stocked (e.g., figure at left above) and fully marine (right-most above) did not have sufficient energy stores to undertake the 6000 km migration to the Sargasso.

Similar diversity of life histories has been found for other anguillids (Daverat *et al.* 2006). Whereas some latitudinal effects have been identified (e.g., Daverat *et al.* 2006, Jessop submitted), our understanding of how habitat choices are formed, and what this means in terms of fitness, is incomplete.

Effects of barriers on inland life histories: case study in Hudson River tributaries, with comparison to other systems

Following up on the work of Morrison and Secor (2003, 2004) and Morrison *et al.* (2003) in the mainstem of the Hudson River estuary, Machut *et al.* (2007) studied dynamics of eels in six representative tributaries that join the tidal estuary. This study involved demographics, but no otolith chemical analyses were performed. Eels were found in extremely high densities below the first barrier encountered in these systems (with the exception of the Wynants Kill, which had a large, iron barrier at its mouth – but nevertheless did hold eels). Barriers, particularly artificial ones, greatly reduced the numbers of eels moving upstream. A “barrier intensity index,” (BII) that included the compounding effects of barrier density (numbers km⁻¹) and cumulative dam height, was inversely correlated with eel condition, but interestingly, was positively correlated with eel growth (Figure 2.4.1).

Dam building occurred throughout the history of European settlement of the Hudson Valley, but the rate of larger (> 2 m) dam construction was actually higher in the latter half of the 20th century (Swaney *et al.* 2006). Similar growth in number of dams is evident in the Lake Ontario drainage basin and has been associated with loss of eels (Dittman *et al.* 2008, Machut *et al.* 2008); likewise, dam construction increased dramatically in Quebec during 1960-2000 (J.-D. Dutil, personal communication), also associated with eel declines. These North American observations are likely to be matched to observations on other continents and anguillid species.

Whether it is beneficial to pass eels up large hydropower dams is a complex issue due to risk of turbine mortality during subsequent downstream migration. However, in smaller tributaries whose dams are not equipped with hydro turbines, eel passage appears to be a successful way to move eels up into otherwise inaccessible habitats, with anticipated benefits. For example, in the Hudson River watershed, an experimental eel ladder was erected at the base of the first dam in the Saw Kill (above two large, natural waterfalls) by Robert Schmidt in 2006. During the first summer, 132

eels ranging from 70 to 550 mm were passed (Limburg *et al.* 2008). Additional benefits of passing eels up to habitats beyond dams include reduced exposure to toxicants in the mainstem of the Hudson, and higher probability that the passed eels become female (based upon our observations of sex ratios: Machut *et al.* 2007).

A gap in our knowledge is the effect on eels of artificial impoundments created by dams. Whereas a great deal of research on ecological effects of impoundments has been done, most of these have addressed biogeochemistry (e.g., Humborg *et al.* 2000, Vörösmarty and Sahagian 2000, Renwick *et al.* 2005) or reservoir fisheries (e.g., Cowx 2002). As we continue to investigate the impacts of dams, we should also consider the impacts (good and bad) of impoundment creation.

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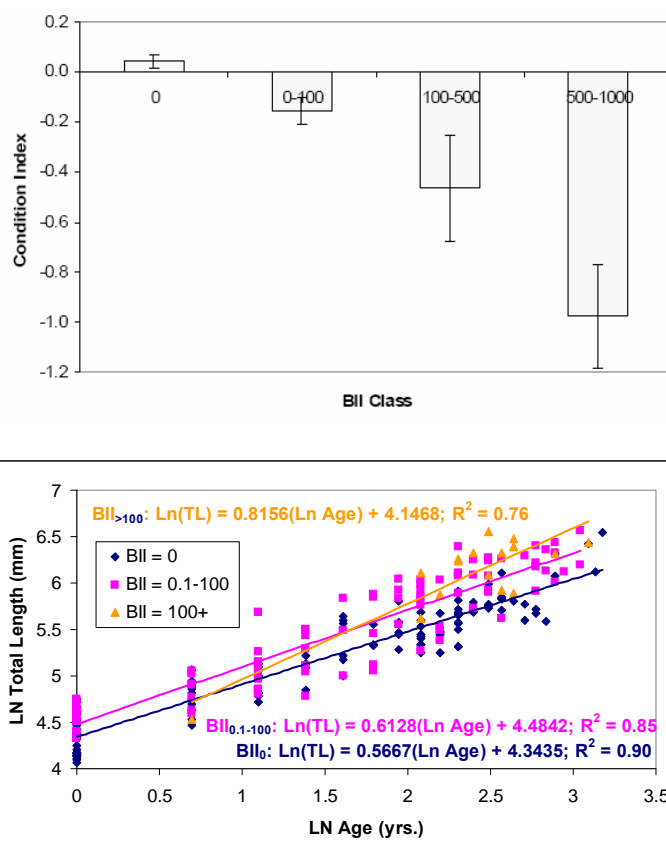


Figure 2.4.1. Effects of barriers, expressed through a barrier intensity index (BII), on eel condition (upper panel) and on growth rates (slopes of lines, lower panel). Source: Machut (2006).

2.5 Migration and habitat association in small eels

In the Southern Gulf of St. Lawrence, eels caught by electrofishing in streams are generally small, with modal lengths about 27 cm (Cairns *et al.* 2007) (Figure 2.5.1). Eels caught in rotary screw traps set in rivers in spring to capture Atlantic salmon smolts are also small, with modal lengths about 31 cm. In contrast, eels caught by fyke nets in freshwater ponds and saline bays and estuaries are much larger, with modal lengths in the range of 50 to 65 cm (Figure 2.5.1). Several factors could potentially explain the observed difference in eel sizes between these habitats.

One possibility is that large yellow eels are under-represented in stream samples. The fact that two very different gear types (electrofishing and rotary screw traps) both catch few large eels makes this seem less likely. However it remains possible that the low numbers of large eels observed in streams is an artefact of gear selectivity.

If eels in streams are male, the small sizes observed there would be explained because male eels mature at a small size. However, all eels from Southern Gulf streams that have been sexed were either undifferentiated or female (Cairns *et al.* 2008).

The paucity of small eels in samples collected in ponds, bays, and estuaries might be explained by the inability of fyke nets to retain small eels. However, length frequency distributions of eels whose lengths were estimated visually from glass bottom boat surveys were similar to those of fyke nets (Figure 2.5.2). On most survey nights visibility was sufficient to detect small objects on the bottom, including eels down to 12–15 cm in length. If small eels were present in significant numbers in the water under the boat during glass bottom boat surveys, they would have been seen.

The difference in size distributions between streams and saline bays and estuaries could be explained if juvenile eels colonize streams soon after arrival from the ocean, but later return to saline waters to complete their growth. However, a review of otolith Sr:Ca studies indicates that net movements in yellow eels are generally towards, rather than away, from fresh water (Lamson *et al.* 2006). These findings suggest that, in general, streams are not nursery areas for eels which complete their growth in saline waters. However, this does not preclude the possibility that streams may serve as nursery habitat in some areas.

Large eels sampled in ponds may have used stream habitat as nurseries. Sr:Ca cannot test this because both habitats are fresh. Sr:Ca results indicate that the majority of large eels in bays and estuaries spent their early years in saline water. Where these eels spent their early years is not known. In the eastern U.S., small eels appear to use deep channels preferentially. However the bays and estuaries in the southern Gulf of St. Lawrence are often shallow, and lack water more than 3–4 deep. Perhaps small eels are active at different times of the day, or they may seek out areas where they can hide under vegetation or debris, and thus avoid detection in glass bottom boat surveys. The paucity of small eels detected in glass bottom boat surveys in ponds, bays, and estuaries suggests a size-based temporal or spatial segregation. Such a segregation could be driven by small eels' need to reduce risk of cannibalism, which is common in eels (Lookabaugh and Angermeier 1992).

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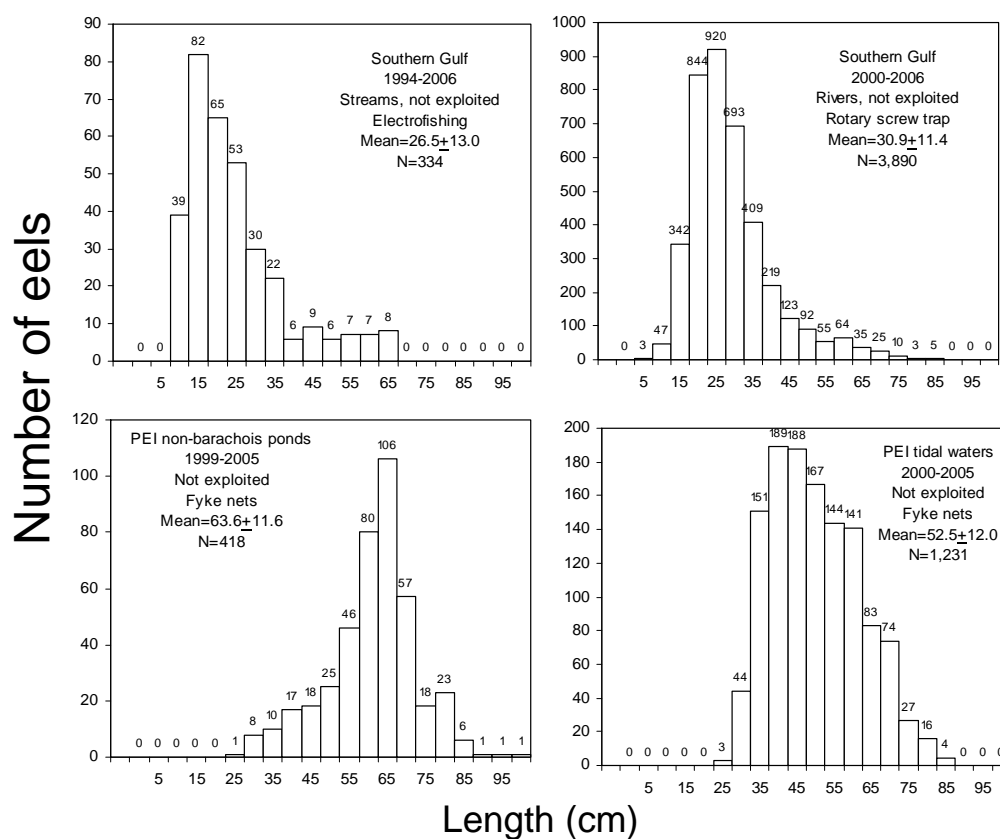


Figure 2.5.1. Length frequencies of American eels in the southern Gulf of St. Lawrence. Data from Cairns *et al.* 2007.

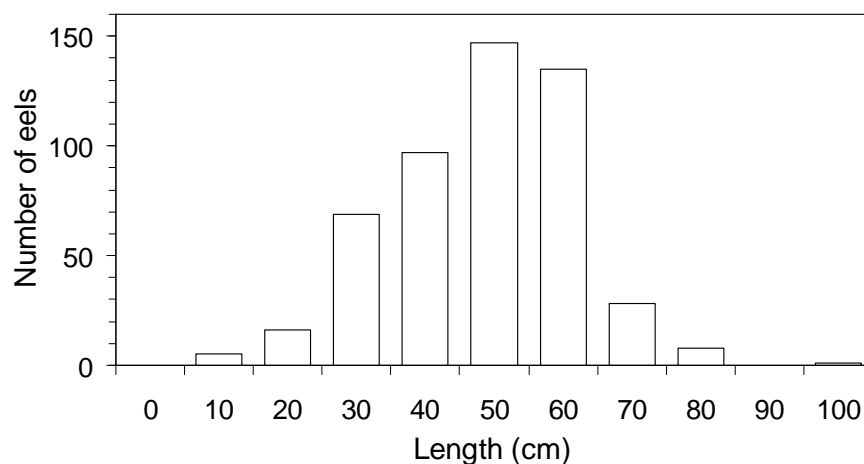


Figure 2.5.2. Frequency distribution of lengths of American eels estimated on glass bottom boat surveys in bays and estuaries of the southern Gulf of St. Lawrence. N = 506.

2.6 Preparation of an atlas of American eel habitat and fisheries on the east coast of North America

Members of SGAESAW are preparing an atlas of American eel habitat and fisheries on the east coast of North America. The atlas will be submitted for publication in a technical report series of the Canadian Department of Fisheries and Oceans, and will be available online. American eel habitat usage profiles in saline have not been pre-

cisely defined. However, the species is known to commonly inhabit estuaries and shallow and sheltered bays. Therefore the mapping of potential eel habitat will be based on criteria of depth and shelter from the open sea. Surface area of potential eel habitat will be calculated from GIS layers that are based on these criteria of depth and shelter. The location of current, and in some cases, historic, fisheries will also be mapped.

The atlas will be oriented towards saline waters. Concurrent efforts are underway to map current and historic potential eel habitat in freshwater in Canada and the U.S. Once total surface areas of potential eel habitats in the fresh water and saline zones are available, comparisons can be made which may shed light on the relative importance of fresh vs. saline habitats for American eel production.

In Canada, there is a broad effort to map freshwaters available to eels under current conditions of river obstructions, and also under scenarios where barriers would be removed or passability improved. Part of this project is the development of a decision tool which will permit managers to evaluate the surface area and potential biological production that would accrue given the mitigation of a given barrier to upstream or downstream migration. This project is a joint initiative among the Department of Fisheries and Oceans, the Quebec Ministère des ressources naturelles et de la faune, and the Ontario Ministry of Natural Resources. In the USA, work is underway to map current and former eel habitat in American drainages of the St. Lawrence system.

2.7 A method for the classification and mapping of sheltered and semi-exposed habitats in estuarine and coastal waters

With the general objective of assessing the importance of marine habitats in support of conservation of eels in North America, a method is proposed to categorize coastal and estuarine habitats based on three parameters: depth, degree of protection from wave action, and temperature. This Section describes the method of categorization by degree of protection from wave action, and applies it to the St. Lawrence River Estuary and Gulf. The method designates three categories: Sheltered, Semi-exposed, and Exposed.

Methods

Topographic vector maps in shapefile format (scale 1:50,000) were downloaded from Natural Resources Canada's web site (Natural Resources Canada 2008) and the data processed with ArcGIS 9.3 and complementary tools available from the web.

Waters in the study area were categorized as Sheltered, Semi-exposed, or Exposed by the following criteria. Sheltered zones were defined with the aid of a 1.5 km diameter circle. The circle was moved towards the coast until it reached two points on the coastline. A cutting line was drawn between these points and was taken as representing the outer boundary of the Sheltered Zone. Semi-exposed Zones were defined using a 15 km diameter circle. Similarly, the circle was moved towards the coast until it reached two points on the coastline. The cutting line was drawn and taken to represent the outer boundary of the Semi-exposed Zone (Figure 2.7.1). Waters outside the Sheltered Zone formed the Exposed Zone.

In situations where small islands lie off a coastline, application of the circle method could lead to designation of Sheltered or Semi-exposed whereas in reality the island would be too small to have any significant sheltering effect. To avoid this, islands fitting inside a 150 m circle were ignored for the purpose of mapping Sheltered Zones

(Figure 2.7.2). Similarly, islands fitting inside a 1.5 km circle were ignored for the purpose of mapping Semi-exposed Zones.

Other criteria were also set. Considering that the work had to be done manually and in order to reduce the processing time, Sheltered and Semi-exposed Zones defined with the circles had to be larger than a minimal surface area as described in Figure 2.7.3. Furthermore, in order to avoid including zones offering minimal protection from open water, a maximal aperture criterion (90°) criterion was used as described in Figure 2.7.4.

Bras d'Or Lake on Cape Breton Island is a large brackish water body with a narrow outlet to the ocean. On the basis of its outlet width, Bras d'Or Lake would be designated Sheltered. However, the Lake is large enough for substantial waves to be generated within it. Therefore a rule was set under which any semi-enclosed salt or brackish body of water large enough to fully enclose a circle of 15 km in diameter is designated as Semi-exposed. Bras d'Or Lake meets this criterion. Bras d'Or Lake was not covered in the maps presented at the March SGAESAW meeting, but the rule will be applied as atlas development proceeds.

The topographic maps used were structured in such a way that the Sheltered and Semi-exposed Zones, as determined using cutting lines, included areas of fresh water. A method was required to remove these areas (Figure 2.7.5). A variety of methods was used because no unique criterion was available for the whole study area: watershed limits were used when available (Quebec), otherwise the lowest indicated contour line was used. In some maps contours were given in metric and in others in Imperial units. It was therefore not possible to apply a uniform criterion for the freshwater boundary, which resulted in some variation or bias among areas.

Results and discussion

The total areas of Sheltered, Semi-exposed and Exposed habitats in the Estuary and the Gulf of St. Lawrence are presented in Table 2.7.1. Sheltered and Semi-exposed Zones represented 1.6 and 4.8% of the study area, respectively (Figure 2.7.6) and are shown by jurisdiction in Figure 2.7.7.

Sheltered and Semi-exposed Zones were broken down by ecoregion (17) as defined by Natural Resources Canada, and weighted by length of coastline. The Quebec Lower North Shore, New Brunswick, and Prince Edward Island were rich in Sheltered areas compared to the St. Lawrence Estuary, the Gaspé Peninsula and Anticosti Island (Table 2.7.2). In contrast, Semi-exposed habitats were better represented in the St. Lawrence Estuary, the southern portion of the west coast of Newfoundland, as well as the New Brunswick coast.

The next steps in this process will involve combining this information (Sheltered and Semi-exposed Zones) with other parameters such as depth, surface temperature and eel density.

The methodology described above will also require further improvements. Data are not always available in the same format and may use different units or scales across regions. Some data are available for some regions and not for others. Automation of the method to generate Sheltered and Semi-exposed areas would make it possible to examine different scenarios by changing any variable and criterion.

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Table 2.7.1. Total areas of Sheltered, Semi-exposed, and Exposed habitats in the Estuary and the Gulf of St. Lawrence.

Exposure category	Total area (km ²)
Sheltered	3,743
Semi-exposed	8,807
Exposed	224,945

Table 2.7.2. Total area of Sheltered and Semi-exposed habitats per ecoregion (unweighted and weighted). Sheltered and Semi-exposed areas for each ecoregion were weighted by dividing them by the coast length of the ecoregion. Ecoregions are based on climatology and were described by Natural Resources Canada (2007).

Ecoregions	Ecozones	Coast length (km)	Total area (km ²)			
			Sheltered	Sheltered weighted	Semi-exposed	Semi-exposed weighted
S. Laurentians	Boreal Shield	114.46	3.06	0.03	881.82	7.70
Cent.Laurentians	Boreal Shield	544.01	66.27	0.12	416.19	0.77
Saguenay	Boreal Shield	99.21	312.72	3.15	312.44	3.15
Mecatina Plateau	Boreal Shield	2062.57	1243.72	0.60	1158.50	0.56
Coastal Barrens	Taiga Shield	89.83	66.56	0.74	25.06	0.28
Strait of Belle Isle	Boreal Shield	340.77	94.92	0.28	245.87	0.72
N. Peninsula	Boreal Shield	343.80	199.46	0.58	241.99	0.70
SW Newfoundland	Boreal Shield	807.17	224.10	0.28	1068.40	1.32
Long range Mtns.	Boreal Shield	8.54	0.29	0.03	0.00	0.00
Anticosti I.	Boreal Shield	537.64	5.56	0.01	101.22	0.19
Iles-de-la-Madeleine	Atlantic Maritime	298.77	114.62	0.38	240.59	0.81
Nova Scotia Highlands	Atlantic Maritime	481.49	67.12	0.14	244.54	0.51
Maritimes Lowlands	Atlantic Maritime	1161.08	639.82	0.55	959.73	0.83
Prince Edward I.	Atlantic Maritime	985.72	571.36	0.58	510.66	0.52
Chaleur Uplands	Atlantic Maritime	318.03	14.15	0.04	277.78	0.87
Appalachians	Atlantic Maritime	784.58	92.69	0.12	1233.14	1.57
St-Lawrence	Mixwood Plains	115.44	26.48	0.23	889.34	7.70
Total		9093.12	3742.91	7.87	8807.27	28.20

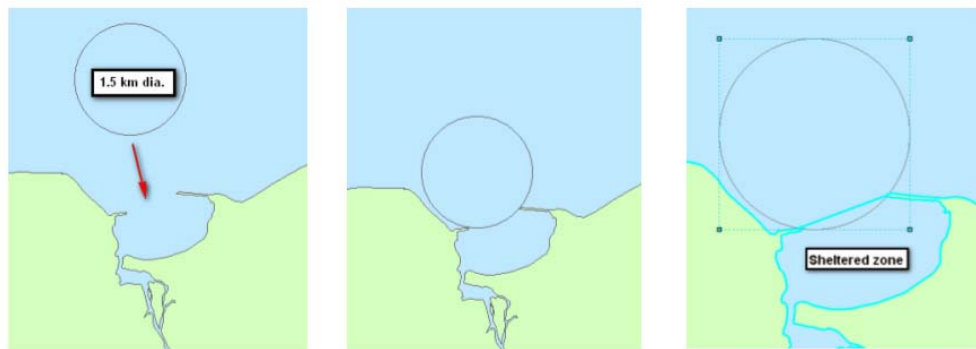


Figure 2.7.1. Sheltered and Semi-exposed Zones were defined using 1.5 and a 15 km diameter circles, respectively.

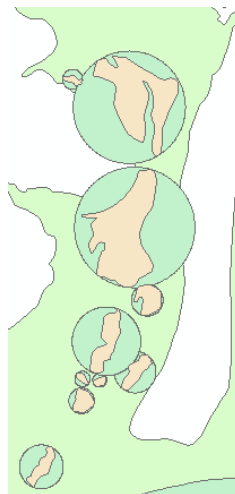


Figure 2.7.2. Circles were generated around islands with ArcGIS complementary tools. Small islands were ignored in the analysis, as described in Methods

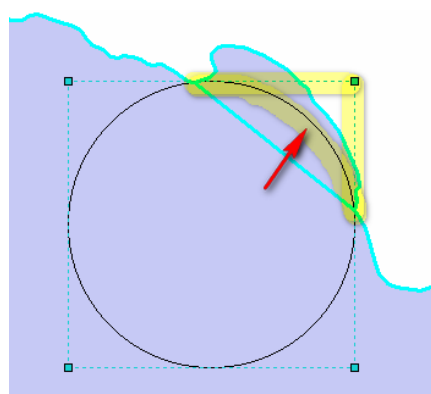


Figure 2.7.3. Area defined by superimposing the 1.5 km (dia.) circle and the dotted square that contains it, as outlined by yellow highlight (0.12071 km²).

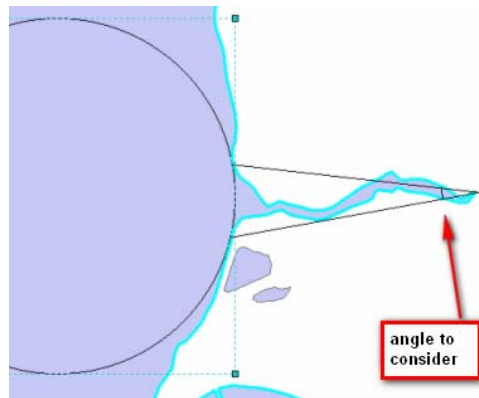


Figure 2.7.4. Angle formed between the innermost point on the coast and the two points on the coastline representing the outer boundary of a zone. The same criterion applies to both Sheltered and Semi-exposed Zones.

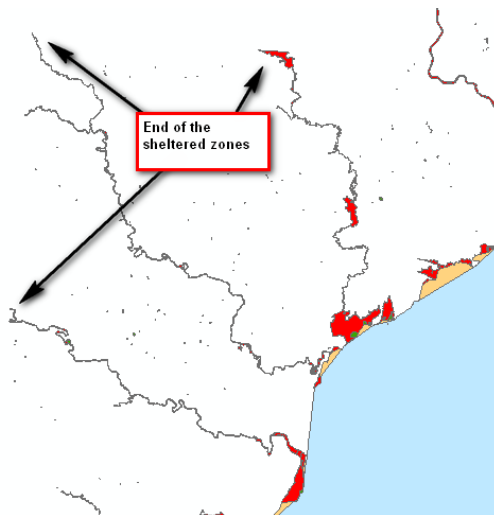


Figure 2.7.5. Example of the extent of some Sheltered Zones. The three zones include large areas of fresh water.



Figure 2.7.6. Example of the mapping of Sheltered (red), Semi-exposed (orange) and Exposed (blue) habitats in the St. Lawrence River Estuary and Gulf – showing Prince Edward Island, Iles-de-la-Madeleine, and part of the coast of New Brunswick.

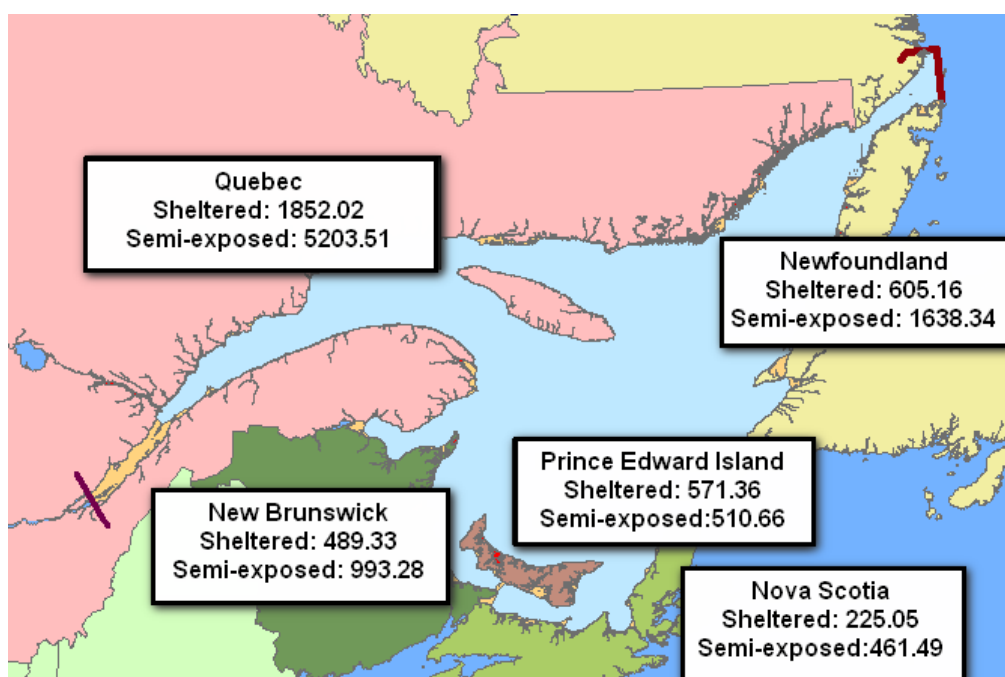


Figure 2.7.7. Total area (km²) of Sheltered, Semi-exposed and Exposed habitats in the St. Lawrence River Estuary and Gulf, by jurisdiction.

2.8 Mapping eel fishing areas in eastern North America

Data on locations of fishing effort were obtained from fishermen's logbooks, phone-out surveys to fishermen, and from government biologists. Known fishing locations are shown in Figs. 2.8.1 and 2.8.2. In eastern Canada, eels are fished in both fresh and saline waters. The fishery in the Southern Gulf of St. Lawrence is concentrated in

saline waters, but elsewhere there is a mix of saline and fresh fishing sites. In the eastern U.S., most eel fishing occurs in saline waters. In both countries there are substantial areas of coastline which are not fished for eels.

U.S. data available for this report have limitations in quality and gaps in spatial coverage. Collection of additional data on location of eel fisheries is ongoing and atlas preparation will proceed as further data are obtained.

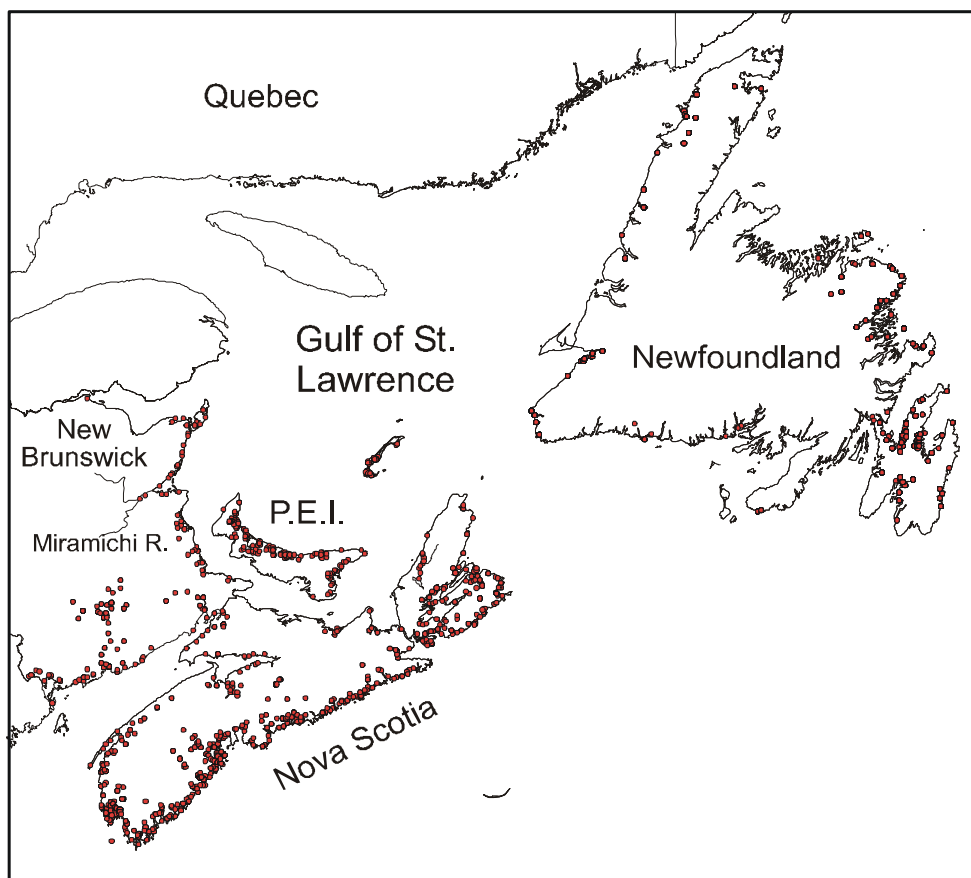


Figure 2.8.1. Current and recent fishing areas for American eels in the Gulf of St. Lawrence and the Atlantic coast of Canada.

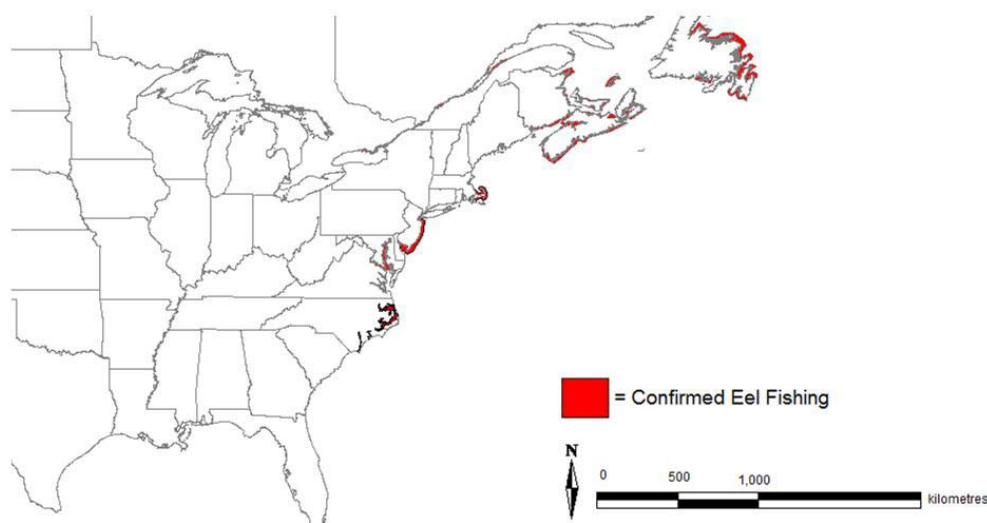


Figure 2.8.2. Current and recent fishing areas for American eels. Data are preliminary. Data are unavailable for Maine, Connecticut, and Virginia.

2.9 Locations of eel fishing in Delaware

American eel support a large fishery in Delaware. Delaware accounted for 12 to 18% of total U.S. annual landings between 1999 (the first year of mandatory landings reporting) and 2007. Mean landings during 1999 through 2007 were 57 t (Delaware Division of Fish and Wildlife 2008). The fishery is conducted with eel pots and the eels are sold for food and bait.

The fishery is pursued almost entirely in saline waters as only tidal waters are open for commercial fishing. There are limited areas of tidal fresh water in the state but they contribute little to Delaware American eel landings. Eels are landed at ports on Delaware River, Delaware Bay, the many tidal tributaries of the river and bay, and Delaware's Inland Bays (Indian River and Rehoboth Bays) (Figure 2.9.1).

The areas fished in Delaware River and Bay were classified by salinity. In oligohaline to mesohaline regions of Delaware Bay and River, which included the Delaware River and upper Bay ports (Delaware City south to Port Mahon), effort occurred in the tidal tributaries and in the nearshore areas of the river and bay. In the mesohaline to polyhaline areas of Delaware Bay, which included Bowers Beach, Mispillion and Lewes, effort was concentrated in the tidal tributaries with little effort occurring in the bay. Fishing effort in the Inland Bays was concentrated in the mesohaline areas of Indian River but effort also occurred in polyhaline areas.

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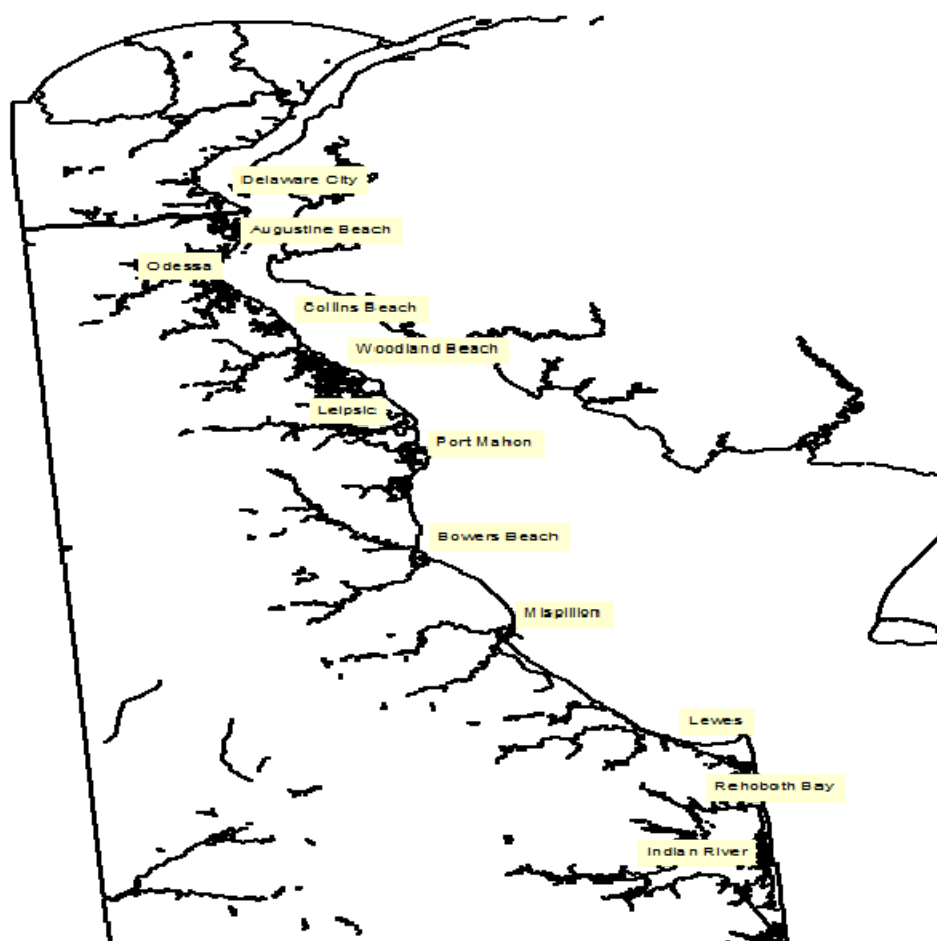


Figure 2.9.1. Delaware Bay, showing ports with reported eel landings during 1999 through 2007. Indian River and Rehoboth Bay constitute Inland Bays.

2.10 Locations of eel fishing in Virginia

The harvest of American eels from Virginia's marine waters is composed of yellow eels. Although primarily a food fishery, during the last decade sales to the recreational fishing sector have grown along with the demand for live eels as bait by anglers targeting cobia, blue catfish, and especially striped bass. Selling eel as bait for the fall striped bass fishery is often more profitable than selling for human consumption.

The fishery is dominated by eel pots, which have accounted for nearly 90% of Virginia's American eel harvest over the last fifteen years. A small percentage of American eels are caught in peeler pots and blue crab pots. There have been very few full-time eel fishermen over the last fifteen years; like many fishermen, those that harvest eel also harvest other species.

American eel harvest has two peak periods during the year: April–June and September–November. On average, approximately 43% of the annual harvest has been taken from April through June and harvest during September through November accounts for another 46%.

Many Virginia eel fishermen will fish an area intensively— exerting enough fishing pressure to get what’s available as long as it is worthwhile —and then move to a new area. Locations that are remote with little or no competition are preferred. A fisherman might return to a previously fished area a year or two later.

Most of the data on where American eels are harvested are provided by the eel fishermen. As of 1993, all licensed commercial fishermen in Virginia are required to submit monthly reports of their daily harvests to the Virginia Marine Resources Commission (VMRC)—the agency responsible for the management of fishery resources in the state’s tidal waters. The fishermen must provide detailed information on both their commercial harvest (fish caught and kept from an area) and landings (fish offloaded at a dock) of marine species in Virginia. The reported harvest and landings areas are assigned numeric codes that have been assigned to specific locations within the Chesapeake Bay, its tributaries, and the state’s coastal waters. Data collected through the mandatory reporting program are considered most reliable starting in 1994, the year after the pilot year of program.

The Chesapeake Bay and its tributaries are largely characterized by saline waters. All areas within the VMRC’s jurisdiction are classified as tidal. Fishermen have reported harvest of American eel by eel and fish pots from almost all areas within the jurisdiction of the VMRC. The mandatory harvest reports indicate that over half of Virginia’s American eel harvest by eel and fish pots has been taken from the James, York, and Rappahannock rivers. A large proportion of the state’s American eel harvest is also attributed to Tangier and Pocomoke Sounds.

Acknowledgement: Lewis Gillingham (VMRC) for sharing his extensive knowledge of Virginia’s eel fishery.

2.11 A preliminary list of survey data sets that may indicate American eel presence or abundance

The use by American eels of estuaries and sheltered bays is well known. The extent to which eels also use deeper or more exposed waters as growth habitat is less clear. Large numbers of eels exit the Bec-Scie River on Anticosti Island, Quebec, Canada, in spring, apparently to spend the summer in exposed marine waters of the Gulf of St. Lawrence (Caron and Raymond 1997, Jessop *et al.* 2008). Stable isotope and Sr:Ca data from eels of rivers of Fundy National Park, New Brunswick, Canada, suggest that at least some of these eels might summer in open marine waters (Section 2.3). For the European eel, Tesch (2003, pp. 280-282) documented extensive trawl fisheries for yellow eels in the open waters of the North Sea in the 1960s and 1970s.

Surveys which may catch eels as bycatch could shed light on eel use of exposed marine waters. Some surveys may also indicate how relative abundance changes with habitat variables, notably depth. A preliminary list of survey data sets which may indicate eel presence/absence or relative abundance in marine waters of eastern North America is presented in Table 2.11.1. This list includes offshore, nearshore and inshore trawl surveys, and surveys using lobster traps without escape vents.

Scientific bottom trawl surveys are conducted annually to assess the abundance of groundfish in the St. Lawrence Estuary and Gulf (Bourdages *et al.* 2008, Hurlbut *et al.* 2008). Between 1971 and 2006, over 12,000 sets have been done at depths ranging from 30 m to 500 m and have failed to catch any American eel, indicating that the deeper portions of the St. Lawrence lower estuary and Gulf do not represent a suitable habitat for American eels (Dutil *et al.* 2006, Scallion-Chouinard *et al.* 2007). Near-shore and shallower water beam trawl surveys conducted between 2004 and 2008 in

the brackish water portion of the St. Lawrence estuary, west of the Saguenay Fjord, have also failed to detect resident eels (Dutil *et al.* 2009), with one exception: a survey conducted in brackish waters in July and August at depths ranging from 6 to 30 m reported two eels (Fournier 2002). A trawl survey in the Northumberland Strait in the southern Gulf has never caught eels (Table 2.11.1).

The Virginia Institute of Marine Science (VIMS) trawl survey in Chesapeake Bay provides a long-term abundance index for eels (Geer 2003, Fabrizio and Tuckey 2008). This and similar trawl surveys typically operate in the day. It is not known whether eels caught in these surveys were in the water or are buried in the substrate at the time when they are caught. Data from trawl surveys can be used to plot relative abundance vs. depth. It is possible that eels in shallow water are more likely to be frightened away by a survey vessel passing overhead than eels in deeper water. This is a potential but unmeasured bias in the use of trawl data to assess the relation between abundance and depth.

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Table 2.11.1. List of surveys that may indicate presence, relative abundance, or density of yellow and silver American eels in estuarine, coastal, and offshore waters of eastern North America.

Area	Survey method and habitat	Survey timing	Comments	Source
Newfoundland and Labrador	Bottom trawl on continental shelf, to depths >1,000 m. Survey operated by DFO.	Series started in 1977. Surveys are conducted in fall.		Brodie 2005
Lower St. Lawrence River between Saint-Pierre-les-Becquets (near Trois-Rivières) and Boischatel (just downstream from Quebec City)	25 m beach seine with 3 mm mesh, in marshes.	May-Oct 2002	No American eels were caught	de Lafontaine et al. 2003
St. Lawrence Estuary west of the Saguenay and east of St-Jean-Port-Joli	Beam trawl, in brackish estuary, range of depths: 5-250 m	2004-2008	No American eels were caught	Dutil et al. 2009
St. Lawrence Estuary west of St-Jean-Port-Joli	Bottom trawl (Yankee), near limit of brackish water, range of depths: 5-25 m	2001	2 eels were caught	Fournier 2002
St. Lawrence Estuary between Pointe des Monts and the Saguenay R.	Compilation of records from observers on commercial vessels and the scientific literature	Covers records from 1930 to 2005	Eels were recorded in literature reports and observer reports, mostly in the coastal zone.	Scallan-Chouinard et al. 2007
St. Lawrence Estuary and the northern Gulf of St. Lawrence	Bottom trawl, with 12.7 mm codend liner. Survey operated by DFO, range of depths: 50-500 m	Series started in 1978. Surveys generally conducted in late summer	No American eels have ever been recorded on this survey.	Dutil et al. 2006, Bourdages et al. 2008
Southern Gulf of St. Lawrence	Bottom trawls. Survey operated by DFO.	Series started in 1971. Surveys are conducted in September.	No American eels have ever been recorded on this survey.	Hurlbut et al. 2008
Northumberland Strait	Bottom trawl survey in waters 5-40 m deep, with 11 mm codend liner. Survey operated by DFO.	Series started in 2001, ongoing. Conducted in Jul-Aug in daytime only.	No eels have been found in 1,400 sets	Mark Hanson, DFO; Comeau et al. 2008, Hanson 2009
Scotian Shelf, Bay of Fundy	Bottom trawls on continental shelf to 730 m depth. Codend has 19 mm liner. Survey operated by DFO.	Series started in 1970. Surveys are conducted in summer.		Branton and Black 2004
Atlantic Coast of Nova Scotia	Beach seines, gillnets, lobster traps without escape vents.	Jul-Nov 2006	No eels were caught in this survey	Bundy et al. 2007
Atlantic Coast of Nova Scotia	Unmodified commercial lobster traps, fished by commercial fishers. Survey operated by Fishermen and Scientists Research Society	2005-2006	6 eels were caught, ranging in length from 48 to 58 cm	den Heyer 2007; A. Bundy, DFO, pers. comm.

Table 2.11.1 (continued)

Area	Survey method and habitat	Survey timing	Comments	Source
Atlantic and Fundy coasts of Nova Scotia	Wire-mesh lobster traps with 25 mm mesh size and no escape vent. These traps are fished as supplements to regular commercial traps. Program operated by the Fishermen Scientists Research Society (FSRS).	Program began in 1999		MacKenzie and King 2007
NE US, Maine to New York	Lobster traps with no escape vent. Program operated by the Gulf of Maine Lobster Foundation and state governments. Uses same gear as FSRS program.	Program began in 2000		MacKenzie and King 2007
Northeast US	Bottom trawls on the continental shelf.	Series started 1963. Surveys conducted in spring and fall.		Northeast Fisheries Science Center 2008
Massachusetts coastal waters	Trawl survey using 65' stern trawler	Series began in 1978	1-4 eels caught per year south of Cape Cod in most years between 1978-1988. No eels caught since 1996.	Massachusetts ASMFC annual compliance report
Rhode Island, Narragansett Bay, Rhode Island Sound, Block Island Sound	Trawl survey in coastal waters		No eels observed in 2007	Rhode Island ASMFC annual compliance report
Rhode Island, Narragansett Bay, Rhode Island Sound	Trawl survey	2007	No eels observed	Rhode Island ASMFC annual compliance report
New Jersey, Atlantic coast	Stratified random trawl survey in waters down to 27 m depth. Codend has 6.4 mm liner. Conducted by NJ Div. of Fish & Wildlife.	Series started in 1988. Since 1991 cruises are conducted in Jan, Apr, Jun, Aug, & Oct.		Jeff Brust, NJ DEP
New Jersey, Delaware River	Seine survey primarily targets striped bass but other species are also recorded. Conducted by NJ Div. of Fish & Wildlife.	Series started in 1980. Since 1997 32 stations are sampled twice per month from Aug to Oct.		Jeff Brust, NJ DEP
New Jersey estuaries	Various estuaries were surveyed with various gears (trawl, gillnet etc.). Conducted by NJ Div. of Fish & Wildlife.	1970s, 1980s		Jeff Brust, NJ DEP
New Jersey, Great Bay to Mullica River	Trawl surveys along a transect. Conducted by Rutgers University.	1988-1990, 1996-present. Trawls conducted in Jul and Sep		Jeff Brust, NJ DEP
New Jersey, various locations	Various ongoing and historic surveys at Tuckerton and also other locations. Conducted by Rutgers University.	Various		Jeff Brust, NJ DEP

Table 2.11.1 (continued)

Area	Survey method and habitat	Survey timing	Comments	Source
New Jersey, Delaware River	Trawl, seine, and impingement surveys. Conducted by the Public Service Enterprise Group.	Ongoing	Part of mandatory monitoring for a nuclear power plant.	Jeff Brust, NJ DEP
Delaware Bay and River tidal tributaries	Trawl survey using 3 m otter trawl with 9.5 mm mesh cod end. Conducted by DE Div. Fish & Wildlife.	Surveys were conducted 1996-2005.	Eel abundance was highest in the middle reaches of the tributaries.	Clark 2006; John Clark, DE DFW
Delaware Bay and River	Juvenile finfish survey using 4.8 m otter trawl with 13 mm mesh cod end. Survey conducted by DE Div. Fish & Wildlife.	Series started in 1981, ongoing. Operates monthly, Apr-Oct.	Eels have been caught at all sites except for 4 sites in the lower Bay.	Michels and Greco 2008; John Clark, DE DFW
Delaware Bay, offshore sites	Adult finfish survey using a 9.1 m otter trawl with a 51 mm mesh codend. Survey conducted by DE Div. Fish & Wildlife.	Series started in 1990, ongoing. Operates Mar-Dec.	25 eels caught since 1990.	Michels and Greco 2008; John Clark, DE DFW
Maryland, Sassafas R.	Research eel pot survey	1998-2000, 2006-2008		Keith Whiteford, MD DNR
Maryland coastal bays	Surveys with 16' trawls, seines	Since 1990	Eel catches are low	Steven Doctor, MD DNR, Murphy and Secor 2006
Chesapeake Bay	Trawl surveys operated by the Virginia Institute of Marine Science. Eel index based on catches in upper half of tributaries	Series started in 1955, although gear changes complicate long-term trend analysis	Eel index based on catches in upper half of major tributaries in Apr-Jun.	Geer 2003, Fabrizio and Tuckey 2008
North Carolina	Trawl survey			

2.12 Eel distribution in Delaware saline waters derived from Delaware Division of Fish and Wildlife trawl surveys

Delaware Division of Fish and Wildlife has two ongoing trawl surveys of Delaware Bay and River and a completed trawl survey of tidal tributaries of Delaware Bay and River. American eels were captured in all three trawl surveys at varying rates. The salinity and depth of American eel capture sites and the timing of the captures provided information on eel distribution.

The juvenile finfish trawl survey uses a 4.8 m otter trawl with a 13 mm mesh cod end liner to sample 39 sites during daylight hours in Delaware Bay and River monthly from April through October (Michels and Greco 2008). Survey data from 1981 through 2007 showed that American eels were captured at all sites except for four in lower Delaware Bay (Figure 2.12.1). The highest American eel CPUE was at the Mahon River site, the only site in a tidal tributary. This site was similar in depth and salinity to nearby sites in Delaware Bay. Salinity was inversely related to CPUE for Delaware River and Bay sites. Depth was not obviously related to CPUE for Delaware River sites.

The adult finfish trawl survey uses a 9.1 m otter trawl with a 5.1-cm mesh cod end to sample 9 offshore sites during daylight hours in Delaware Bay from March through December (Michels and Greco 2008). Only 25 eels were caught in all tows from 1990

through 2007. American eels were captured at two upper bay, two middle bay, and two lower bay sites at depths ranging from 9 to 17.5 m and salinities ranging from 13 to 28.5 ppt (Figure 2.12.2). American eels were only caught at the lower bay sites in December.

The tidal tributary trawl survey used a 3 m otter trawl with a 9.5 mm cod end liner to sample six sites during daylight hours in each of six Delaware River and Bay tidal tributaries during 1996 through 2005 (Clark 2006). The three tidal tributaries with the strongest salinity gradients—the St. Jones, Mispillion, and Broadkill rivers—showed similar patterns in eel distribution (Figure 2.12.3). Eel abundance was lowest in the uppermost sites, which had low oligohaline salinity, and the lowest tributary sites, which had high mesohaline to polyhaline salinity. Eel abundance was highest in the middle reaches of the tidal tributaries in oligohaline and mesohaline salinities. The tidal tributary trawl survey results suggested that eel distribution was influenced by salinity in systems with steep salinity gradients.

American eels caught in Delaware Division of Fish and Wildlife trawl surveys were most abundant in oligohaline to mesohaline waters of Delaware Bay and River and their tidal tributaries. American eels were more abundant in shallow, inshore Delaware Bay waters than in deeper, offshore waters but abundance was not related to depth in Delaware River. Although eel abundance was low in polyhaline areas of Delaware Bay and its tidal tributaries, their presence in these polyhaline waters showed that American eels exploited habitats over the full range of salinities in the Delaware estuary.

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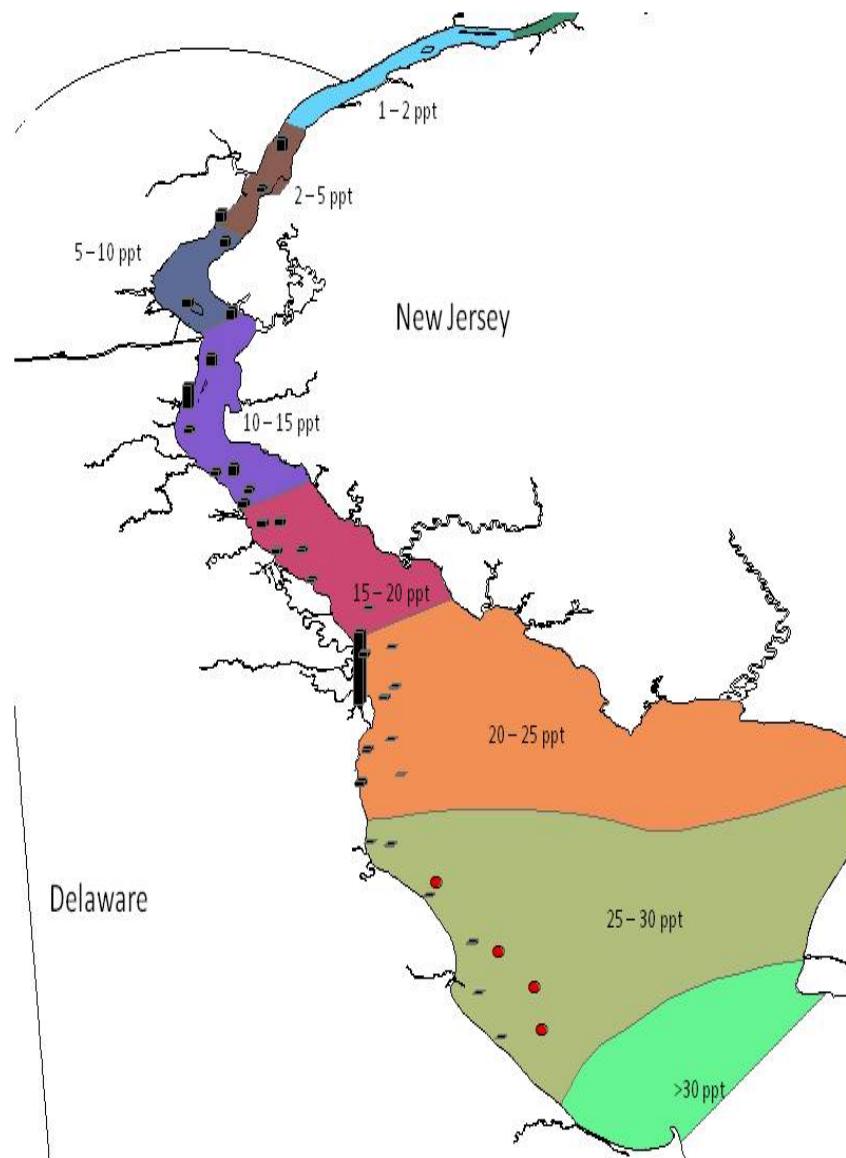


Figure 2.12.1. Delaware juvenile finfish trawl survey sites in Delaware River and Bay. Black bars represent American eel geometric mean CPUE for 1981 through 2007. Red circles are sites at which no eels were caught. Tallest bar is the Mahon River site.

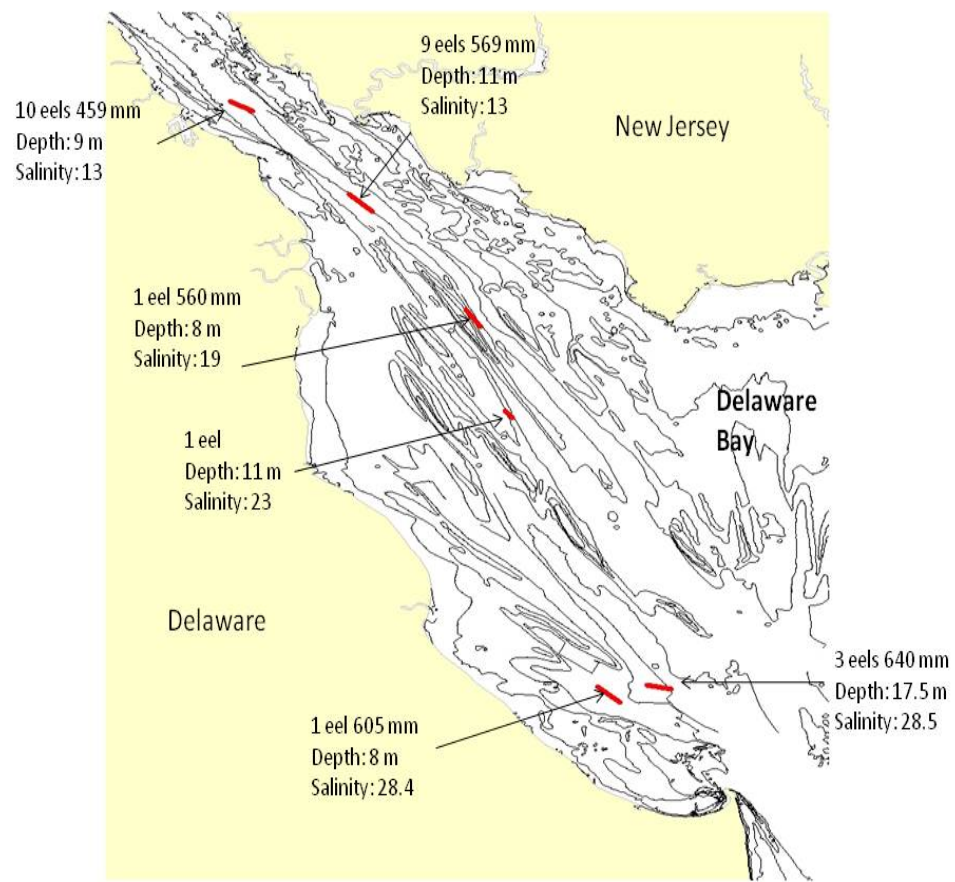


Figure 2.12.2. Delaware adult finfish trawl survey sites in Delaware Bay sampled during 1990 through 2007. Labels are total eels caught, and mean length, depth and salinity during period for each site.

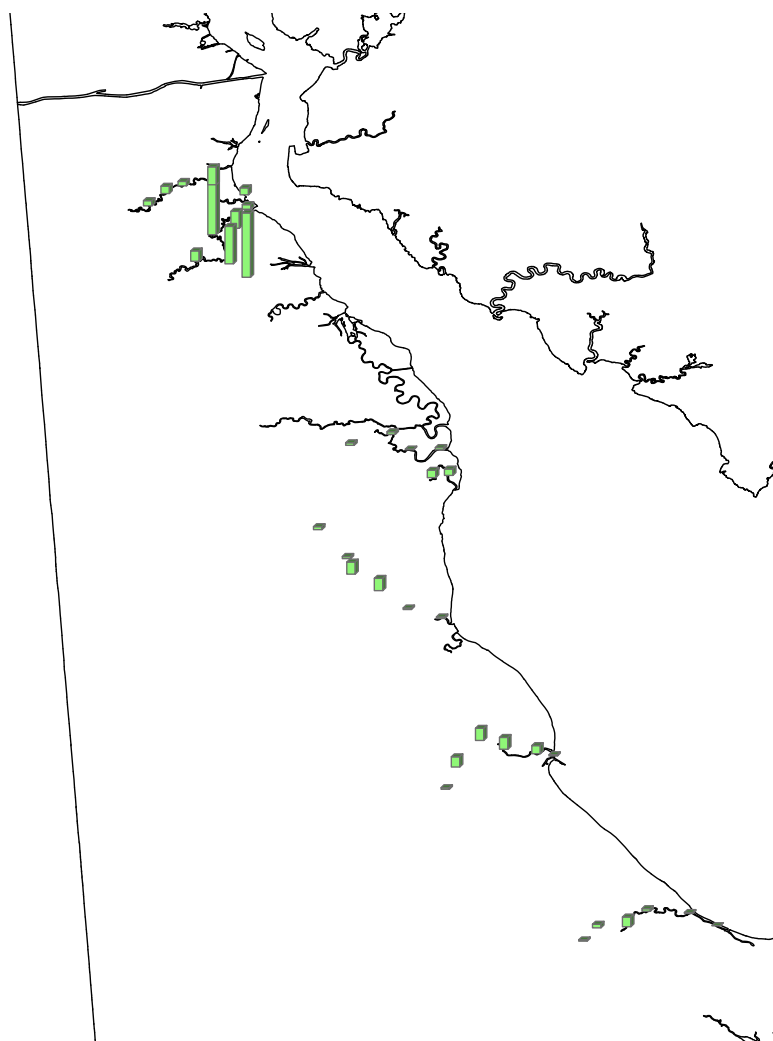


Figure 2.12.3. Delaware tidal tributary trawl survey sites sampled during 1996 through 2005. Bars represent geometric mean CPUE of American eel at each site. The tidal tributaries sampled from north to south were the Appoquinimink, Blackbird, Mahon, Simons, St. Jones, Mispillion, and Broadkill rivers.

2.13 Eel ecology, movements, and growth in the St. Jones River, Delaware

The St. Jones River is tidally influenced and flows approximately 18 km from a dam at Silver Lake, Dover, Delaware, to Delaware Bay. Salinities range from approximately 20 ppt at the river mouth to tidal fresh (< 1 ppt) within the last few kilometres below the dam. During a three year fishery-independent mark-recapture program utilizing commercial eel pots (76x30x30 cm with 1.3 cm coated wire mesh), a total of 10,115 American eel were individually tagged of which 3,352 were recaptured. An additional 2,384 American eel were recovered through a cooperative agreement with the primary commercial harvester who accounted for >95% of landings for the St. Jones River.

Catch-per-unit-effort (CPUE) declined with increasing river kilometre (Figure 2.13.1). Catches were highest in the lower, high salinity portion of the St. Jones River (22.0 eel/day). CPUE was lowest in the upstream, less saline reaches of the river (5.76

eel/day). American eel catches were positively correlated with salinity ($R^2 = 0.608$; Figure 2.13.2) and American eel were usually absent or in very low abundance (<5 eel/day) from upper river sampling locations. This trend of decreasing catch rates in the upper portion of the river was also observed among years. Catch per unit effort in all regions of the St. Jones River increased in each year of the study. In 2005, CPUE was at its lowest levels (8.8 #/day) and increased to 14.0 #/day in 2006. In 2007, CPUE was at its highest levels during this study at 18.5 #/day.

Growth rates were calculated using an equation modified from Oliveira (1997):

The divisor is defined as the number of days an individual was at liberty when the water temperature was $\geq 10^\circ\text{C}$. Growth rates for recaptured American eels were calculated spatially (by location strata) and by size class (small: 152–305 mm, medium: 306–457 mm, and large: >457 mm) to examine variation in growth rates. Growth rates generally increased with the size of American eel, with large American eels expressing the highest mean growth rates (Table 2.13.1). Mean growth rates in the lower portion of the St. Jones River (sites 1–14) were higher than for both the middle (sites 15–25) and upper (sites 26–40) areas of the river. Growth rates were significantly higher ($p < 0.05$) in the higher salinity sites when compared to the upper, less saline portions of the St. Jones River. Large American eels experienced significantly higher growth rates ($p < 0.05$) than medium and small American eels. The results of the interaction effect indicate that the effect of size and location was significant ($p < 0.05$).

During periods of non-harvest, apparent survival (S) estimates for both medium ($S = 0.798$; 95% CI = 0.756, 0.833) and large size American eels ($S = 0.792$; 95% CI = 0.731, 0.842) were maximized in the non-harvested portion of the St. Jones River. Small American eels in the occasionally harvested portion of the St. Jones River exhibited the lowest apparent survival probabilities ($S = 0.388$; 95% CI = 0.294, 0.492) during the non-harvest months. In non-harvest months, estimated apparent survival probabilities for American eels in the area of intense harvest pressure were generally similar for American eels of all three size classes, ranging from 0.656 (95% CI = 0.481, 0.798) for large American eels, 0.661 (95% CI = 0.584, 0.730) for small American eels, and 0.700 (95% CI = 0.641, 0.753) for medium American eels.

Capture probabilities (p) were highest for the non-harvested upper portion of the St. Jones River ($p = 0.349$; 95% CI = 0.315, 0.385) and decreased as one moved downstream through the zone of occasional harvest ($p = 0.218$; 95% CI = 0.194, 0.244). Capture probabilities were lowest in the lower most intensively harvested zone ($p = 0.136$; 95% CI = 0.123, 0.150). Recovery probability (r) estimates for American eel harvest by the commercial fishery were greatest in the intense harvest zone ($r = 0.491$; 95% CI = 0.451, 0.530) and decreased with a move into the occasionally harvested region of the St. Jones River ($r = 0.339$; 95% CI = 0.275, 0.409).

In general, downstream movement transition probabilities were higher than upstream movement transition probabilities. Estimated upstream movement probabilities ranged from 0.006 (95% CI = 0.001, 0.024) for large American eels to 0.016 (95% CI = 0.011, 0.024) for medium American eels. During the winter months, there was no upstream movement for American eels of any size class. Transition probabilities representing downstream movement in non-winter months were comparatively higher than upstream movement estimates, with the exception of the large American eels, who exhibited no downstream movement in non-winter months. The highest movement transition probability was for small American eels exhibiting downstream movement over winter, which was estimated at 0.179 (95% CI = 0.029, 0.617).

From May–November 2006 a total of 974 American eel were collected during supplemental sampling using commercial eel pots in Delaware Bay waters adjacent to the mouth of the St. Jones River. Catches in bay waters were minimal (9.4% of total landings) until the months of October and November when the vast majority of harvest was recorded. These data, when coupled with increased downstream transition probability estimates, provide support for anecdotal reports by commercial harvesters who believe that large segments of American eel exit tidal creeks during the winter months to occupy more saline, warmer regions of Delaware Bay.

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Table 2.13.1. Mean growth rates (mm/growing season days at liberty) and variances of American eels in the St. Jones River by size class and location strata, 2005–2007.

Mean Growth Rate by River State	Small	Medium	Large	Location Means
Sites 1–14	0.248	0.329	0.516	0.327
Sites 15–25	0.286	0.272	0.350	0.288
Sites 26–40	0.159	0.194	0.263	0.214
Size Means	0.253	0.275	0.343	

Variance on Mean Growth Rates	Small	Medium	Large	Location
Sites 1–14	0.027	0.055	0.066	0.054
Sites 15–25	0.039	0.036	0.049	0.040
Sites 26–40	0.023	0.019	0.029	0.024
Size	0.031	0.042	0.052	

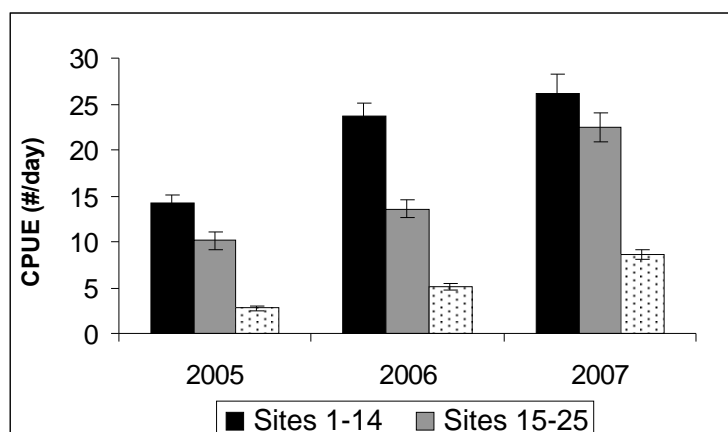


Figure 2.13.1. Annual variation in mean catch per unit effort (CPUE) values with standard deviation by strata location, 2005–2007.

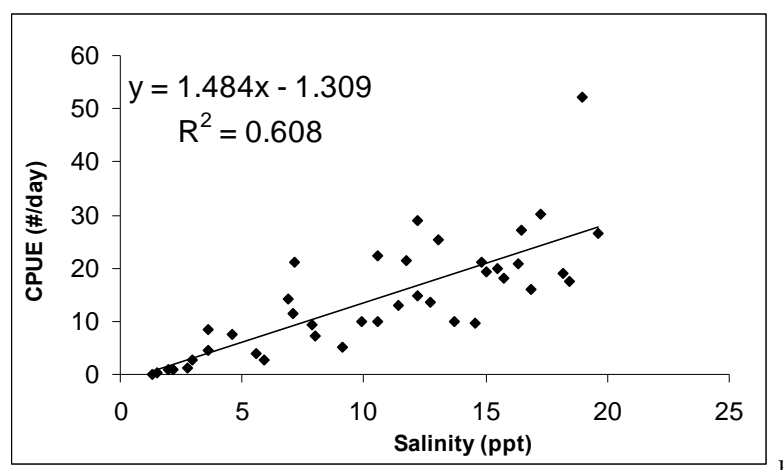


Figure 2.13.2. Mean site American eel catch per unit effort (CPUE; #/day) versus mean site salinity (ppt) in the St. Jones River, 2005–2007; regression equation inset.

2.14 Habitat choice and diet of 0+ eels in coastal waters

Background

There is no established method for monitoring the early year-classes of yellow eel. A simple sampling method for epibenthic fauna on shallow soft-bottoms has been in use in Sweden since the early 1970s (Pihl and Rosenberg 1982). A rectangular box made of aluminium sheet with an open bottom is dropped down. The contents are then emptied of all macroscopic animals using dip-nets with <2 mm mesh-width (Figure 2.14.1).

The drop-trap was used extensively for surveys in areas shallower than 1 meter along the whole Swedish West- and South coast between 1975 and 1985. Those studies have been synthesised by Degerman *et al.* (1986), who found that small eels, down to the glass-eel year class, were caught in about 30% of the approximately 100 localities that were sampled with 10 to 20 random drops at each site.

The data from all drops where one or more eels were caught were analysed for bottom substrate, vegetation type and vegetation cover. All eels were found in drops with high vegetation coverage although a large fraction of the drops were with no or little vegetation (Figure 2.14.2). The average eel abundance found during 1975–1985 was 0.5 eels/m² in the 0–1 m depth interval at localities with more than 40% vegetation cover.

Those observations were used to help design a sampling method to study juvenile eels during the Environmental Impact Assessment (EIA) of the Öresund Link project. A larger trap which sampled an area of 1 m² and was adjustable allowing depths of 2 to 2.5 m to be sampled was used. The trap was emptied using an ejector pump (Westerberg *et al.* 1993). The fisheries investigations in the Sound took place during 1992 to 2002 and during this period approximately 2700 drops were made at 3 localities on the Swedish side and 2 on the Danish side, with a smaller number of samples at 3 localities in Kattegat and Skagerrak intended as controls. The general results of the EIA were presented in Anon. (2005). This study presents a further analysis of the 10 years of data.

It was assumed when designing the sampling strategy that eels were associated with vegetation. The sampling was stratified to the vegetated parts of the station and the average abundance of eel for the whole locality was calculated using the result of the vegetation survey. Though vegetation-free areas were not sampled the vegetation coverage in individual drops varied from almost 0 to 100%. The linear relationship between coverage and abundance is what should be expected if the abundance of eel was directly related to vegetation cover, but only in those areas with vegetation (Figure 2.14.3).

Habitat choice in the Sound

There was a clear dominance of small eels. If 130 mm total length is used to separate the 0+ year-class from the older eels and 250 mm is considered the separation point between juveniles and adults, then 92% of the total catch were juveniles and 67% were 0+ eels.

All eels were found at shallow depth (Figure 2.14.4). There were relatively few drops made at depths greater than 1.5 m, as the trap became unstable in waves at deeper deployment. Instead a simple survey technique was developed to work semi-quantitatively at depths down to 2–3 m. The ejector pump, bow-sieve and sorting table used with the drop trap was connected by a flexible hose to a short PVC pipe mounted on a long steel pipe and a wheel (Figure 2.14.5). The steel pipe was held vertically with the nozzle following the bottom while the boat moved at approximately 1 m/s. The function of the nozzle was monitored by a video camera. By inter-calibrating with drop-trap data from previously surveyed locations the effective sampling width of this “vacuum cleaner” was found to be roughly 1 cm. Several transects down to about 3 m depth confirmed the very low abundance of small eels below a depth of 1.7 m.

The vegetation type and coverage was recorded for each individual drop. The mean number of small eels (<250 mm) per m² vegetated area was calculated according to which was the dominant vegetation type in the drop (Table 2.14.1). Eels were found in all kinds of vegetation as well as in detritus. The highest eel density was associated with green macro-algae. The presence of *Ulva lactuca* indicated high nutrient load and a relatively undisturbed environment.

The sediment type at the sites sampled in the Sound was relatively uniform, consisting of sand and silt. There was no difference in eel abundance between sediment types.

Diet

A study was made of the stomach and intestine contents of 119 small eels caught in the Sound during 1993. The contents of the stomach and intestine were weighed and analyzed by taxonomic group. The proportion of a specific group was estimated to within 1/3 of the total weight of the stomach and intestine. The mean weight of the gut contents as a percentage of the total weight of the eel was 3.7 % ranging from 0 to 7% (Table 2.14.2).

For all sizes of eel crustaceans dominated the diet (Table 2.14.3). The amphipod *Corophium voluactor* was a major component of the diet of 0+ eel. Older eels had a more varied diet. The dominant insect was Chironomid larvae.

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Table 2.14.1. Mean abundance of young eels in relation to vegetation type. Abundance is shown as number/m² of vegetation.

Dominant Vegetation type	N	Mean	95% conf
Zostera	260	0.37	0.149
Ruppia	1549	0.61	0.081
Other fanerogames	44	0.17	0.195
Cladophora	141	0.96	0.265
Ulva	200	1.62	0.293
Rhodophyteae	62	0.69	0.336
Phaeophyceae	156	0.42	0.152
Epiphytic algae	272	0.31	0.101
Detritus	60	0.35	0.240

Table 2.14.1. Frequency distribution of the weight of food items from the stomach and intestine as a percentage of total body weight, counts in 0.5% bins, percentage shows bin centre.

Percent gut content	Total number	0+	>=1+
0.00%	1		1
0.50%	3	2	1
1.00%	1	1	
1.50%	3	3	
2.00%	9	3	6
2.50%	17	8	9
3.00%	15	6	9
3.50%	13	7	6
4.00%	22	14	8
4.50%	11	7	4
5.00%	8	2	6
5.50%	3	2	1
6.00%	6	5	1
6.50%	5	3	2
7.00%	2		2

Table 2.14.3. Diet composition by weight for all 119 eels and by year-class.

	All	0+	≥1+
Crustaceans	61.8%	71.4%	59.6%
Polychaets	20.8%	1.8%	25.0%
Insects	9.3%	21.4%	6.7%
Other	8.2%	5.5%	8.7%

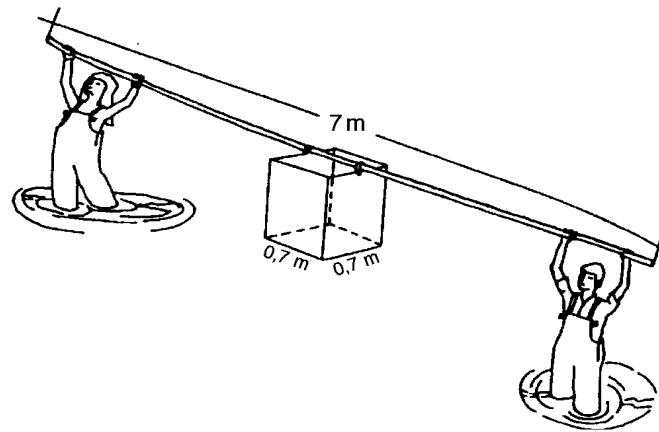


Figure 2.14.1. The drop-trap.

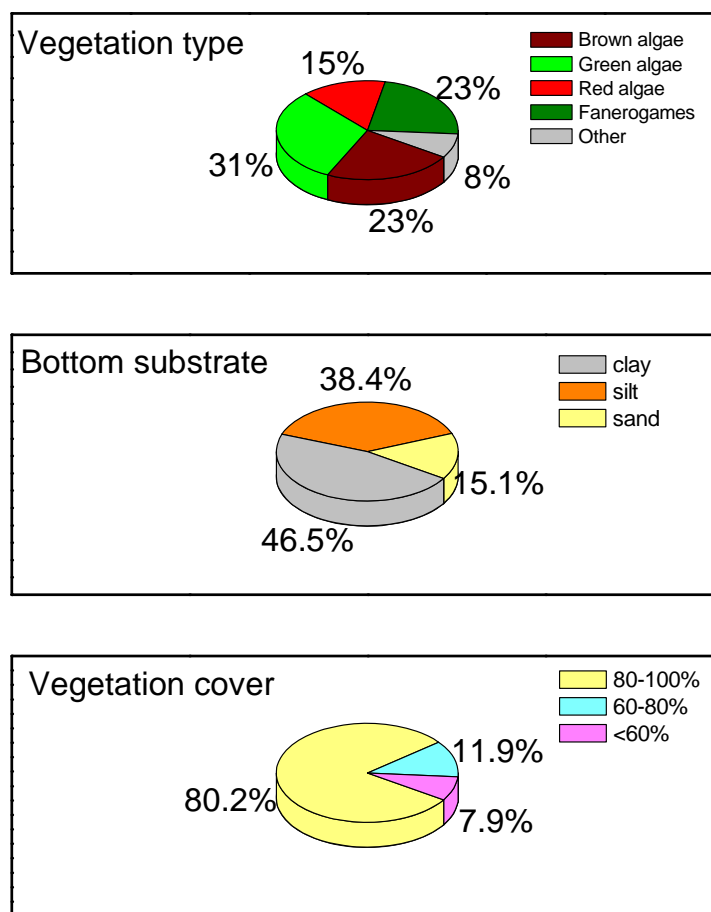


Figure 2.14.2. Average characteristics at 30 sites with eels on the Swedish West-coast.

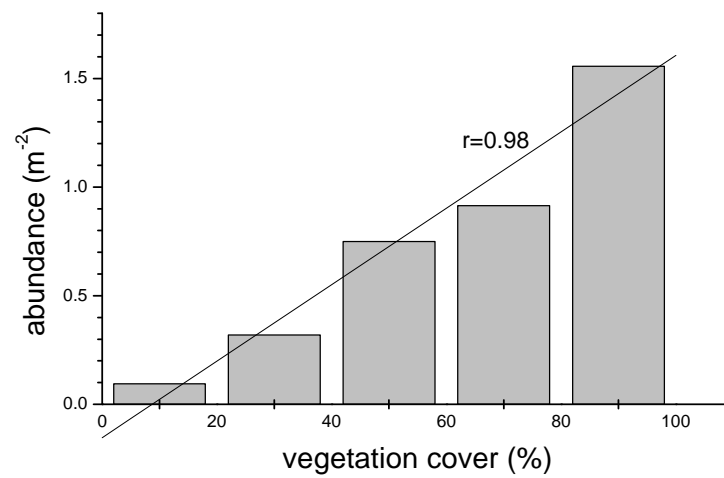


Figure 2.14.3. Observed eel abundance as a function of vegetation cover in a drop-trap in Öresund.

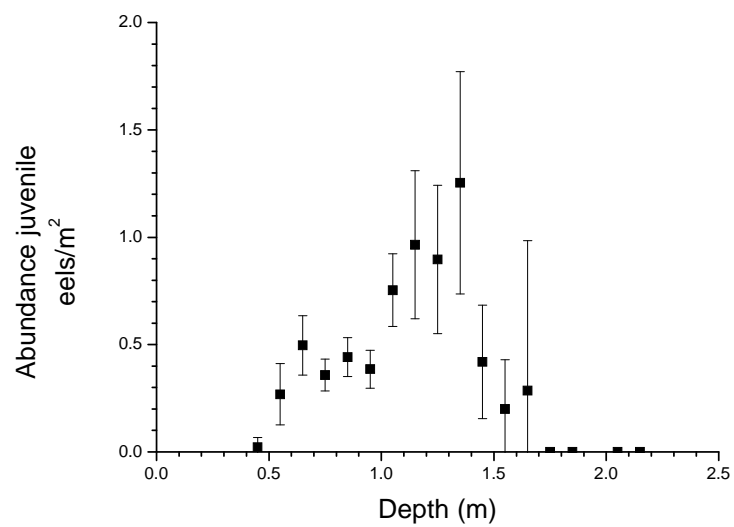


Figure 2.14.4. The depth distribution of juvenile eels in Öresund, showing mean abundance and 95% confidence interval.

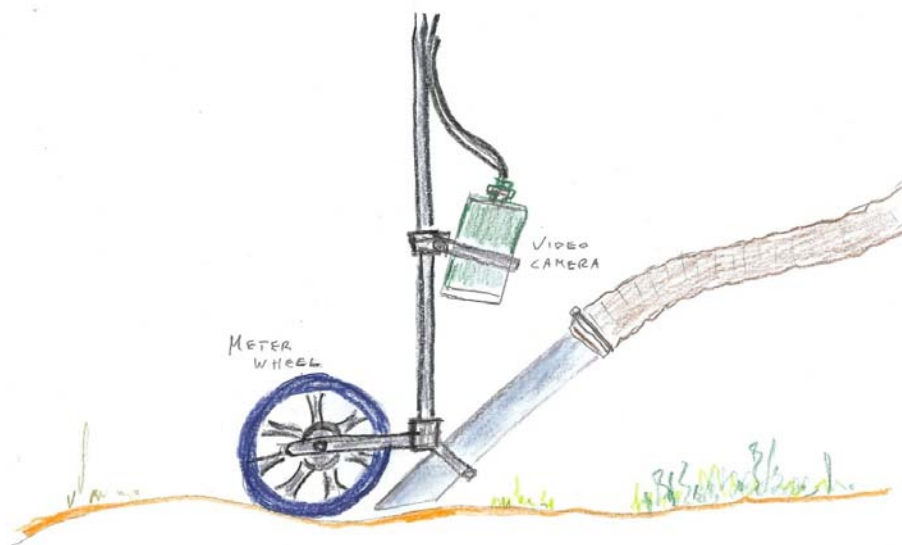


Figure 2.14.5. The suction nozzle and fixture used for continuous survey of juvenile eels.

2.15 Migratory behaviour and habitat use of Japanese eel in the estuary as revealed by both conventional mark-recapture method and otolith elemental signature

Abstract

To understand the migratory behaviour and environmental history of Japanese eels in continental waters, a total of 3263 yellow eels (wild and cultured) were marked by different methods and released in Da-Pong Bay, a coastal lagoon, and the estuary of the Kao-Ping River in southwestern Taiwan in 2002, 2003, 2005 and 2006. The temporal change of Sr/Ca ratios in otoliths of the eels was measured by Electron Probe Micro-Analysis (EPMA), which indicated that estuarine resident eels were dominant, constituting 60% of the catch in the bay and 75.5% in the river, followed by freshwater residents (25% in the bay and 22% in the river), and seawater residents (15% in the bay and 2.5% in the river). Temporal changes in otolith Sr/Ca ratios also indicated that the eels, after release in the bay, moved quickly to the freshwater entrance but remained longer in the high salinity area. However, those in the river tended to stay in the brackish to freshwater zones similar to the behaviour of the wild populations. The mark and recapture data also indicated that the facultatively diadromous eels exhibit home range behaviours.

Purpose of this study

The Japanese eel spawns to the west of the Mariana Islands in the Pacific Ocean (Liao *et al.* 1996, 1999; Tsukamoto 1992, 2006) and is traditionally viewed as growing in fresh water. Recent studies on otolith Sr/Ca ratios have indicated that the migration of these eels is facultative; i.e. a part of the eel population skips the freshwater life phase and completes its life cycle in seawater (Shiao *et al.* 2003; Tsukamoto *et al.* 1998; Tsukamoto and Arai 2001; Tzeng *et al.* 2000, 2002; Tzeng 2003). These inferences are

based on the positive relation between eel otolith Sr/Ca ratios and the salinity of ambient water (Daverat *et al.* 2006, Kawakami *et al.* 1998, Lin *et al.* 2007, Tzeng 1996). However, the detailed migratory process of the eel in the yellow stage is still not completely understood.

To understand the eel's migratory behaviour, various marks and tags were applied to eels, including liquid nitrogen brands (LN), oxytetracycline (OTC) and alizarin complexone (ALC), micro-chips and coded wire tags (CWT) (Thomassen *et al.* 2000) and the clipping of pectoral and caudal fins. Strontium (Sr)/ Calcium (Ca) ratios in otoliths can be used as a natural tag to discriminate fish migration between seawater and freshwater (Kraus and Secor 2004, Lin *et al.* 2007, Tzeng 1996). Thus, the environmental history of marked eels after release can be reconstructed by the temporal change of Sr/Ca ratios in the otolith. This study uses both artificial marks and tags and the natural tag of otolith Sr/Ca ratios to evaluate the migratory behaviours of Japanese eels in a lagoon and river (Figure 2.15.1).

Results

- Temporal change in recapture rates

The recapture rate of eels in Da-Pong Bay in 2006 and in the Kao-Ping River in 2003, 2005 and 2006, all decreased sharply after the second month post-release except in the Kao-ping River in 2003 (Figs. 2.15.2a, b and c). This indicates that the population size of wild eels in the river is low.

- Spatial change in recapture rates

The percentage of all recaptures of eels in the river sharply decreased with increasing distance from the release sites between 1-10 days after release (Figure 2.15.3). This indicates that most eels dispersed after release but did not move far away from the release sites. Approximately 80% of eels were recaptured within 1 km of the release sites (Figure 2.15.3). The maximum distance of daily movements of the eels released in the northern and southern areas of Da-pong Bay was estimated to be 2.48 and 2.21 km per day, and 2.09 km per day in the Kao-ping River. Of the 143 eels recaptured from Da-Pong Bay, 93.9% were recaptured in areas of freshwater entrance where salinity was low (5-7 psu). Similarly, 99% of the 296 eels recaptured from the Kao-ping River were recaptured near their release sites in the estuary.

- Migratory behaviours and habitat use by wild yellow eels

The temporal changes in otolith Sr/Ca ratios from the elver check (EC) to the otolith edge differed among wild eels in Da-pong Bay (n= 60), and could be classified into 3 migratory types: (1) freshwater resident, with the Sr/Ca ratio less than 4×10^{-3} (25%, n= 15, Figure 2.15.4a), (2) seawater resident, with the Sr/Ca ratio higher than 4×10^{-3} (15%, n= 9, Figure 2.15.4b), and (3) estuarine resident (60%, n= 36, Figs. 4c and d), where the Sr/Ca ratios varied around 4×10^{-3} . Estuarine residents was further divided into 2 sub-types: (i) where the eels changed their habitats only once (Figure 2.15.4c), and (ii) where the eels migrated to different habitats (Figure 2.15.4d). These were vagabonds as defined by Daverat *et al.* (2006). One wild eel had a seasonal migration behaviour while the other eels migrated without a seasonal cycle.

Similarly, the migratory behaviours and habitat use by wild eels in Kao-Ping River (n= 209) can also be classified into freshwater eels, estuarine eels and seawater eels. From all sites, estuarine residents constituted 75.5% of the eels examined from 2003 – 2006 (n = 157), followed by freshwater residents 22% (n = 47) and a few seawater residents 2.5% (n= 5).

- Migratory behaviours of eels after release

The temporal changes in otolith Sr/Ca ratios after the OTC mark for the 4 eels recaptured in Da-Pong Bay changed from 3×10^{-3} to 7×10^{-3} (Figure 2.15.5a). This means that these eels after release remained in the high salinity environment.

However, the eels released in the downstream area of the Kao-Ping River in 2005 tended to migrate to the brackish estuary (Figure 2.15.5b), while those released in 2006 tended to migrate to the freshwater and brackish estuary because most of the otolith Sr/Ca ratios were less than 4×10^{-3} (Figure 2.15.5c). Over a period of 194 days, one eel released in the freshwater upstream area of the Kao-Ping River, as indicated by Sr/Ca ratios less than 2×10^{-3} after release, moved to the downstream estuarine area (Figure 2.15.5d). The recapture rates of the eels were significantly higher in the downstream than in the upper reach of the river ($p < 0.05$). Recapture rates did not significantly differ between cultured and wild eels ($p > 0.05$).

Conclusions

Conventional marking and tagging techniques together with the analysis of otolith elemental signatures are promising methods to analyze migratory behaviour and environmental history of eels. Mark-recapture data indicated that released eels did not move far from the release sites. On the other hand, the otolith Sr/Ca ratios indicated that the recaptured eels preferred estuarine brackish waters, and that migratory environmental histories were divergent among individuals.

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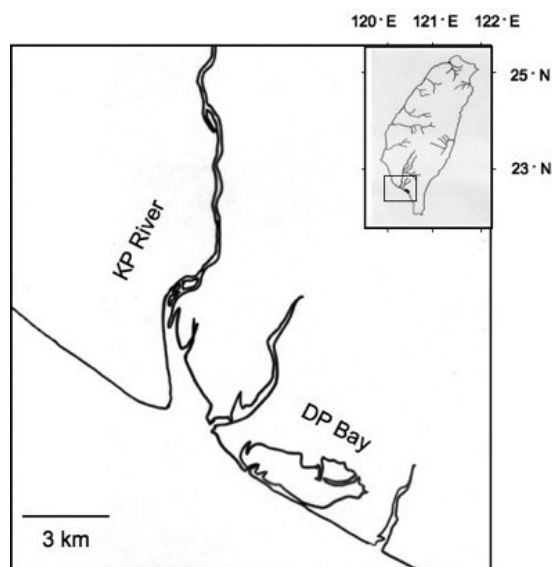


Figure 2.15.1. The release sites for Japanese eels in Da-pong Bay (DP) and the estuary of the Kao-ping River (KP) in southwestern Taiwan.

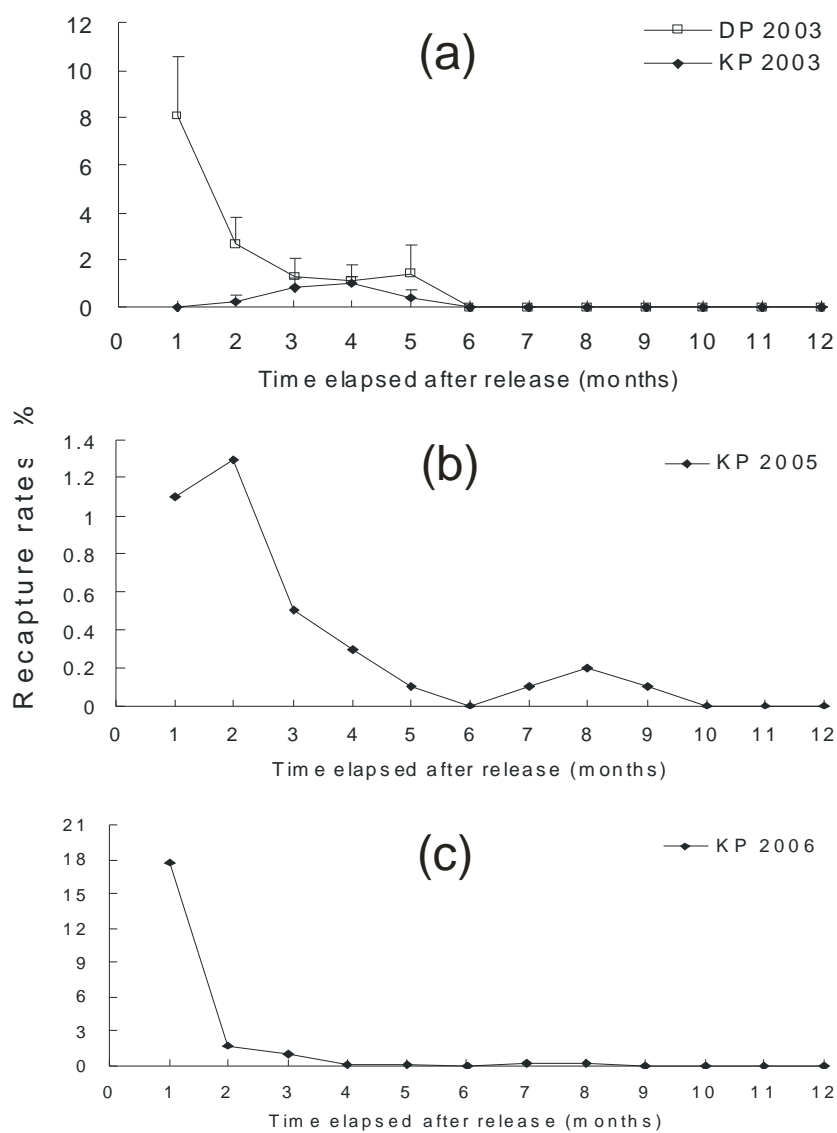


Figure 2.15.2. The monthly change of mean (\pm SD) eel recapture rates in the first year after release in Da-Pong Bay and the Kao-Ping River in 2003(a), 2005(b) and 2006(c).

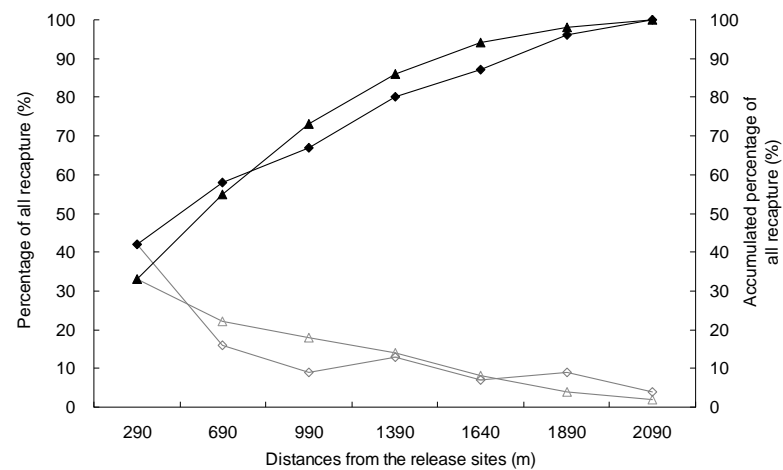


Figure 2.15.3. The spatial frequency distribution of Japanese eels in the 10 days (diamond) and 24 hours (triangles) after release in the estuary of Kao-Ping River. Left axis and open symbols: Percentage of all recaptures by distance from the release site; Right axis and filled symbols: accumulated percentage of all recapture by distance from the release site. Diamonds: the 783 eels released on 15 August 2006 and recaptured up to August 25, 2006 (n=204); Triangles: the 195 eels recaptured from 15 August up to 25 August 2006 and released on 25 August and recaptured on 26 August 2006 (n=45).

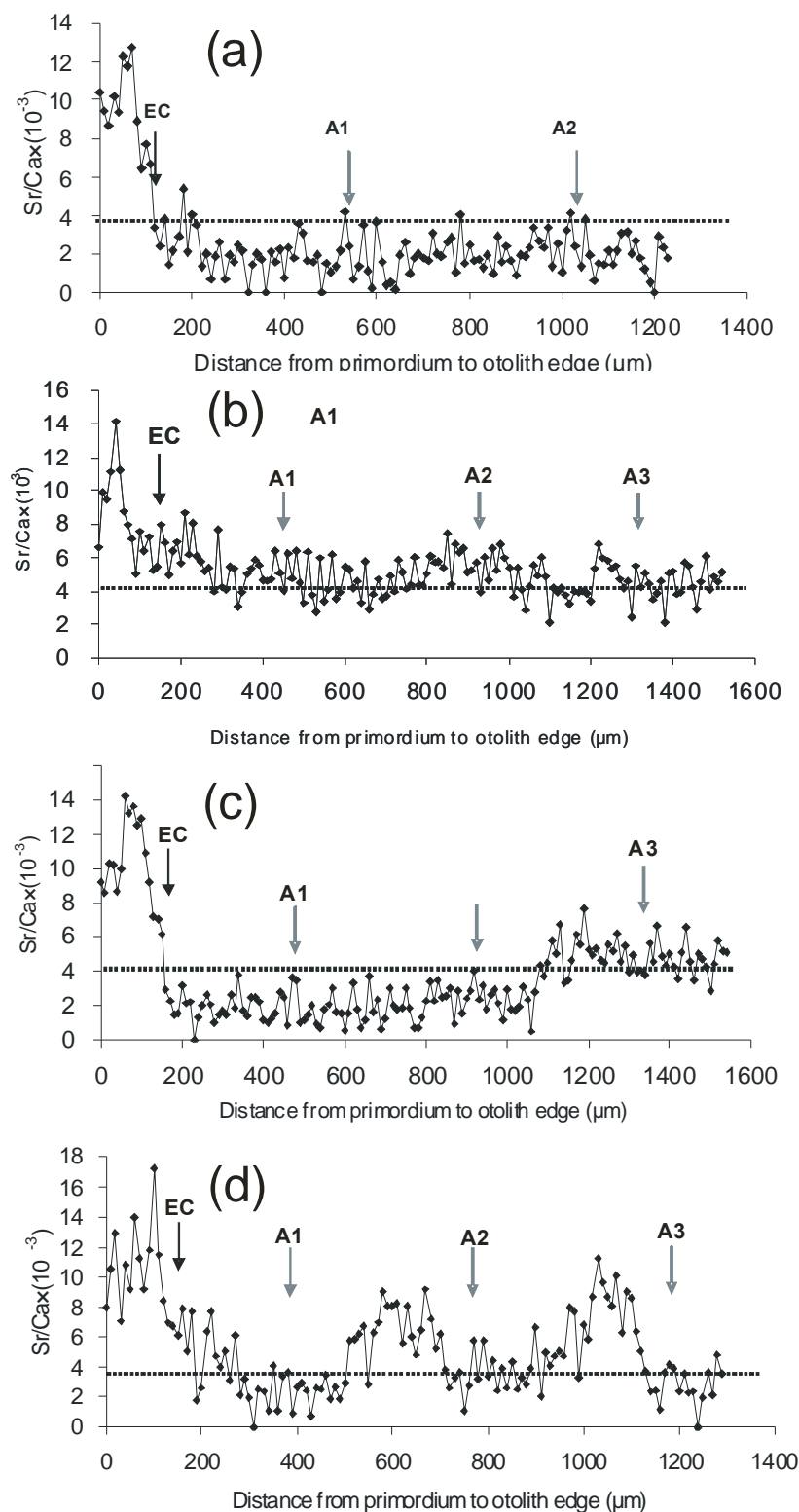


Figure 2.15.4. Temporal changes in otolith Sr/Ca ratios between the primordium and the edge of wild Japanese eels in Da-pong Bay. According to the pattern of otolith Sr/Ca ratios, migratory behaviours were classified into 3 types: freshwater eel (a), seawater eel (b) and estuarine eel (c, d). EC = elver check, A: annual increment. Sr/Ca ratios 4 ‰ were the boundary of seawater and freshwater.

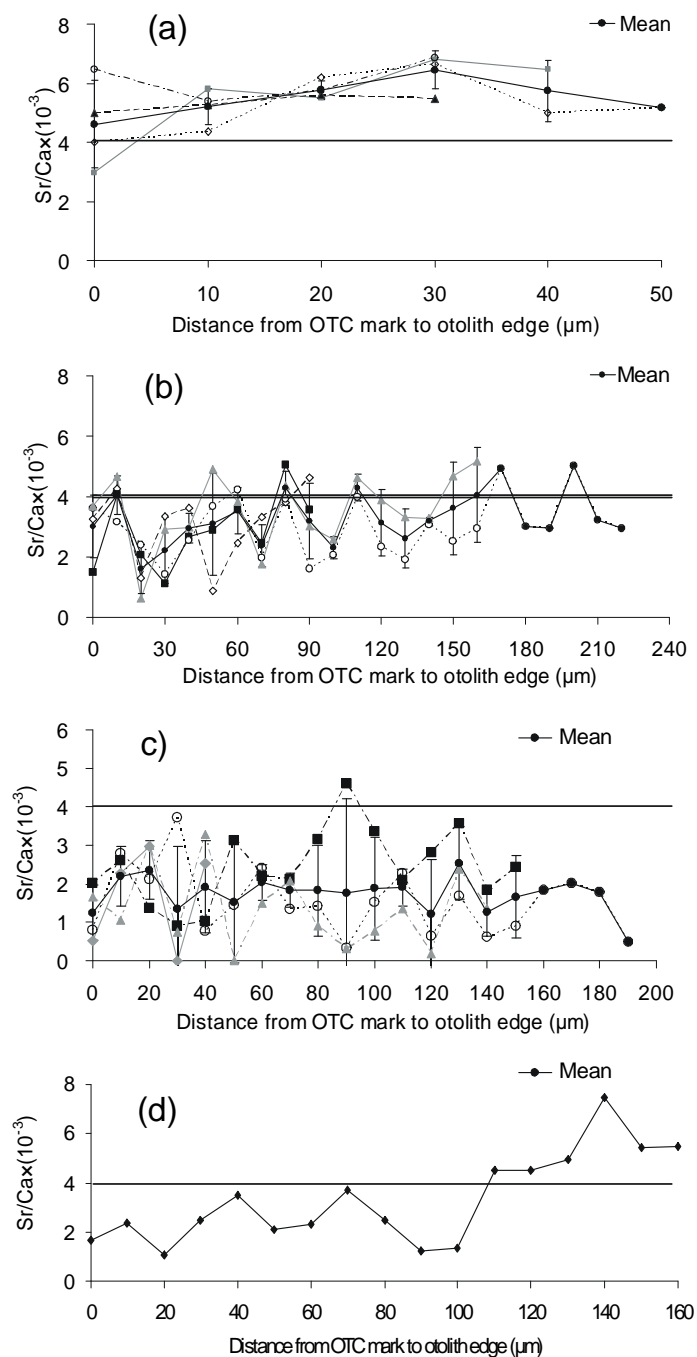


Figure 2.15.5. Temporal changes in otolith Sr/Ca ratios from the OTC mark to the edge of 4 Japanese eels, which were released and recaptured in (a) Da-pong Bay in 2003; (b) Kao-ping River in 2005; (c) Kao-ping River in 2006 and (d) Kao-ping River released in 2004 and recaptured downstream 194 days later in 2005. Sr/Ca ratios 4 ‰ were the boundary of seawater and freshwater.

2.16 European eel movements during continental life in the Rhône River delta (South of France): high level of sedentarity revealed by otolith microchemistry

Migrations between estuarine and freshwater environments are still unclear in the European eel (*Anguilla anguilla*) due to the multiplicity of water bodies colonised by the species. Sedentarity is assumed to occur during the continental life (Crivelli *et al.* 2008), but inter-habitat migrations have also been described around the world for several *Anguilla* species (Arai *et al.* 2004, Daverat *et al.* 2005, Shiao *et al.* 2006). Investigating these movements and testing for European eel sedentarity during continental life is of paramount importance for the conservation of this species.

Within the Rhône river delta, only one freshwater habitat, the Fumemorte canal, communicates with the brackish ecosystem that is connected to the sea. This offers a unique opportunity to test for eel sedentary during continental life (Figure 2.16.1), by investigating the lifetime movements of silver eels caught in the canal using otolith Sr:Ca ratios, which is widely recognised as a proxy of a fish's individual salinity history. Thus, if all individuals are sedentary, otolith Sr:Ca ratios should remain the same after their arrival in the canal, with values well below the ones observed in early continental life, during the migration through the brackish ecosystems connected to the sea.

Between 1997 and 2005, 58 silver eels (ages 4 to 11) were collected within the Fumemorte canal. Their otoliths were extracted using acid-washed plastic forceps and scraped clean in ultrapure water. Otolith images were first digitized under a binocular microscope to allow detection of annual growth increments (opaque zones), following a validated method for age estimation in eel (Panfili and Ximenes 1994). To reconstruct individual past migratory behaviour, variations of Sr:Ca ratios were measured on sagittal otolith sections, along a transect covering the whole continental life history, i.e. going from the nucleus transition mark (arrival in continental waters) to the posterior edge (capture). For technical comparisons, 28 otoliths were analysed using Laser Ablation Inductively-Coupled Plasma Mass Spectrometry (LA-ICPMS) and 30 with Electron Probe Micro-Analysis (EPMA). Mean Sr:Ca ratios on otolith edges (freshwater environment) were identical ($t = -0.345$, $df = 56$, $p = 0.731$) for the two analytical instruments, LA-ICPMS ($2.72 \pm 0.32 \cdot 10^{-3}$) and EPMA ($2.67 \pm 0.59 \cdot 10^{-3}$), indicating that measurement accuracy and precision are reliable for both tools. For each transect, the first and the last Sr:Ca values were used as references for the Sr:Ca signatures in the brackish (mean $5.22 \pm 1.39 \cdot 10^{-3}$) and the freshwater (mean $2.70 \pm 0.47 \cdot 10^{-3}$) ecosystems respectively. Using these signatures, a linear discriminant analysis (LDA) was constructed to assign the eel to be either in the freshwater or in the brackish water for each Sr:Ca value of the transect.

Six distinct types of migratory behaviour were identified for the population of the freshwater canal: eels entered the canal either directly (67%) or after one to two years in the lagoon (33%), with a subsequent majority of freshwater residents (55%), but also some occasional migrants (≤ 2 intrusions in the lagoon) and a few regular migrants (> 2 intrusions in the lagoon) (Figure 2.16.2). Table 2.16.1 summarises the different percentages of migratory types.

These results stress the value of LDA for reconstruction of eel inter-habitat use during the continental life, which is fundamental for population management and conservation. In addition, the relative majority of freshwater residents in the Fumemorte canal could have a direct impact on population management.

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Table 2.16.1. Relative abundance of migratory patterns of silver European eels in the Fumemorte Canal between freshwater (FW) and brackish water environments.

Number (%)	Type			
Entrance	FW resident	Migrant	Occasional migrant	Total
1-2 year old	9 (15 %)	5 (9 %)	5 (9 %)	19 (33 %)
Direct	23 (40 %)	3 (5 %)	13 (22 %)	39 (67 %)
Total	32 (55 %)	8 (14 %)	18 (31 %)	58 (100 %)

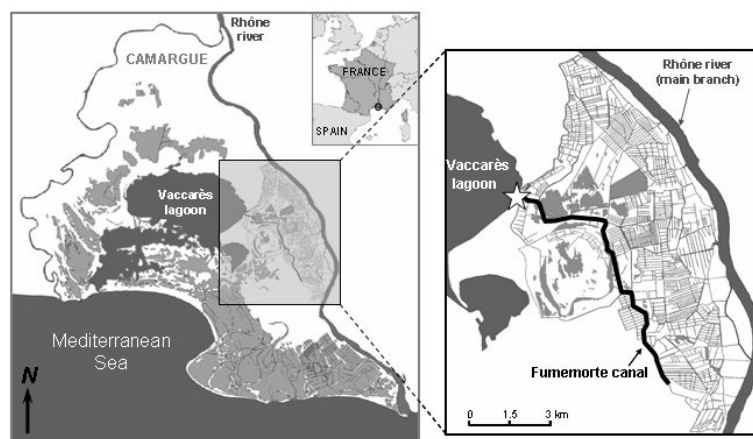


Figure 2.16.1. Location of the Vaccarès lagoon and the Fumemorte canal within the Camargue hydrological complex (Rhône river delta, South of France). The star indicates the sampling point at the dam (outlet of the Fumemorte canal). This is the only route by which eels can migrate between the lagoon and the freshwater canal.

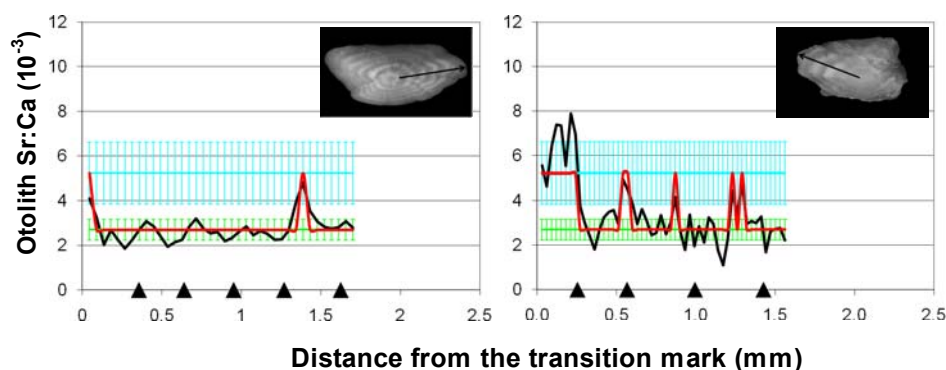


Figure 2.16.2. Two migration types identified from otolith Sr:Ca variations in Fumemorte silver eels. For each fish, black triangles on the X axis (▲) represent the successive years of life (start of otolith annuli) and, for all the Sr:Ca values (black line) measured along the analysis transect, the corresponding LDA assignment to either brackish water or freshwater is indicated by the red line. Average Sr:Ca values (\pm SD) for brackish water (in blue) and freshwater (in green) are represented to help interpretation of the Sr:Ca patterns observed. Analysed individuals fell into 2 groups: those entering directly in freshwater (left) and those entering after 1 or 2 years of lagoon life (right). Two different migration patterns are presented: occasional migrant (left) and migrant (right).

2.17 Using stable isotopes and fatty acids to examine salinity habitat use in European eels

Our understanding of the ecology of anguillid eels, including that of the European eel has recently undergone considerable re-evaluation (Tsukamoto *et al.* 1998, Tzeng *et al.* 2003). We now know that yellow eel stocks include components that display distinct migratory behaviours, and that some individuals do not enter freshwater, live in brackish water, or follow a mixed strategy migrating between freshwater and marine habitats. As many current management and conservation measures only relate to eels following 'typical' catadromous migratory behaviour, there is a pressing need for means to assess how yellow-phase eel populations structure themselves with regard to salinity. Many workers have examined variation in eel otolith Sr:Ca along salinity gradients (Cairns *et al.* 2004, Daverat *et al.* 2005, Tsukamoto and Arai 2001), and this has proven to be an extremely powerful, but expensive technique. In an attempt to develop a less expensive and more readily available means to examine this problem, we previously (Harrod *et al.* 2005) used stable isotope analysis (SIA) to show strong evidence for population sub-structuring along a short and abrupt salinity gradient in European eels inhabiting the Screebe catchment in Western Ireland (Figure 2.17.1: sites freshwater (FW), brackish water (BW) & marine-influenced water (MW), salinity range = 0-25). Here we have expanded our focus to include eels from fully marine habitats (Figure 1: SW, salinity = 34), and to add fatty acid analysis (FAA), as it can provide a useful indicator of salinity variation (LeBlanc *et al.* 1989). Hence we combine SIA and FAA to examine the relative efficacy of these techniques to identify spatial structuring in a coastal eel population.

Eels were captured using summer fyke nets in each salinity zone (FW: $n = 30$; BW: $n = 16$; MW: $n = 31$; SW: $n = 29$). Eel non lipid-treated $\delta^{13}\text{C}$ values ranged between -26.1 and 15.0‰, with marked differences between eels captured from the different salinity zones (ANOVA: $p < 0.0001$). Lipid-removal had a significant effect on eel $\delta^{13}\text{C}$ ($p < 0.0001$), with mean (\pm 95% CI) $\delta^{13}\text{C}$ values being depleted by $-1.1 (\pm 0.2)$ ‰. Individual lipid-treated $\delta^{13}\text{C}$ values varied between -23.9 and -14.4‰, and differed in eels cap-

tured in the different capture zones ($p < 0.0001$). Although eels captured in FW were most ^{13}C -depleted, and SW most ^{13}C -enriched, there was considerable overlap between individual values in eels captured in the FW/BW and MW/SW habitats. Comparison of mean individual differences between $\delta^{13}\text{C}$ and lipid-free $\delta^{13}\text{C}$ values varied between salinity habitats ($p = 0.019$), suggesting between-habitats differences in muscle lipid content. Individual eel $\delta^{15}\text{N}$ values varied between 9.0 and 14.0‰. Although there was considerable overlap in individual values, mean $\delta^{15}\text{N}$ differed between salinity zones ($p < 0.0001$). Individual C:N values varied between eels (3.18 – 6.9): however, there was little evidence of mean differences between the different salinity zones ($p = 0.497$). LOESS smoothed scatterplots revealed strong negative and non-linear relationships between C:N and $\delta^{13}\text{C}$ that varied in form between salinity zones, suggesting C:N values provided some means of discriminating between salinity zones.

Discriminant analysis, based on lipid-free $\delta^{13}\text{C}$, $\delta^{15}\text{N}$ and C:N values, resulted in two significant discriminant functions and allowed separation of eels from the different salinity zones (Figure 2.17.2A: $p < 0.0001$). Jack-knifed classification success (Table 2.17.1A) was generally high (71%). However, the model had little power to discriminate eels captured from BW habitats (13%).

A total of 32 Fatty Acid Methyl Esters (FAME) were recorded from the eels. The FAME profile was dominated by saturated fatty acids (mean (\pm SD) $49.5 \pm 9.3\%$), followed by polyunsaturated (PUFAs: $21.3 \pm 7.6\%$) and monounsaturated Fatty acids (MUFAs: $29.1 \pm 10.1\%$). The FAME profile of eels was dominated by C16:0 ($35.5 \pm 9.2\%$), C18:1 (n-9) ($16.9 \pm 6.8\%$), C18:0 ($9.4 \pm 3.8\%$), and C16:1 (n-9) ($5.3 \pm 3.0\%$). Comparison by ANOVA showed considerable variation in the mean abundance of individual FAMEs along the salinity gradient. The relative abundance of n3-fatty acids was similar across the salinity gradient (mean \pm SD = $10.34 \pm 4.8\%$). Overall, the relative abundance of n-6 fatty acids was similar to n-3 fatty acids (mean n3:n6 ratio, $p = 0.379$). However, comparison of n3:n6 ratios by ANOVA showed that the relative contribution of n-6 fatty acids fell with increased salinity ($p < 0.0001$). A DFA based on individual concentrations of the 32 separate FAMEs (arcsine square-root transformed) showed large differences in FAME profiles for eels from the different salinity zones (Figure 2.17.2B: $p < 0.0001$). Jack-knifed classification success was higher than for SIA and C:N data (Table 2.17.1B), with a total classification success of 76 %. Although the classification success of BW eels increased (from 13 to 50%) relative to the SIA/C:N DFA, it was still low relative to eels from the other salinity zones (mean classification success = 81%). When SIA and FAA data were combined in a single DFA, the results were striking, with almost complete discrimination of eels by salinity zone (Figure 2.17.2C: $p < 0.0001$). Total classification success increased to almost 90%: again classification success was lowest for BW eels (81%) but the discriminatory power was similar for eels from the other salinity zones (Table 2.17.1C).

Previously, using SIA, we demonstrated strong population structuring in the coastal eel population by salinity (Harrod *et al.* 2005). In the current study, we extended sampling to cover eels collected from across the entire salinity gradient (i.e. 0 – 34), and also expanded our analytical protocol to include FAA. Our results showed that variation in eel $\delta^{13}\text{C}$, $\delta^{15}\text{N}$ (Figure 2) and C:N was considerable, and sufficient to allow eels to be reliably (ca. 70%) identified to salinity zone. This represents a marked decrease in discriminatory power relative to our earlier study (e.g. total classification success was reduced from 85% to 71%). This partly reflects the tendency for eels from the two extremes of the salinity gradient in the extended dataset to cluster together (i.e. FW/BW and MW/SW) and the large variation in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values in eels from

the BW salinity zone. In the previous study, BW eels were also the most isotopically variable, and we discussed possible reasons (Harrod *et al.* 2005). Briefly, this area of the system is the most heterogeneous in terms of salinity and other physicochemical characteristics, and it is possible that eels move between FW and BW habitats. Although SIA and C:N data are not sufficient to reliably identify eels from the BW salinity zone, FAA data performed far better, whilst the combined use of SIA and FAA performed best. We suggest that these techniques offer considerable scope for eel biologists interested in habitat structuring by salinity.

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Table 2.17.1. Jack-knifed classification matrices from the three discriminant function analyses examining eel structuring by salinity using A) $\delta^{13}\text{C}$, $\delta^{15}\text{N}$ and C:N data; B) FAMEs and C) $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, C:N & FAME data.

A) $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, C:N		<i>n</i> classified to zone			
Eel capture location	FW	BW	MW	SW	Classification success
FW (n = 30)	27	3	0	0	90 %
BW (n = 16)	13	2	1	0	13 %
MW (n = 31)	0	0	24	7	77 %
SW (n = 29)	0	0	7	22	76 %
Total (n = 106)	40	5	32	29	71 %

B) FAME		<i>n</i> classified to zone			
Eel capture location	FW	BW	MW	SW	Classification success
FW (n = 30)	23	1	4	2	77 %
BW (n = 16)	1	8	6	1	50 %
MW (n = 31)	2	3	25	1	81 %
SW (n = 29)	0	1	3	25	86 %
Total (n = 106)	26	13	38	29	76 %

C) $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, C:N & FAME		<i>n</i> classified to zone			
Eel capture location	FW	BW	MW	SW	Classification success
FW (n = 30)	28	2	0	0	93 %
BW (n = 16)	2	13	0	1	81 %
MW (n = 31)	0	1	27	3	87 %
SW (n = 29)	0	0	4	25	86 %
Total (n = 106)	28	17	33	28	89 %

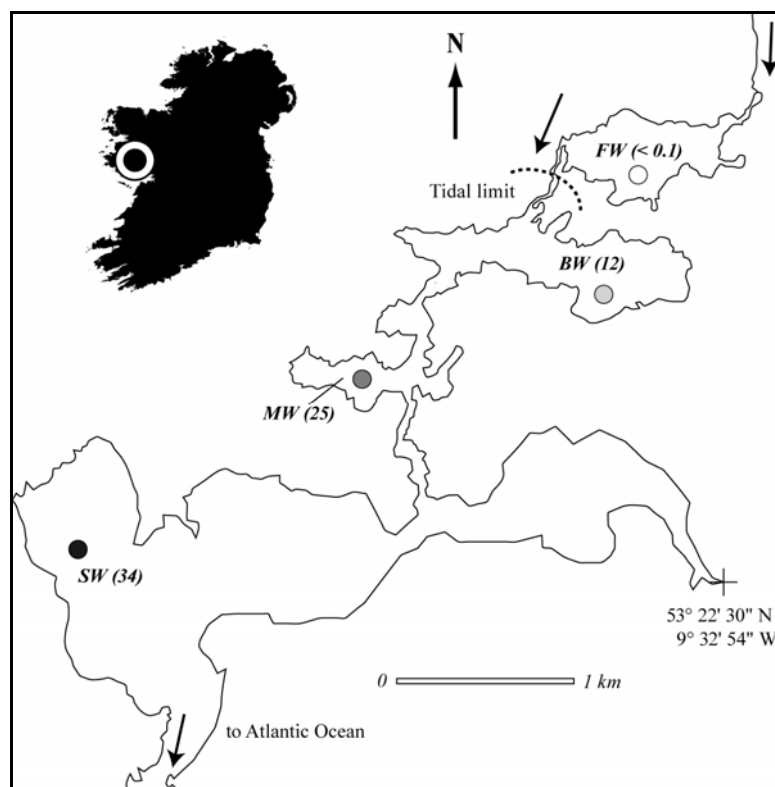


Figure 2.17.1. Map showing the location of study sites. Figures in parentheses indicate median benthic salinity values.

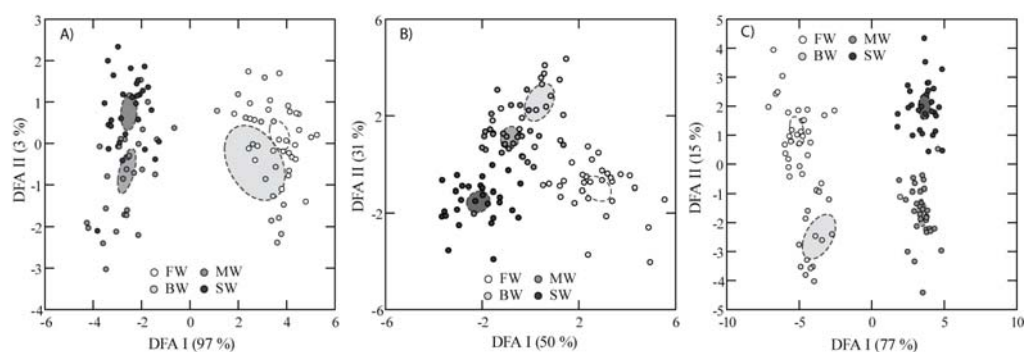


Figure 2.17.2. Canonical plot scores from discriminant analysis of: A) stable isotope ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$), and elemental ratio (C:N) data; B) FAME data; and C) combined stable isotope, elemental ratio and FAME data, from yellow-phase European eels collected from four contrasting salinity zones. Gaussian bivariate 95% confidence ellipses are centred on group centroids.

2.18 Discussion - habitat use in saline and fresh water

Implications for stock assessment and management

Habitat availability may vary with catchment. Eels that occupy a habitat may be an attractant to new recruits, but the relation of recruitment to population density is not known. Recruitment supply and colonization of eels to different areas may vary greatly, e.g. high in saline habitats of western Ireland, low in eastern Ireland. At least in some areas, eels that occupy saline waters in summer may move to fresh water for

wintering, meaning that both habitats need protection to achieve effective conservation.

Research needs

Determine whether data for one *Anguilla* species can extend across other species, whether migratory behavioural patterns are discrete or a continuum, whether one assessment approach fits all habitats, what habitats small eels use, what factors in addition to salinity should be considered (distance from spawning grounds, prey, vegetation), the selectivity of pots relative to fyke nets, the relation of recruitment to population density, and methods to sample silver eels from the mouth of an estuary.

Research methods

Eels can be sampled by fyke net, baited pot, beach seine, drop trap, glass bottom boat, trawl, vacuum sampling, habitat trap, and ramp trap. Habitat use can be evaluated by otolith strontium:calcium analysis, mark-recapture, stable isotopes, telemetry and through the North American atlas project. Eel pots can be fished in more exposed areas than fyke nets. These two gears may trap a different length-frequency distribution of eels.

A standardized method for sampling glass eels as they enter fresh water would be useful. Four small mats at the head of tide on the River Bann have caught 805,000 glass eels in a season. However, habitat traps have the limitation that their efficiency is reduced when a lot of vegetation is available. Habitat traps are difficult to standardize because they are not a true trap, in that eels are free to leave whenever they wish.

3 Anguillid eel demographic characteristics in saline and fresh water

3.1 Characteristics of yellow eel along a North Sea-Baltic gradient

Arriving in the North Sea coastal areas, the glass eel gradually becomes pigmented and changes into the juvenile yellow eel stage. Some juvenile eels remain in coastal areas while others migrate into the Baltic Sea and into streams and rivers. Upon becoming sexually mature the eel transforms and as a silver eel starts migrating out from the Baltic Sea and back towards the Sargasso Sea. This means that eel can spend their juvenile yellow eel stage in different habitats, ranging from marine conditions to pure fresh water. The differences in salinity could result in, for example, differences in growth and onset of maturation which is common for other species that occur in both marine and brackish water.

In order to investigate the characteristics of yellow eel along a North Sea - Baltic Sea gradient, data from sampling of Swedish commercial yellow eel fyke net fisheries were used. The sampling covered a salinity gradient from 30 PSU in ICES SD 20 to 7 PSU in SD 27 (Figure 3.1.1). During 2002–2008 over 11,500 yellow eel were sampled for individual length, total and somatic weight, sex and prevalence of *Anguillicola crassus*. All but 128 were female and the males were mainly recorded on the Skagerrak coast in SD 20 resulting in a female biased sex ratio of 97% in SD 20 and 99% in the other areas. Age readings exist for 2,700 individuals, but most of the otoliths were stored and not analysed after the 2005 catch year. The sampling programme started as an initiative of the Swedish Board of Fisheries and is now part of the Swedish contribution to the DCR. In addition, sampling of silver eel from commercial pound net catches targeting silver eel started in 2005. To date, length and weight records and

otoliths were collected from 4,100 silver eels and 1,200 age readings were performed. The silver eel data are used to infer size and age at silvering.

There was a similar size composition of yellow eel in the Kattegat, the Öresund area and the southern Baltic coast (SD 21, 23 and 25), but a dominance of smaller individuals in Skagerrak (SD 20) and larger individuals in central Baltic Proper (SD 27) (Figure 3.1.2). Mean length for SD 20 (456 ± 72 mm) as well as mean length for SD 27 (594 ± 84 mm) differs significantly from the other areas (SD 21= 484 ± 70 mm; SD 23= 490 ± 69 mm; SD 25= 484 ± 89 mm; ANOVA, $p < 0.001$; Tamhanes post-hoc test, $p < 0.001$). This means that there is a pattern of increasing size going from the saline water in SD 20 to brackish water in SD 27. This is partially taken into consideration in the Swedish minimum legal landing size for eel which is 40 cm in SDs 20, 21 and 23 and 65 cm in SDs 24-30.

Plots of age distribution in yellow eels reveal no geographic gradient although mean age significantly differs among areas with the youngest eels in the southern Baltic (SD 25) and the oldest in Baltic Proper (SD 27) (SD 20= 8.9 ± 1.8 ; SD 21= 8.4 ± 2.1 ; SD 23= 9.2 ± 1.9 ; SD 25= 7.0 ± 1.8 ; SD 27= 10.1 ± 2.2 , ANOVA, $p < 0.001$) The samples from SD 25 probably represent the first good habitat for yellow eel recruits on their path of migration from the west coast into the Baltic Sea. The relatively low mean age in unsorted fyke net landings in SD 25 indicate that migrants in transit might make up a considerable proportion of the catches.

The size at age pattern is close to linear for both length and weight in all areas (Figure 3.1.3). Bias is probably introduced for younger ages as a consequence of gear selectivity and in higher ages as a consequence of silvering. Yellow eel from SD 27 in the central Baltic were considerably longer and heavier than in other areas, a 10 year old female being, on average, 57 cm and 314 g in the former area compared to 49.5 cm and 192 g on the Skagerrak coast (SD 20). This means that yellow eel show a larger size at age in brackish water than in salt water habitat.

Somatic condition (Fulton index) is also higher in the Baltic samples and increases with increasing age (Figure 3.1.4). The possibly transiting eels in SD25 thus were in better condition than eels from the west coast, but had otherwise grown at approximately the same rate. Condition increasing with increasing age is seen in all areas except SD 20. Despite the better condition in more brackish areas, the prevalence of *Anguillicola crassus* increased along the North Sea - Baltic gradient (Table 3.1.1).

Size and age distribution of silver eels sampled in different areas was used to infer size at silvering in a gradient from Kattegat to northern Baltic Proper. It is however important to note that we do not know if the sampled silver eels have grown up as yellow eel in the sampled area or if they come from other areas. Nevertheless, the size distribution of silver eels shows a clear geographic pattern with increasing size the further into the Baltic (Figure 3.1.5). Unfortunately no samples were taken in SD 21 and only 8 eels in SD 20. Mean length differs significantly among sampled areas (ANOVA, $p < 0.001$; SD 20= 541 ± 122 mm; SD23= 654 ± 95 mm; SD24= 692 ± 86 mm; SD25= 699 ± 65 mm; SD27= 777 ± 67 mm).

Age at silvering appears to vary geographically, with increasing ages in more brackish areas (SD 23= 11.0 ± 2.6 ; SD 24= 12.3 ± 2.6 ; SD 25= 12.01 ± 2.4 ; SD 27= 13.8 ± 2.4). SD 23 and SD 24 are not different from each other but all other pair-wise comparisons are significant (ANOVA, $p < 0.001$, Tamhanes post hoc test, $p < 0.001$).

In conclusion, brackish water areas seem to constitute a better habitat compared to marine areas for yellow eels, resulting in a larger size at age and better condition.

This occurs despite the fact that prevalence of *Anguillicola crassus* infection is higher in the Baltic Sea. Both size and age at silvering are also higher in brackish areas compared to saline areas. The differences in age and size distribution in the eels from different areas highlight the need for geographically differentiated minimum legal size limits. In particular, the low minimum size in SD 23, 40 cm, could be questioned if the purpose of the regulation is to spare a significant part of the population, since the mean size of yellow eels is 49 cm and size at silvering 65 cm in that area. Apart from salinity, other factors like predator abundance could be the reason behind observed differences and need to be investigated.

Table 3.1.1. Prevalence of *Anguillicola crassus* in yellow eel samples from different ICES SDs.

	20	21	23	25	27
Not infested	1829	781	530	476	975
Infested	173	124	470	753	1255
Prevalence	8.6	13.7	47.0	61.3	56.3

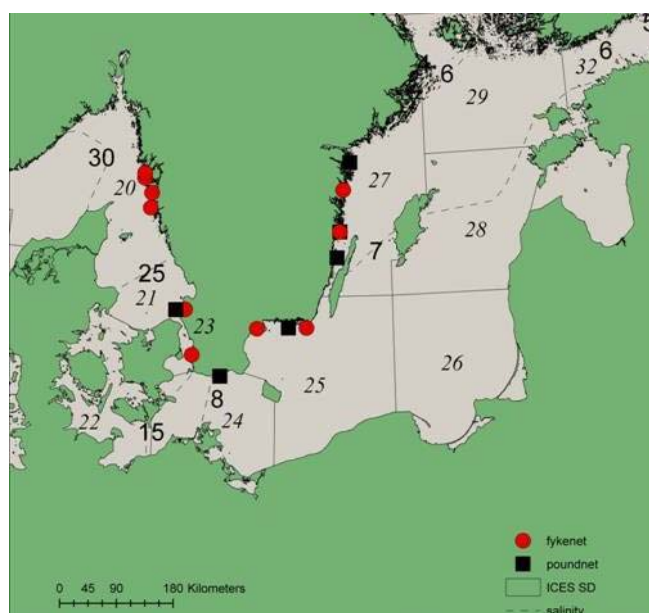


Figure 3.1.1. Sampling of yellow eel from commercial fyke net fishery (circles) and silver eel from commercial poundnet fisheries (squares) in different ICES SDs and different salinities.

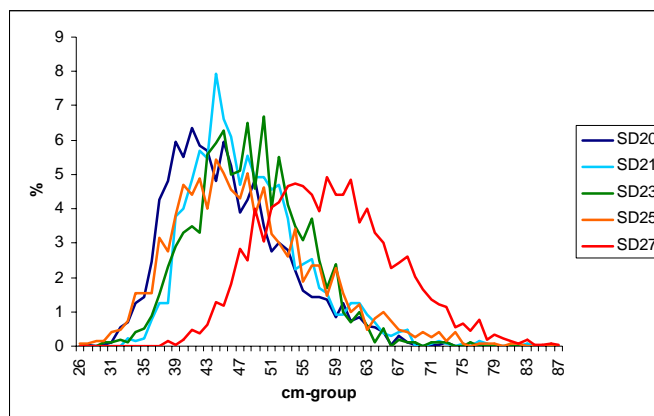


Figure 3.1.2. Length composition of yellow eel from commercial fyke net catches in samples collected in 2002–2008 in Skagerrak and Kattegat (ICES SDs 20–21) and the Baltic Sea (ICES SDs 23, 25 and 27). Samples from SDs 25 and 27 are based on an unsorted mixture of landings and discards.

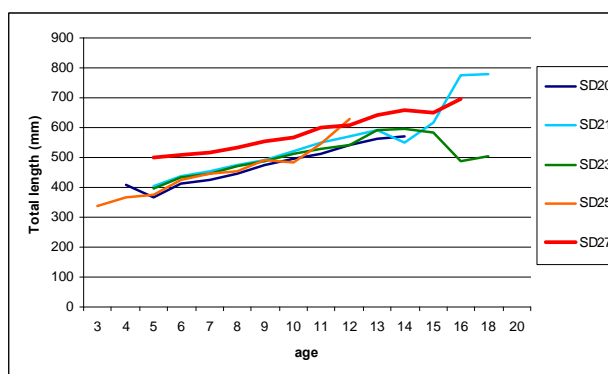


Figure 3.1.3. Total length at age in yellow eel sampled 2002–2008 in different ICES SDs.

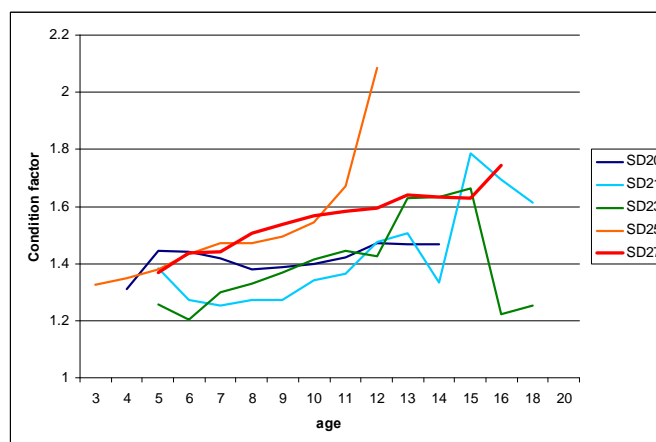


Figure 3.1.4. Fulton's condition factor at age for yellow eel sampled 2002–2008 in commercial fyke net fisheries in different ICES SDs.

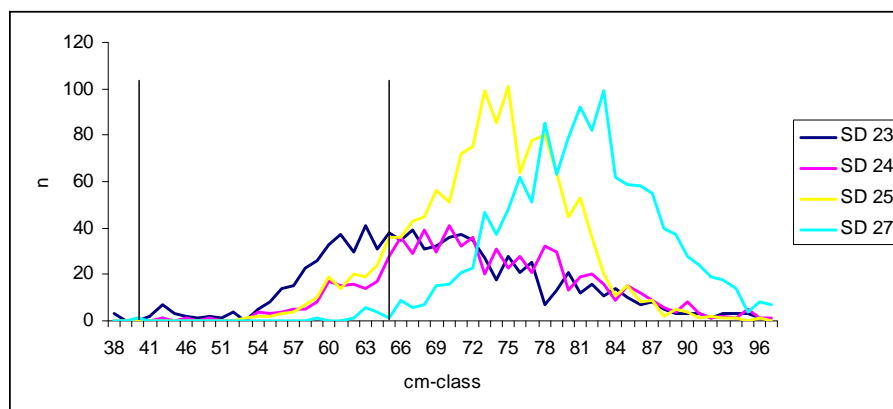


Figure 3.1.5. Total length of silver eels from pound net catches, 2002–2008, in different ICES SDs. Vertical bars indicate legal size limits in ICES SDs 20–23 (left) and in ICES SDs 24–30 (right).

3.2 Naturally-recruited and restocked eels in Latvia: discrimination and growth comparison

The European eel has been restocked in Latvia for many years, but the contribution of restocked eels to the local population has been little examined. This may be due to the lack of appropriate marks or tags to discriminate restocked eels from naturally-recruited eels. Otolith Sr:Ca ratio is a useful natural mark to discriminate fish from freshwater and saltwater habitats (Tzeng *et al.* 1997, Campana 1999, Tzeng *et al.* 2000). Eels that naturally recruit to Latvia experience the brackish Baltic Sea at an early age because elvers must migrate across the Baltic Sea to reach Latvia, while restocked eels do not experience saline water at the same age because they are artificially transported to Latvian fresh waters from UK and or France (Shiao *et al.* 2006). Therefore, otolith Sr:Ca ratios could be used to discriminate restocked eels from naturally-recruited eels based on differences in salt/freshwater experiences. This method also allows the growth of restocked eels to be compared to that of naturally-recruited ones.

A total of 75 female eels was collected, including 31 in Daugavgrīva, 16 in Lake Ķīšezers, and 28 eels in Mērsrags, in August–September 2005. Their largest otoliths (sagittae) were removed, processed and Sr and Ca otolith concentrations (% wt) were measured from the primordium to the edge at 10 μ m intervals by electron probe microanalyzer (EPMA). The critical otolith Sr:Ca ratio indicating freshwater residency was set at 2.24×10^{-3} (Shiao *et al.* 2006). After EPMA analysis, otoliths were repolished and etched with 5% EDTA to estimate age (Tzeng *et al.* 1994). The growth rate (GR) was calculated as $(TL - L_0)/\text{Age}$ where L_0 is mean length of elvers (Wang and Tzeng 2000), and the lengths-at-age were back-calculated by the Dahl-Lea method.

The otolith of naturally-recruited (Nat) eel appeared a brackish signal of higher Sr:Ca ratios from $4-8 \times 10^{-3}$ when the eel migrated through Baltic Sea and then decreased to less than 2×10^{-3} at recruitment to the freshwater environment (Figure 3.2.1a). On the other hand, the restocked (Rst) eels were imported from France or UK at elver stage and released in the freshwater. They didn't migrate through Baltic Sea and thus mean otolith Sr:Ca ratios remained at a low value of around 1.5×10^{-3} from the elver stage until the otolith edge (Figure 3.2.1b). This demonstrates that the temporal change of Sr:Ca ratios in otolith can be used to discriminate Nat and Rst eels. In addition, the incremental width between annuli in otolith was significantly narrower in Rst than Nat eels, indicating that Nat grew faster than Rst eels (Figure 3.2.1).

The growth rates of the eel were significantly influenced by origins (i.e. Rst and Nat), sampling sites and their interaction (2-way ANOVA, all $p < 0.0001$). The mean growth rate (GR) was significantly slower in Rst than Nat eels in both Daugavgriva and Mērsrags ($p < 0.001$ and $= 0.01$). However the growth rate was not significantly different between Nat and Rst eels in Lake Ķīšezers (Table 3.2.1). The back-calculated lengths-at-age of Rst eels after age two were significantly smaller than those of Nat eels in Daugavgriva (Figure 3.2.2, Mann-Whitney U Test, $p < 0.05$), but they were not significantly different for eels in Lake Ķīšezers ($p > 0.05$). The results of mean GR and lengths-at-age for the comparison between Rst and Nat eels were not consistent. This may be due to the inter-habitat changes of the eel.

The proportions of Nat and Rst eels were also significantly different among sites (χ^2 test, $p = 0.0145$, Table 3.2.1). The relative abundance of Rst in each of the sampling sites depends on the amount of the eel restocked and the movement behaviour of the eel after releasing as well as the physical barrier of the river. The proportions of Rst eels has been greater than those of Nat eels in both Lake Ķīšezers and Daugavgriva (refer to GMM project final report 2004-2007), which appeared reasonable because Rst elvers were released in some midland lakes connecting with the Gulf of Riga through River Daugava, and then possibly dispersed to Lake Ķīšezers in the lower reach and the river mouth, Daugavgriva. However, the outlets of the lakes were equipped with eel weirs that might obstruct the downstream movement of Rst eels. Dams in River Daugava without fish ladders further limited this movement. Therefore, the existence of Rst eels in Daugavgriva and Lake Ķīšezers implied that some Rst eels passed these obstructions successfully, contrary to previous views. The Rst eels probably passed these obstructions during periods of high water discharge, but more evidence is needed to confirm this.

The differences in growth between Rst and Nat were complex. Productivity was similar among the three nearby collecting sites, and the slower growth rate of Rst eels in Daugavgriva might be due to their having escaped from midland lakes with low productivity, in which eel growth is slow (Lin *et al.* 2007). The significant site-origin interaction in this study further indicates that the influences of sampling site and restocking on the growth of the eels might be site-specific. Rst eels did not always grow slower than Nat eels, and apparently the release sites (productive lower reaches or oligotrophic midland lakes) played a more important role in determining eel growth.

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Table 3.2.1. *Anguilla anguilla* collected in Daugavgriva, Lake Ķīšezers and Mērsrags, Latvia with mean salinities (‰) in brackets. The eel was classified by origins (Nat: natural-recruited, Rst: re-stocked eels). And their mean (\pm SD) total length (TL, cm) and weight (TW, g), age (years) and growth rate (GR, cm year⁻¹) were calculated. ND = data not available.

Site	Daugavgriva (4.2)		Lake Ķīšezers (0)		Mērsrags (5.6)	
Origin	Nat	Rst	Nat	Rst	Nat	Rst
N	19	12	11	5	26	2
TL	58.7 \pm 9.9	69.3 \pm 9.9	80.3 \pm 7.0	83.6 \pm 7.0	78.7 \pm 6.3	68.3 \pm 11.3
TW	ND		949 \pm 236	1047 \pm 291	1021 \pm 244	691 \pm 389
Age	10 \pm 2	22 \pm 5	14 \pm 2	13 \pm 4	14 \pm 2	18 \pm 4
GR	5.5 \pm 1.1	3.0 \pm 0.6	5.4 \pm 0.8	6.2 \pm 2.4	5.5 \pm 0.9	3.7 \pm 1.4

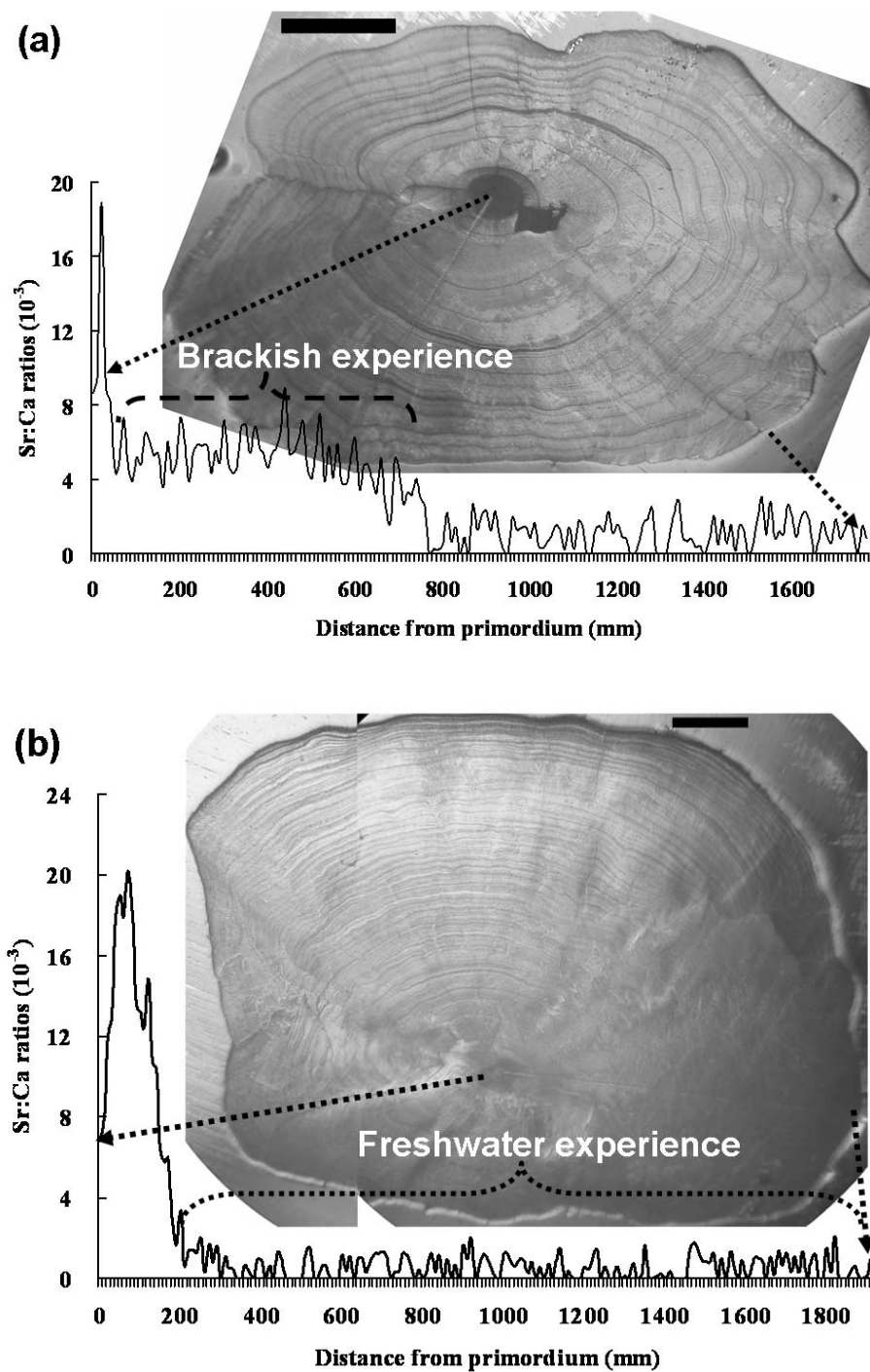


Figure 3.2.1. Temporal changes of Sr:Ca ratios and annuli in the otolith sagittal section of (a) naturally recruited and (b) restocked *A. anguilla* from Latvia. Scale bar = 500 μm .

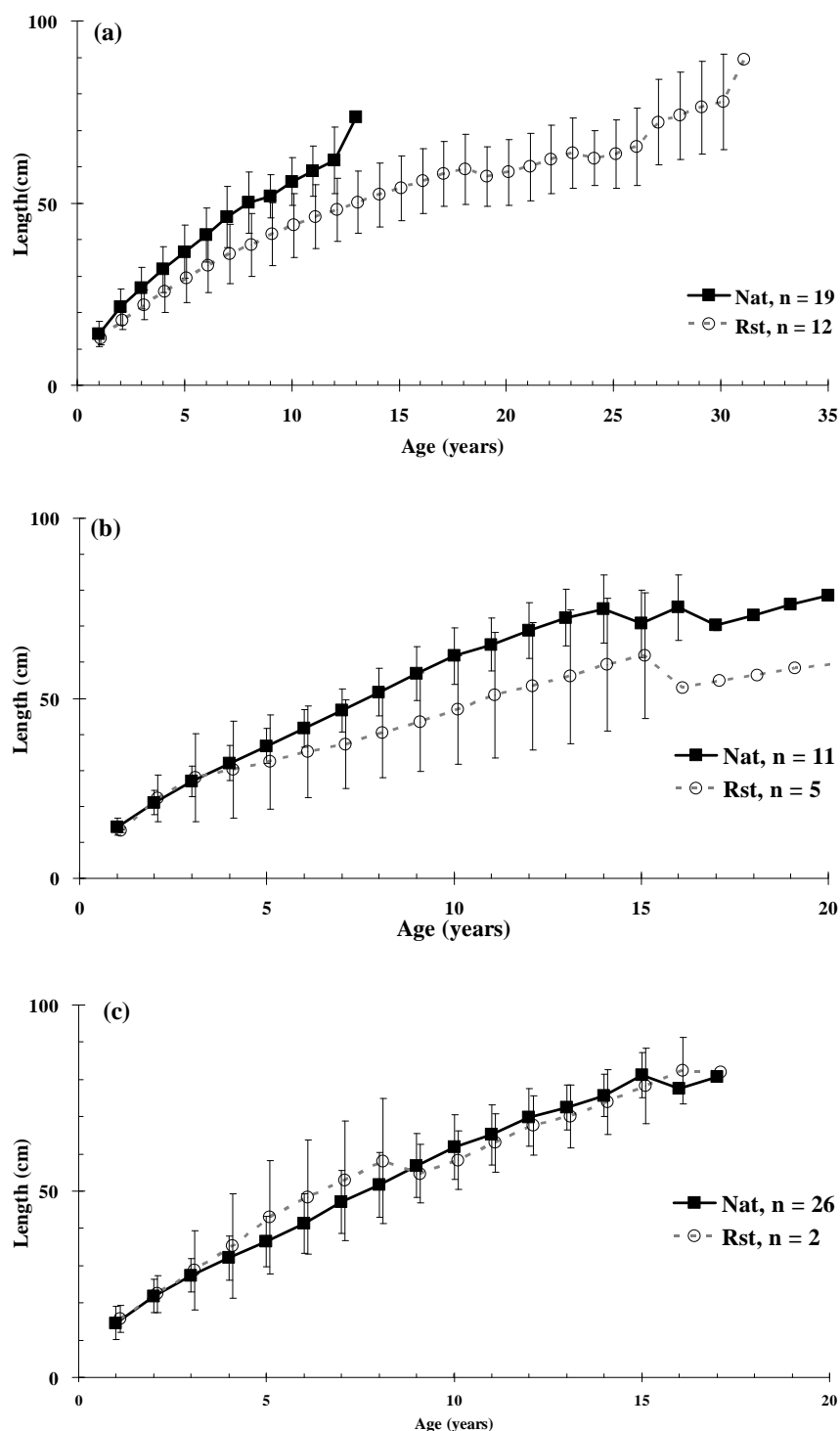


Figure 3.2.2. Back-calculated lengths-at-age (\pm SD) of female naturally-recruited (Nat) and restocked eels (Rst) collected from (a) Daugavgriva, (b) Lake Kisezers and (c) Mersrags.

3.3 The effects of ambient salinity on eel spawner quality

Otolith microchemistry has proven to be a powerful tool to trace the migration routes of diadromous fish. In a holistic approach we correlated migration patterns of European yellow and silver eels as revealed by LA-ICP-MS methodology to detailed information on individual fitness by investigating a total of 370 eels sampled in the North Sea, the Baltic Sea and various northern German freshwater sites for otolith

trace element profiles (Figure 3.3.1). We then combined individual life history information with potential fitness parameters like habitat-specific growth, parasite infestation and virus infections to better understand the effects of ambient salinity and habitat choice on European eel spawner quality.

Migrations of eels in northern German waters are complex and cannot be explained by a facultative catadromous behaviour. Pre-spawning habitat shifts were found to occur in all directions and did not follow uniform patterns. Individual variability in migration patterns therefore speaks against a genotypic predetermination, but corroborates the hypothesis of habitat shifts as an opportunistic adaptation to unfavourable conditions. For the marine sampling site off the island of Helgoland in the North Sea, no evidence was found that any eels spent their whole life in the marine environment, questioning the existence of purely marine anguillid eels.

Strontium-calcium ratios were also identified to represent a powerful tool to differentiate between wild and stocked eel in Baltic Sea tributaries, since the brackish signal of this hyposaline inland sea must be present in trace element profiles of naturally ascended individuals. Preliminary results point to a percentage of stocked eels in the Western Baltic of less than 20%. Considering the high stocking efforts in Western Baltic tributaries over the last decades, this implies either a high natural recruitment or alternatively a low survival of stocked eels. Strontium marking of farm-raised eels as an obligatory management measure would facilitate the differentiation of stocked versus naturally recruited eels and therefore the evaluation of the success of stocking programs.

Investigations on the infection rate of northern German eels with *Herpesvirus anguillae* (HVA) revealed a remarkably low overall prevalence of 2%. The results showed the presence of latent HVA infections in apparently healthy eels from a single freshwater system (river Eider) as well as the marine sampling site near Helgoland Island, but the virus apparently is still absent from many fresh and brackish water locations (Jakob *et al.* 2009a). Restocking plans with juvenile eels should consider the risk of anthropogenic introduction of HVA into virus-free habitats.

The comparative examination of the parasite fauna of the different sampling sites shows clear differences in parasite species composition and diversity, and a distinct negative correlation between species diversity and salinity gradient (Jakob *et al.* 2009b). *Anguillicola crassus* and *Pseudodactylogyrus* spp. were found at all freshwater and brackish water sampling sites with rather high prevalence. As a result, only eels that move early to the marine environment are suspected to be at lower risk to get infected with neozoon parasites and may have a better chance to reach their spawning grounds in good condition (Figure 3.3.2).

In conclusion, it can be stated that eels staying in a purely marine environment are at lower risk of getting infected with pathological parasites and may therefore have higher chances to reach spawning grounds in good condition. The common practice of catching glass eel in river estuaries for an unselective restocking of freshwater systems all over Europe might therefore worsen the problem of declining eel stocks by further decreasing the number of eels that would stay in marine coastal habitats.

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Jakob, E., K. Zumholz, S. Klimpel, and R. Hanel. 2009b. Habitat dependent parasite infestations of the European eel *Anguilla anguilla* (L.) in northern Germany. ICES J. Mar. Sc. 66:358-366.

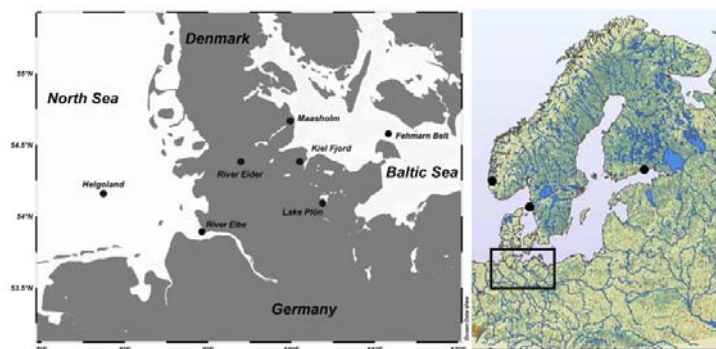


Figure 3.3.1. Sampling coverage.

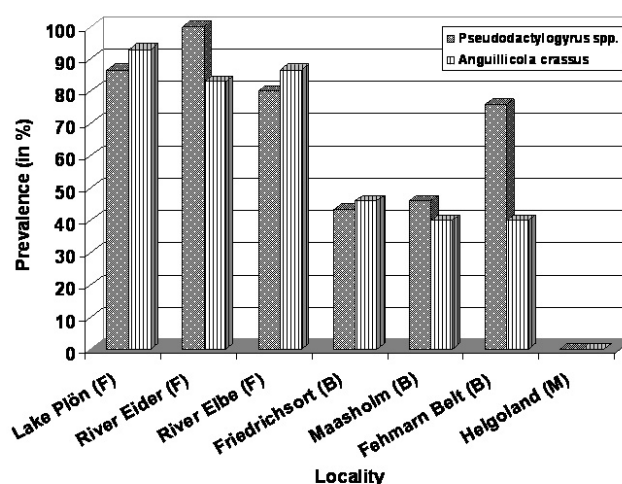


Figure 3.3.2. Prevalence (%) of infection for *Anguillicola crassus* (right columns) and *Pseudodactylogyrus* spp. (left columns) for different freshwater (F), brackish (B) and marine (M) locations in northern Germany.

3.4 Demographic differences between freshwater and estuarine eels in the Severn, England

There is very poor understanding of eel in UK estuaries and coastal waters (Knights *et al.* 2001). This study describes the growth and sex ratio of eel caught in the Severn estuary and compares these demographic parameters with those from freshwater sites in the lower reaches of the river.

Two sites were sampled using conventional fyke nets, in the upper estuary, under neap tide conditions. Freshwater sampling was carried out at 27 sites in the lower river. All freshwater sites were within 30 km upstream of tidal influence. The sites were wadeable, enclosed with “micromesh” stop nets (3 mm mesh) and fished either three or four times in succession using pulsed D.C. electric fishing equipment (240 v,

50 Hz; supplied by a 3.5 Kva generator). Hand nets with a three-millimetre mesh size were used to collect any eel.

The total length of each individual was measured to the nearest millimetre. Otoliths were removed and aged according to Aprahamian (1987), and the data presented here refer to the number of years spent in fresh water. Sex was assessed macroscopically (Sinha and Jones 1966). Growth was modelled using the Von Bertalanffy model (von Bertalanffy 1957) for eel in the estuary, and by least squares regression (Graynoth 1998) for eel in fresh water.

Growth in the estuary was best described by the Von Bertalanffy growth model. In the upper estuary eel had a higher asymptotic length (L_{∞}) and lower growth coefficient (k) when compared with samples taken lower down the estuary at Oldbury Power Station (Bird *et al.* 2008) (Table 3.4.1). In freshwater, growth was best described by a least square regression of the form:

$$\text{Length (mm)} = 86.9 + 18.4 * \text{Age (years)} \quad (n=2\ 395)$$

When compared with eel from freshwater growth in the estuary was substantially higher (Figure 3.4.1) by approximately 40% (Figure 3.4.2).

Of the 153 eel caught in the estuary 134 could be sexed of which females dominated the sample (79.1%). In fresh water 2 477 eel were caught, the majority of which were undifferentiated (74.2%). Of the 637 specimens where sex was determined, males dominated (63.2%) (Figure 3.4.3). The number of males, females and undifferentiated eel according to three size categories (Table 3.4.2) shows a higher proportion of male in fresh water compared to the estuary in all three size categories (Figure 3.4.4).

The higher growth rate in the estuary compared to fresh water is presumed to reflect higher productivity in the estuary and also higher temperatures during the summer feeding period.

The main limitation of the study was that different methods were used to sample eel from the two habitats and that the residence time of eel in each habitat is unknown. The difference in method between the two habitats is not considered to influence the conclusion that eel caught in the estuary grew faster than those obtained from fresh water. As regards sex ratio the breakdown according to size in part mitigates against the selectivity of different methods suggesting that the proportion of males in the estuary are lower when compared with freshwater sites in the lower river.

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Table 3.4.1. von Bertalanffy growth parameters derived from lengths at age of *Anguilla anguilla*, from the Severn estuary

Location	L_{∞} (mm)	k (year ⁻¹)	t_0 (year)	n	Ref.
Upper estuary	734	0.066	-1.81	152	This study
Oldbury Power St.	508	0.17	-0.9	91	Bird <i>et al.</i> (2008)

Table 3.4.2. Number of male, female and undifferentiated eel in relation to size and habitat.

Location	Sex	300–349 mm	350–399 mm	400–449 mm
Estuary	Male	19	9	0
	Female	12	22	31
	Undifferentiated	8	1	0
Freshwater	Male	261	77	2
	Female	65	78	48
	Undifferentiated	72	2	0

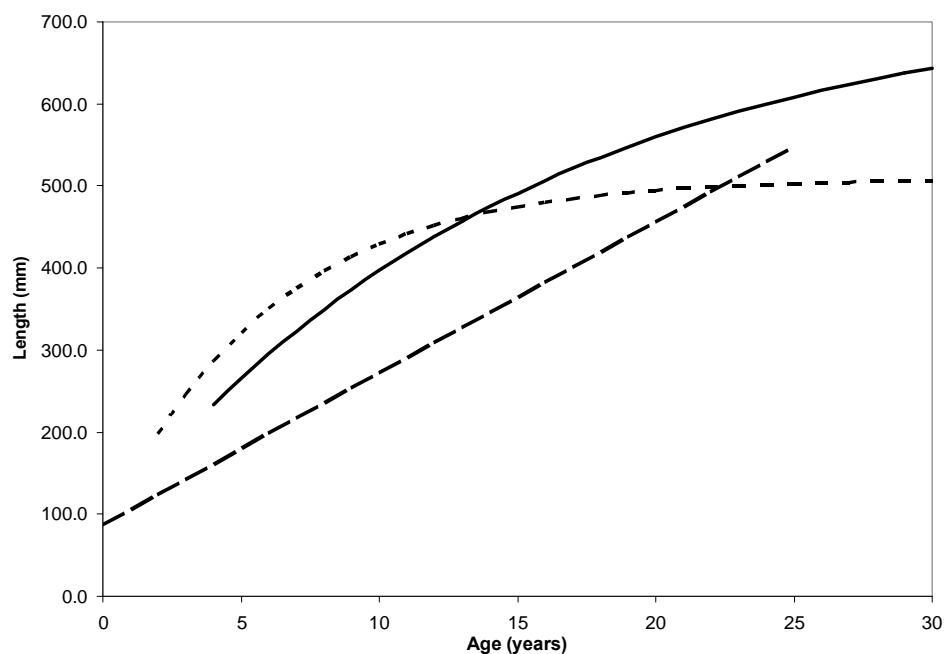


Figure 3.4.1. Length at age of eel from the upper estuary (solid line), lower estuary at Oldbury Power Station from Bird *et al.* (2008) (dotted line) and from freshwater sites from the lower river (dashed line).

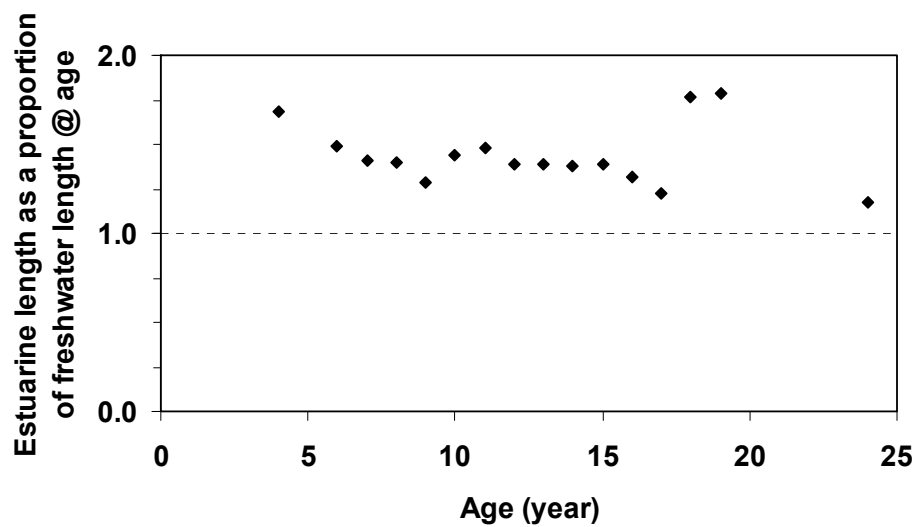


Figure 3.4.2. Comparison of estuarine length of eel in relation to freshwater length by age.

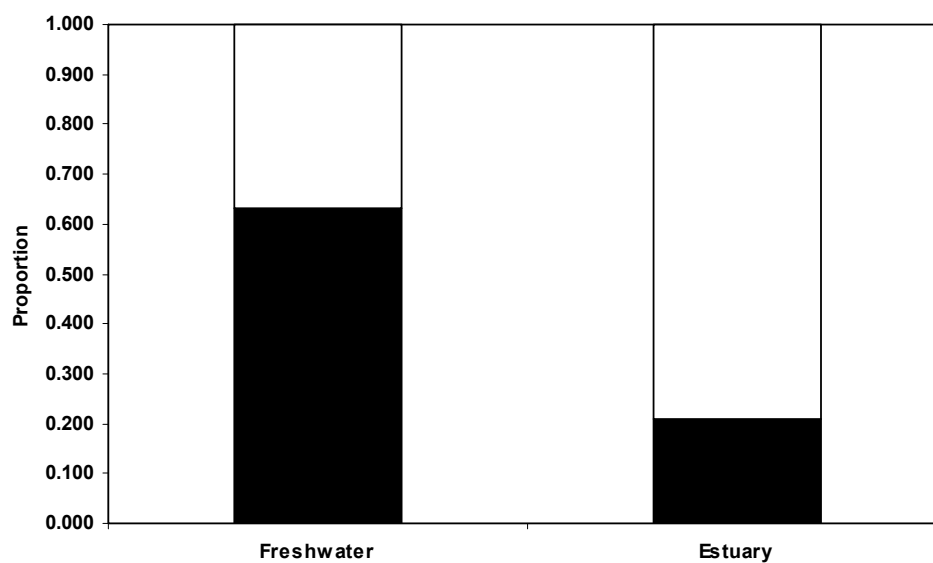


Figure 3.4.3. Proportion of males (solid column) and females (open column) in relation to habitat, n = 637 and 134 for freshwater and estuary respectively.

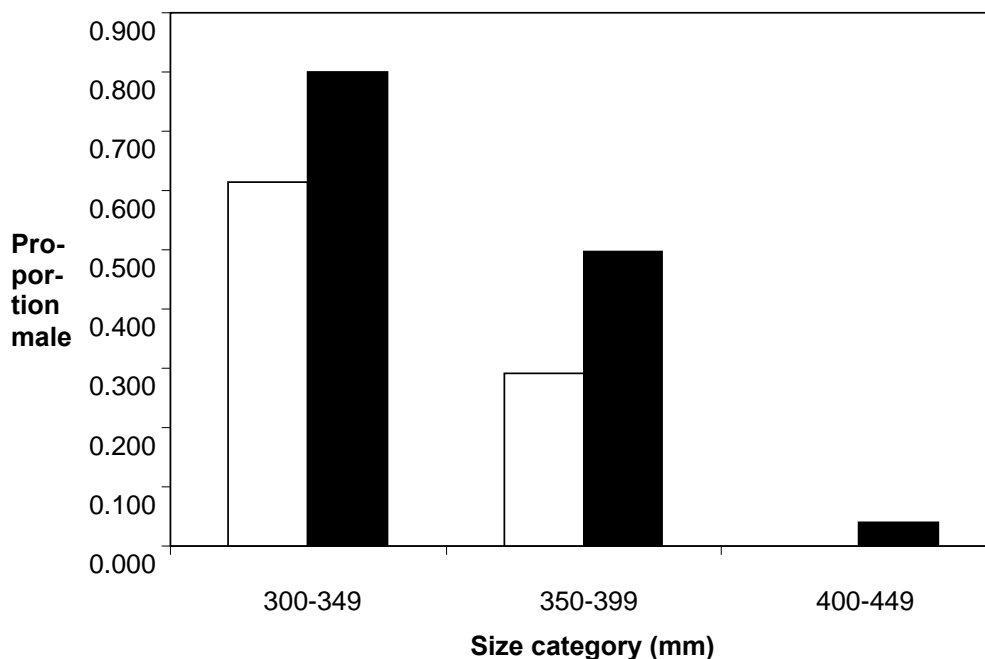


Figure 3.4.4. Proportion of male eel in fresh water (solid column) and in the estuary (open column) in relation to size.

3.5 Population dynamics of European eel in a Mediterranean lagoon

Introduction

This chapter presents the first model of eel demography that accounts for all of the following features of the continental phase of eel life cycle: (1) density dependent survival of juveniles (Vøllestad and Jonsson 1988, De Leo and Gatto 1995); (2) body growth characterized by strong sexual dimorphism and high interindividual variability (De Leo and Gatto 1995, Krueger and Oliveira 1999); (3) sex differentiation and maturation, as well as natural mortality, related to body size rather than age (Melià *et al.* 2006, Bevacqua *et al.* 2006); (4) fishing mortality depending on maturation stage, body size and gear selectivity (Bevacqua *et al.* 2009); and (5) severe fluctuations of annual glass eel recruitment (Vøllestad and Jonsson 1988). The model was calibrated and validated on a long-term dataset (1993-2006) regarding the European eel population of the Camargue lagoons (Rhône River delta, Southern France), and accounted for monthly variations in parameters in order to explicitly consider seasonal changes in recruitment, maturation processes and fishing effort. Catch data were provided by Tour du Valat (TdV) Biological Station that has monitored the Camargue lagoons since 1993.

Study site

The Camargue water system comprises two major interconnected water bodies: the Impériaux lagoon (2.800 ha) and the Vaccarès lagoon (6.400 ha). The lagoons are isolated by dykes from the two arms of the Rhône River (Grand Rhône and Petit Rhône) and from the Mediterranean Sea. The water flow from the lagoons to the sea and back is regulated by Fourcade sluice gates, near Saintes Maries de la mer (Crivelli *et al.* 2008). In the study period, water management was mainly aimed at maintaining low

water levels (around 1–2 m to prevent the inundation of Saintes Maries de la mer) and low salinity levels (around 4–12 ppt to avoid damage to rice fields) in the lagoons. Water temperature ranges from 4 to 32°C, with an average annual value of 15°C. Commercial fishing takes place both in Impériaux and Vaccarès through the use of fyke nets while recreational fishing is banned. From the socio-economic viewpoint, eel fishing accounts for more than half of the income of the professional lagoon fisheries in France (Crivelli *et al.* 2008).

Results

Figure 3.5.1 shows expected versus observed TdV catches in terms of biomass, from spring 1999 to autumn 2006, aggregated over trimesters. The correlation between observed and estimated TdV catches is 0.67 ($r^2 = 0.40$) in 1999–2003 and 0.78 ($r^2 = 0.55$) in the validation period 2004–2006.

Calibration procedures permitted the assessment of still unknown parameters involved in eel population dynamics such as density dependent mortality between the glass eel and elver phase and different fishing mortality rates between yellow and silver eels.

The estimated relationship between yellow eel settlement R and glass eel recruitment G is shown in Figure 3.5.2. This relationship is responsible for dampening R oscillations with respect to G oscillations. Thus, although the number of glass eels that entered the lagoons in a given year varied considerably during the study period (from 1 million to 1 billion), the consequent abundance of eels successfully colonizing the lagoons never exceeded 10 million (about 1000 ind./ha).

During 1999–2006 eel stock abundance varied between 1 and 18 million with undifferentiated eels (i.e. < 300 mm) comprising over 90% of the population. Yellow males and females comprise the remaining 10% while silver eel abundance in the stock is negligible due the fact that silver eels that escape fishing mortality leave the lagoons to migrate to the spawning grounds. In terms of biomass, the stock varied between 50 and 250 t (4.5–22.7 kg/ha) with undifferentiated eels comprising 30% of the population, yellow males and females comprising 68% and silver eels accounting for the remaining 2%. Both stock biomass and abundance show strong seasonal oscillations. Stock abundance quickly rises in spring due to settlement of newly recruited eels and then decreases until the next recruitment wave. Stock biomass falls in autumn due to silver eel escapement and high fishing pressure, and increases during the rest of the year due to body growth of resident and newly recruited individuals.

The model also allowed an assessment of professional fisheries harvest. Monthly harvest was estimated to fluctuate between 1 t (0.1 kg/ha) and 25 t (0.25 kg/ha). Annual harvest varied between 55.2 and 95.5 t (5.0–8.7 kg/ha). Undifferentiated eels, sexually differentiated yellow eels, and silver eels account for 15, 60 and 25% of harvest biomass, respectively. Although silver eels are fished only in autumn, they account for a remarkable fraction of annual harvest with a minimum in 2006 (19%) and a maximum in 2004 (38%).

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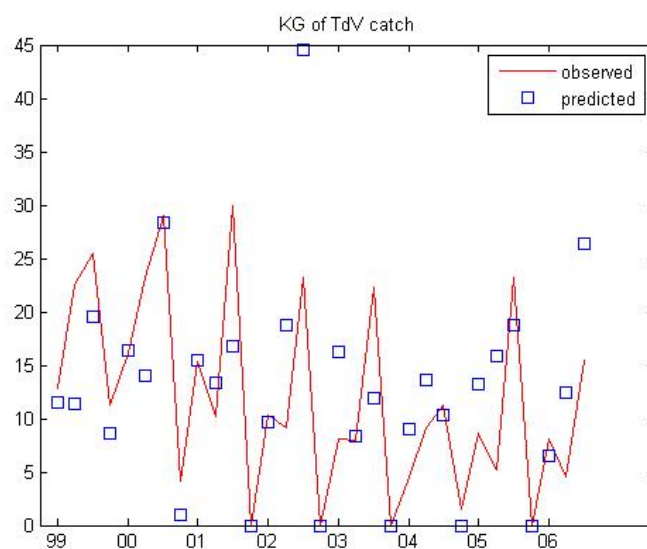


Figure 3.5.1. Predicted (lines) vs. observed (symbols) harvested biomass from spring 1999 to fall 2006.

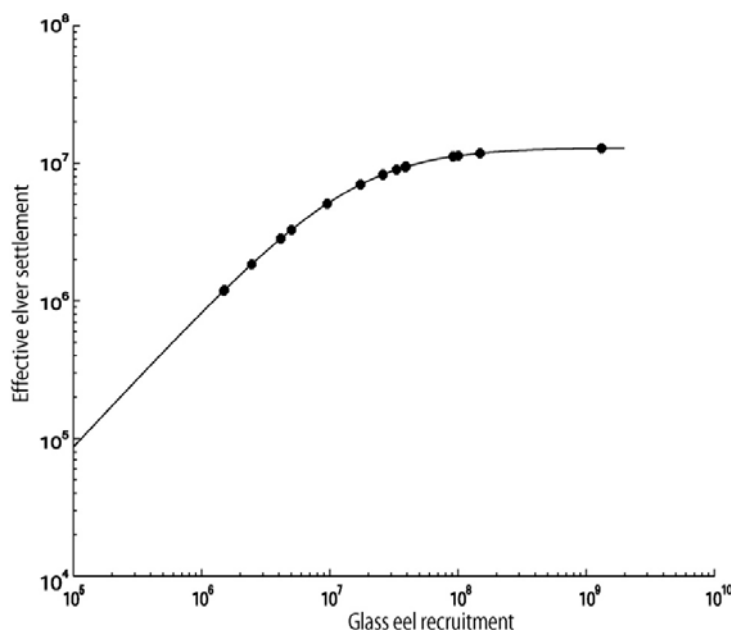


Figure 3.5.2. Relationship between glass eels recruitment and settled elver abundance. Dots indicate estimated glass eel recruitment and the corresponding yellow eel settlement estimated by the model.

3.6 Eel growth and quality issues from Mediterranean lagoons

Introduction

Temperate eel growth rates vary widely in relation to eel habitats such as lagoons, lakes and streams (De Leo and Gatto 1995). For instance, residence in oligotrophic habitats typically yields slower growth rates (Moriarty 1988; Poole and Reynolds 1996a,b) than those of mesotrophic (Aprahamian 2000, Lin *et al.* 2007), or eutrophic habitats (Rosell *et al.* 2005, Simon 2007). However, growth rate is known to vary not only in relation to environmental factors like latitude, temperature, salinity and food supply, but also to demographic factors of population size and density (Moriarty 1973, Panfili *et al.* 1994).

The aim of this study is to examine the demographic characteristics of populations of eel from four different habitats in Italy, one from a river and three from saline coastal lagoons, against the parameters of growth, age and sex ratio, whilst quality issues will be represented through *Anguillicola crassus* status.

Material and methods

The study was conducted during the eel fishing season 2007/2008 in order to catch both yellow and silver eels. Sampling sites were three saline lagoons and a freshwater habitat in Italy. Two lagoons were the small coastal lakes of Fogliano and Caprolace, central Italy, on the Tyrrhenian coast, whilst the third site is the Lesina lagoon, southern Italy, on the Adriatic coast. The fourth site is the lower stretch of the Tiber River, central Italy, from the estuary to the first dam. The descriptive parameters of the four sites are summarized in Table 3.6.1. Yellow and silver eels were collected from each site with the same sampling modality, by fyke netting (mesh size 6 mm). Total length and weight were determined, and individuals were then sacrificed in order to collect otoliths for age evaluation (grinding and polishing method, ICES 2009), gonads for sex determination (macroscopically whenever possible, otherwise by histological preparation and microscope examination), and swimbladders for evaluation of nema-

tode *Anguillicola crassus* infestation. Epidemiology of anguillicolosis was described using the conventional terms of prevalence and mean intensity as defined by Bush *et al.* (1997). Prevalence is the proportion of infected host in a sample (%) whilst mean intensity is the average number of parasites per infected hosts in a sample.

Mean length and age of both sexes of silver eel were analysed through application of Analysis of variance (ANOVA; $P < 0.05$). Theoretical growth was calculated using von Bertalanffy's model. The index of growth performance (Φ) (Pauly and Munro 1984) was calculated using the following equation: $\Phi = \log K + 2 \log L_{\infty}$; where: L_{∞} and K are the growth parameters of the von Bertalanffy equation.

Results

Length distribution is similar for the three lagoon samples: sizes ranged from 20 to 80 cm and the prevailing size classes were 35, 40, 45 cm. Mean length of females in the Lesina lagoon was ca. 10 cm greater than female length in the other 3 sites, and was the only site where length differed significantly. The Tiber population showed a narrower size range (20 to 65 cm), with prevailing classes of 25 and 30 cm and 90% of the eels were lower than 45 cm. The four populations display different sex ratios, ranging from 13% (Tiber) to 100% (Lesina) of females, while the two lagoons of Caprolace and Fogliano have a higher percentage of female (respectively 76% and 62.5%). Table 3.6.2 shows mean length and age of both sexes in the four sites. No significant differences of mean length and age were found for all male silver eel fractions. However, female silver eels from Lesina were significantly different in length and age than those from the other sites.

Theoretical growth was calculated by von Bertalanffy's model for the male and female portions of the four populations. Lesina and Tiber females showed the highest K values (0.34 and 0.4 respectively), but females from Fogliano are shown to be longer at a specified age.

Index of growth performance (Φ) was estimated separately for male and female eel from each lagoon. Additionally, Φ has been calculated also for other Mediterranean lagoons, i.e. Comacchio (northern Italy, Adriatic coast), Vaccarès–Impériaux and Fumemorte (southern France), described by Melià *et al.* 2006. Φ values for males and females of all populations considered are plotted against average salinity (Figure 3.6.1). Growth performance is inversely correlated to salinity, which is more marked in females.

The prevalence in *A. crassus*, i.e. infection rate, found was 45.9% in the Lesina Lagoon and 76.5% in the Tiber River. No infected eels were found in Caprolace or in Fogliano. Mean infection intensity, i.e. mean number of *A. crassus* per infected eel, was higher in eels from the Tiber (3.4) than in eels from Lesina (2.2).

Conclusions

These results represent preliminary findings of some case studies from the Mediterranean area. A more rapid growth is observed for the populations from the sites at lower salinity and in the Tiber River, but it must be considered that such populations may also differ on the basis of demographic traits, density and diet. Each of the study sites differed in various ecological traits such as presence/absence of freshwater inputs, tidal exchanges, plant cover and trophic status. It must also be noted that lagoons with lower salinities or narrower salinity ranges are influenced by varying quantities of freshwater input, thus the extent of this must be considered as this may affect eel growth rates.

The assumption that growth for European (Daverat and Tomas 2006), American, (Jessop *et al.* 2008; Lamson *et al.* 2009) and anguillid eels in general (Cairns *et al.* 2009) is faster in brackish and salt water relies on observations of habitat use from Sr:Ca ratios in addition to observed length at age. It will be of great interest to examine these features simultaneously in Mediterranean environments.

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Table 3.6.1. Descriptive features of the four study sites.

	Caprolace	Fogliano	Lesina	Tevere (Tiber)
Latitude	41° N	41° N	41° N	41° N
Surface area (ha)	2.26	4.08	51.4	40 km (length)
Max/average depth (m)	2.9 / 1.3	2 / 0.8	1.5 / 0.7	10
Average temperature (°C)	19	18.6	18.3	17.2
Average salinity (psu)	37.7	38.2	15.8	0
Tidal range (m)	0.261	0.261	0.156	-
Trophic status	Intermediate	Intermediate	High	High
Tidal canals	1	1	2	-
Eel fishing	yes	Yes	yes	Yes

Table 3.6.2. Mean length and age \pm standard deviation values of silver eels in the four sample sites for both sexes. Values in red differ significantly from the others (ANOVA; $p < 0.05$)

		Caprolace	Fogliano	Lesina	Tevere (Tiber)
Male	Length	37.7 \pm 2.6	38.2 \pm 1.8	---	39.1 \pm 3.9
	Age	6.3 \pm 1.3	5.2 \pm 1	---	6 \pm 2.1
Female	Length	56.9 \pm 8.1	55 \pm 9.8	65.5 \pm 9.2	54.2 \pm 12.7
	Age	8.6 \pm 2.2	7.7 \pm 1.8	5.6 \pm 1.7	7.1 \pm 2.5

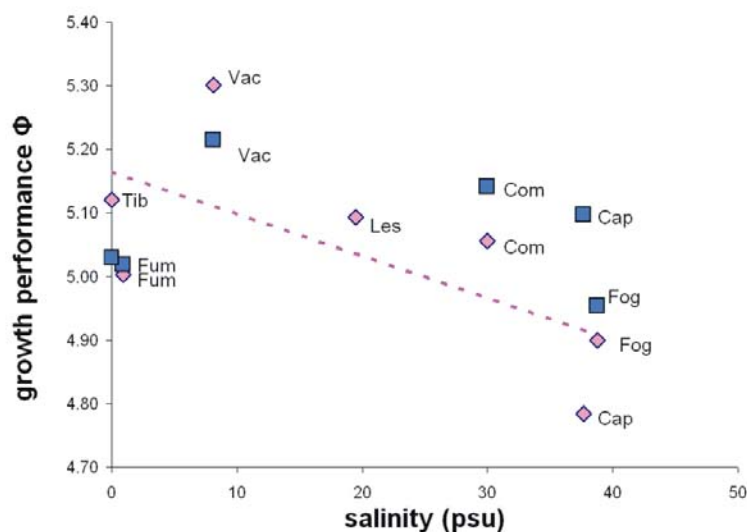


Figure 3.6.1. The relation between the index of growth performance and average salinity for both sexes in Caprolace, (Cap), Fogliano (Fog), Lesina (Les) lagoons, Tiber River (Tev) and other three Mediterranean lagoons: Vaccarès–Impériaux (Vac), Fumemorte (Fum) and Comacchio (Com), (Melià *et al.* 2006). Squares indicate males and diamonds indicate females.

3.7 Discussion - demographic characteristics in saline and fresh water

Implications for stock assessment and management

Currently, knowledge of European eel biology is concentrated on the freshwater side, and it would be hazardous to extrapolate to saline areas. At the present time knowledge is insufficient to define consequences to management of habitat-related differences in eel biology.

Research needs

Measurements of habitat-specific natural mortality rates and other demographic parameters, clarification of the influence of salinity or other habitat-related factors on growth and sex determination. Most studies have been at an observational level, but it's important to understand mechanisms and processes that underlie observations.

Research methods

Research can proceed by gathering data on individual characteristics (physical attributes, habitat history, eel quality, stocked/non-stocked origin), and by modelling. Modelling should take into account individual variation, and be followed by field experiments to test outcomes. Investigations that stack multiple enquires on a single collection campaign are cost- and time-efficient may yield answers that are greater than the sum of individual projects. The Eel Working Group might be a forum to help coordinate this.

4 Anguillid eel densities, populations, and relative abundance in saline and fresh water

4.1 Synthesis of American eel monitoring work on the Saint-Jean water system, Québec, Canada, 2001–2007

Introduction

This section summarizes the extended report of Caron *et al.* (2009) which describes American investigations in the Saint-Jean system, in the Gaspésie Peninsula, Québec, Canada (48°46'08"N, 64°26'51"W), from 2001 to 2007. The Saint-Jean water system has a watershed area of 1124 km² and its main stem is approximately 115 km in length. At its mouth, there is a 5.4 km² saline water estuary connecting to the sea. The extended report of Caron *et al.* summarizes the results on eel abundance estimates and growth rates obtained in lake, river and estuary habitats, as well as on eel movements observed within the Saint-Jean water system.

Abundance and density estimates

Eel abundance was estimated in Lake Sirois which has a surface area of 18 ha, using five hoop nets and 4 lines of minnow traps over 13 days in July 2004. Using a mark-recapture method (Rivest and Lévesque 2001), lake abundance was estimated to vary from 2610 to 3178 yellow eels of 144 to 601 mm in length. This represents a density from 145 to 177 eels/ha. Estimation of eel abundance was also attempted in three other lakes (Ross, Bazire and Pauline), but no eels were found in these habitats during the sampling periods.

Eel abundance was also estimated in the river using electro-fishing (2004; 22 stations of 100/m²) and both electro-fishing and mark-recapture methods (2005; 12 stations of 100/m² and 6 hoop nets respectively). Densities were estimated to vary between 0 and 1.5 eel/100 m² using electro-fishing methods in both years (up to 150 eels/ha). Eels ranged between 162 and 654 mm in length. Highest densities were found in the first 6 km from the river mouth. Comparison of the electro-fishing and the mark-recapture method in 2005 revealed that electro-fishing might underestimate abundance by a factor of 3 or 4.

In the estuary, nine hoop nets distributed within four different sectors of the bay were used to estimate abundance using mark-recapture in July 2005. Captured eels varied between 70 to 795 mm in length. Abundance of <245 mm eels could not be estimated because they were not recaptured after being released 120 m away from their respective traps, suggesting limited movements in this eel size class. Most recaptures of mid size class eels (245 to 420 mm) occurred within the 120 m area. Abundance estimates associated with each trap were extrapolated for each sector. By adding abundance estimates from each sector, the total abundance for 245 to 420 mm eels in the estuary was estimated at 271 431 or 645 eels/ha. Large size class eels (>420 mm) could be recaptured at either the traps of the sector. By adding abundance estimates from each sector, abundance of >420 mm eels in the estuary was estimated at 8 554 or 20 eels/ha. Total eel abundance from all size classes >245 mm was estimated at 279 985 or 665 eels/ha in the estuary. Eels were the most abundant in the northern side of the estuary where eelgrass is present and where the substrate is mainly soft mud (52% of 245-420 mm eels and 44% of >420 mm eels concentrating in this area). Two important prey species, *Fundulus heteroclitus* and *F. diaphanous*, are also very abundant in this area.

Sampling in some of the locations was repeated during summer 2008 in Lake Sirois and in the estuary (4 hoop nets). These samplings gave concordant catch per unit effort (CPUE) estimates, suggesting abundances of similar ranges in both habitats between the different time periods (lake: 6.8 and 9.5 CPUE in 2004 and 2008; estuary: 13.9 and 17.4 CPUE in 2005 and 2008 respectively) (unpublished data).

Abundance estimates during spring and fall migration

Between 2003 and 2007, abundance was also estimated in spring for yellow eels migrating from the river to the estuary using a rotary fish trap and the mark-recapture method. On the Saint-Jean River, spring migration occurred between mid-May and the end of June, and included eels from 121 to 660 mm in length. Abundance of eels migrating to the estuary was estimated to be between 15 037 and 40 921 depending on the year, with no clear increasing or decreasing trend.

Abundance of silver eels migrating to sea at the end of the summer for reproduction was also estimated using the same method. Fall migration was observed from the beginning of September to mid-October on the Saint-Jean River and included eels from 143 to 720 mm in length. Only eels from 320 to 720 mm in length were considered to be potential reproductive migrants and their abundance was estimated at 1 985 eels in total (range: 807–3969).

Growth rate

Length at age was compared in the three habitats by relating total length to age of captured eels. Age was determined from otolith reading of 285 eels captured in summers 2004 and 2005 (40 in Lake Sirois, 115 in the river, 130 in the estuary). Age varied between 2 to 24 years, but only 2% of the eels were above 15 years old. Based on the association between age and length, eels in the estuary showed the highest growth rate, followed by eels in the river and finally eels captured in the lake.

Between 2004 and 2007, a total of 7 875 eels were tagged with microtags and 276 of them were recaptured 1, 2 or 3 years later, which allowed annual growth determination. On average, eels grew between 37 to 48 mm per year, but growth rate varied from 15 to 72 mm per year.

Movements

An acoustic telemetry study was conducted from mid-May to mid-October 2004 on 40 yellow eels ranging between 491 to 640 mm in length (17 captured in the river and 23 in the estuary). The study is detailed in Thibault *et al.* (2007a). Briefly, of the 17 eels captured in the river, 7 migrated to the estuary during the summer, 6 stayed in the river, and 4 were lost. Of the 23 eels captured in saltwater, 17 stayed in the estuary, mainly in the northern section (sector 2), and 6 were lost. These results suggested that part of the downstream migrants exploited the estuary as a summer feeding area and revealed that eels were active at night but selected a resting site during the day (home range: night time = 16.8 ± 4.9 ha, daytime = 0.38 ± 0.19 ha).

Analyses of otolith strontium:calcium (Sr:Ca) ratios in 162 yellow and silver eels also gave complementary information on migration patterns of this species in the Saint-Jean water system. This study is detailed in Thibault *et al.* (2007b) and reveals the co-existence of three main migratory patterns: freshwater residency (20%), brackish water residency (38%) and the predominance of an amphidromous migratory behaviour (42%). Higher growth rate was found for eels spending more time in the estuary compared to those spending more time in the freshwater environment. However, it is

possible that some eels classified as brackish water residents may have had seasonal migrations to fresh habitats that were undetected in otoliths Sr:Ca analysis.

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4.2 American eel landings and densities, by habitat salinity

Table 4.2.1 presents reported landings of American eels in Canada, the United States, Mexico, and the Dominican Republic, broken down by salinity zone. Breakdowns are not yet available for some jurisdictions. On the basis of data available to date, eel fisheries in Canada target a mix of fresh and saline water. The fishery in the U.S. is almost entirely conducted in saline water, although some of the harvested eels may have been produced in fresh water but shifted to saline water. FAO data indicate that all eel fisheries in Mexico are prosecuted in marine waters, while all eel fisheries in the Dominican Republic are prosecuted in inland waters.

Table 4.2.2 presents estimated densities of American eels. Nearly all densities estimated for streams are from electrofishing surveys. Densities estimated in ponds, lakes, bays, and estuaries are from a mix of capture-mark-recapture studies, counts of poisoning experiments, and transect surveys conducted at night with a glass bottom boat equipped with underwater lights. Results of glass bottom boat surveys are minimum estimates because eels that are buried in the substrate at the time of the survey are not counted. Estimated eel densities in saline bays and estuaries have a similar distribution to those estimated for freshwater ponds in the same area, with modal values between 0 and 100 eels/ha, and an extended right tail of the distribution up to several 100 eels/ha (Figure 4.2.1). Most eel densities in streams are under 3,000 eels/ha, but some range up to 25,000 eels/ha. Comparisons between densities estimated for ponds, bays and estuaries vs. streams are complicated by the fact that eels in streams as sampled by electrofishing are generally much smaller than those sampled in ponds, bays, and estuaries. Estimated densities of eels in streams are plotted against latitude in Figure 4.2.2. The highest estimated densities are found at mid-latitudes, but there are too few samples at high and low latitudes to confirm any relation between density and latitude.

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Table 4.2.1. Reported landings of yellow and silver American eels, in metric tonnes, by region, fishing location, and phase.

Region	Total reported landings ^a	Fishing location										Comments, source of breakdown by habitat and life stage	
		Fresh non-tidal			Fresh tidal			Saline tidal					
		Total ^b	Yellow	Silver	Total	Yellow	Silver	Total	Yellow	Silver			
										Total	From fresh growth areas		From saline growth areas
Fed./ State Prov.													
<u>Canada</u>													
St. Lawrence River system													
Ontario	0.0												
Quebec	118.8	0.3 f	16.3 f	0.0 f	47.8 f	4.5 f	43.3 f	54.7 f	0.0 f	54.7 f	54.7 e	0.0 e	Landings in Lac St. Pierre and the Quebec City area are reported in the fresh tidal category.
Gulf of St. Lawrence													
Quebec	5.3	1.1 f	1.1 e	0.0 e				4.2 f	4.2 e	0.0			Landings are for les Îles de la Madeleine, from Richard 2008
New Brunswick	102.2	888.0			5.0 r	4.5 r	2.5 r	97.2 r	87.5 r	9.7 r	1.0 r	8.8 r	
Nova Scotia	7.0	2.1 f	0.0 f	2.1 f				4.9 e	4.4 r	0.4 r	0.0 r	0.4 r	
Prince Edward Island	81.5	0.0 f			0.0 f			81.5 f	73.3 r	8.1 r	0.8 r	7.3 r	
Newfoundland	38.7												
Newfoundland - Atlantic	32.4												
Nova Scotia - Atlantic & Fundy	46.1												
New Brunswick - Fundy	45.8												
<u>United States</u>													
Maine	4.6												
New Hampshire	0.0												
Massachusetts	0.1	1.3						1.3 f	1.3 f				Landings and breakdown from MA Compliance Report for 2007
Rhode Island	0.0												
Connecticut	0.4												
New York	1.9												
New Jersey	74.6	82.1							77.1 f	5.0 r			Landings of silver eel are 5 t or less. Source: Jeff Brust, New Jersey DEP
Pennsylvania	0.0												
Delaware	61.6								60.7 r	0.9 r			John Clark, Delaware DFW

Table 4.2.1 (continued)

Region	Total reported landings ^a		Fishing location									Comments, source of breakdown by habitat and life stage		
			Fresh non-tidal			Fresh tidal			Saline tidal					
			Total	Yellow	Silver	Total	Yellow	Silver	Total	Yellow	Silver			
	Fed./ State Prov.									Total	From fresh growth areas		From saline growth areas	
Maryland	145.6					2.5 f	2.5		143.1 f	142.8 f	0.3 f	0.1 e	0.2 e	Keith Whiteford, Maryland DNR
District of Columbia														
Virginia	28.8													
North Carolina	17.1	16.4		9.9			0.0			6.4				
South Carolina	0.0													
Georgia	0.0													
Florida Atlantic	0.0	3.44	0.78 f	0.78 f	0.00 e	2.61 f	2.59 f	0.02 e	0.05 f	0.00 e	0.05 e			Kim Bonvechio, Eustis Fisheries Research Lab
Florida Gulf of Mexico	0.0	0.13	0.00 f	0.00 f	0.00 f	0.00 e	0.00 e	0.00 e	0.13 e	0.00 e	0.13 e			Kim Bonvechio, Eustis Fisheries Research Lab
<u>Mexico</u>	2.0								2.0					FAO reports all landings as from "marine areas."
<u>Dominican Republic</u>	14.0		14.0											FAO reports all landings as from "inland waters."
Total	828.6		906.3	28.1	2.1	57.9	14.1	45.8	389.1	457.8	79.4	56.6	16.7	

^aFor Canada, landings are for 2005. Sources are federal (DFO) and provincial statistics as compiled by Cairns et al. 2008. Landings for the US are for 2007. Federal landings are from http://www.st.nmfs.noaa.gov/st1/commercial/landings/annual_landings.html and state landings are from personal communications with state biologists. Data for Mexico and the Dominican Republic are from the Food and Agricultural Organization (www.fao.org).

^bf - firm data; e - educated guess; r - rough guess

Table 4.2.2 Densities of American eels by salinity of capture location.

Country	Prov./state, region	Location	°N lat.	Habitat	Salinity	Years	Method ^a	Approx. min. size counted (cm)	Eel density		Source
									Number/ ha	kg/ ha	
Canada	NL Labrador	Sand Hill R	56	Stream	Fresh	1971	E-fish		127		Fletcher and Anderson 1973
Canada	QC Gulf N. Shore	Matamek R	51	River	Fresh	1974	CMR	30	133	17.9	Dolan 1975
Canada	QC Anticosti I.	Bec-Scie R, Castor Brook	50	Stream	Fresh	1988-1996	E-fish		1,144		Caron and Verreault 1997
Canada	QC Gaspé Pen.	Saint-Jean R Estuary	49	Estuary	Saline	2005	CMR	25	665		Section 2.4.2 and Caron et al. 2009
Canada	QC Gaspé Pen.	Lac Sirois, Saint-Jean R	49	Lake	Fresh	2004	CMR	15	161		Section 2.4.2 and Caron et al. 2009
Canada	QC Gaspé Pen.	Lac Ross, Saint-Jean R	49	Lake	Fresh	2004	CMR	15	0		Section 2.4.2 and Caron et al. 2009
Canada	QC Gaspé Pen.	Lac Bazire, Saint-Jean R	49	Lake	Fresh	2004	CMR	15	0		Section 2.4.2 and Caron et al. 2009
Canada	QC Gaspé Pen.	Lac Pauline, Saint-Jean R	49	Lake	Fresh	2004	CMR	15	0		Section 2.4.2 and Caron et al. 2009
USA	VT	Lake Champlain	44	Lake	Fresh	1979	CMR		429	26.1	LaBar and Facey 1983
Canada	NB Gulf	Pokemouche R Estuary	48	Estuary	Saline	2008	GBB	30	51.3		Table 4.4.1
Canada	NB Gulf	Tracadie Bay	48	Estuary	Saline	2008	GBB	30	62.5		Table 4.4.1
Canada	NB Gulf	Tabusintac R Estuary	47	Estuary	Saline	2008	GBB	30	31.7		Table 4.4.1
Canada	NB Gulf	Baie Sainte Anne	47	Estuary	Saline	2008	GBB	30	22.4		Table 4.4.1
Canada	NB Gulf	Kouchibouguac R	47	Estuary	Saline	2007	GBB	30	38.7		Table 4.4.1
Canada	NB Gulf	NW Branch Richibucto Estuary	47	Estuary	Saline	2008	GBB	30	34.7		Table 4.4.1
Canada	NB Gulf	St. Nicholas River, Richibucto	47	Estuary	Saline	2007	GBB	30	58.9		Table 4.4.1
Canada	NB Gulf	Village Bay	47	Estuary	Saline	2008	GBB	30	32.0		Table 4.4.1
Canada	NB Gulf	Cocagne R Estuary	46	Estuary	Saline	2008	GBB	30	17.3		Table 4.4.1
Canada	NB Gulf	Shediac Bay	46	Estuary	Saline	2008	GBB	30	10.0		Table 4.4.1
Canada	NB Gulf	Kinnear R Estuary	46	Estuary	Saline	2008	GBB	30	19.2		Table 4.4.1
Canada	NB Gulf	Restigouche River	48	Stream	Fresh	2000-2007	E-fish	10	117.3	7.7	Cairns et al. 2007
Canada	NB Gulf	Tabusintac R	47	Stream	Fresh	1999-2001	E-fish	10	0.5	0.0	Cairns et al. 2007
Canada	NB Gulf	Miramichi River	47	Stream	Fresh	2000-2007	E-fish	10	87.3	5.7	Cairns et al. 2007
Canada	NB Gulf	Richibucto R	47	Stream	Fresh	2000-2005	E-fish	10	192.7	12.6	Cairns et al. 2007
Canada	NB Gulf	Buctouche R	46	Stream	Fresh	2000-2005	E-fish	10	86.2	5.6	Cairns et al. 2007
Canada	NS Gulf	Pictou Harbour	46	Estuary	Saline	2008	GBB	30	18.5		Table 4.4.1
Canada	NS Gulf	Little Harbour, Pictou Co.	46	Bay	Saline	2008	GBB	30	47.6		Table 4.4.1
Canada	NS Gulf	Merigomish Harbour	46	Estuary	Saline	2008	GBB	30	40.7		Table 4.4.1
Canada	NS Gulf	Pomquet Harbour	46	Estuary	Saline	2008	GBB	30	55.0		Table 4.4.1
Canada	NS Gulf	Tracadie Harbour	46	Estuary	Saline	2008	GBB	30	14.9		Table 4.4.1
Canada	NB Gulf	Margaree R	46	Estuary	Saline	2007	GBB	30	67.6		Table 4.4.1
Canada	NS Gulf	R Phillip	46	Stream	Fresh	2000-2002	E-fish	10	0	0.0	Cairns et al. 2007
Canada	NS Gulf	Wallace R	46	Stream	Fresh	2000-2002	E-fish	10	144	9.4	Cairns et al. 2007
Canada	NS Gulf	East R Pictou	45	Stream	Fresh	2000-2002	E-fish	10	0	0.0	Cairns et al. 2007
Canada	NS Gulf	West R Antigonish	45	Stream	Fresh	2000-2002	E-fish	10	0	0.0	Cairns et al. 2007
Canada	NS Gulf	Margaree River	46	Stream	Fresh	2000-2007	E-fish	10	33.4	2.2	Cairns et al. 2007
Canada	NS Gulf	McCormick Lake	45	Lake	Fresh	1930s	Poisoning		0.0		Smith and Saunders 1955
Canada	PEI	Mill River Estuary	47	Estuary	Saline	2007	GBB	30	191.0		Table 4.4.1
Canada	PEI	Grand River Estuary	46	Estuary	Saline	2007	GBB	30	49.2		Table 4.4.1
Canada	PEI	Trout River Estuary, Roxbury	47	Estuary	Saline	2007	GBB	30	75.8		Table 4.4.1
Canada	PEI	New London Bay	46	Bay	Saline	2007	GBB	30	53.7		Table 4.4.1
Canada	PEI	Hope River Estuary	46	Estuary	Saline	2007	GBB	30	259.9		Table 4.4.1

Table 4.2.2 (continued)

Country	Prov./state/ region	Location	°N lat.	Habitat	Salinity	Years	Method	Approx. min. size counted (cm)	Eel density ^a		Source
									Number/ ha	kg/ ha	
Canada	PEI	Hunter River Estuary, Rusticoville	46	Estuary	Saline	2007	GBB	30	246.4		Table 4.4.1
Canada	PEI	Wheatley River Estuary, Cymbria	46	Estuary	Saline	2007	GBB	30	124.1		Table 4.4.1
Canada	PEI	Covehead Bay	46	Bay	Saline	2006-2007	GBB	30	48.2		Table 4.4.1
Canada	PEI	Morell River Estuary	46	Estuary	Saline	2006-2007	GBB	30	418.7		Table 4.4.1
Canada	PEI	Basin Head	46	Bay	Saline	2005-2006	GBB	30	70.3		Table 4.4.1
Canada	PEI	Lake of Shining Waters	47	Coastal pond	Fresh	2000	CMR	35	20.1	6.7	Cairns et al. 2007
Canada	PEI	Clarks Pond	47	Coastal pond	Fresh	2000, 2001	CMR	35	21.3	8.2	Cairns et al. 2007
Canada	PEI	Rollings Pond	47	Coastal pond	Fresh	2000, 2001	CMR	35	191.8	67.8	Cairns et al. 2007
Canada	PEI	Long Pond, Dalvay	46	Coastal pond	Fresh	2000, 2003	CMR	35	121.5	33.3	Cairns et al. 2007
Canada	PEI	Campbells Pond, Dalvay	46	Coastal pond	Fresh	2000, 2001	CMR	35	22.9	6.4	Cairns et al. 2007
Canada	PEI	Schooner Pond	46	Coastal pond	Fresh	2000	CMR	35	28.1	7.8	Cairns et al. 2007
Canada	PEI	Murphys Pond Trout R Millvale	46	Pond	Fresh	2007	GBB	30	0.0		Cairns et al. 2009
Canada	PEI	Bells Pond Hunter R	45	Pond	Fresh	2007	GBB	30	370.9		Cairns et al. 2009
Canada	PEI	Cass Pond	45	Pond	Fresh	2006	GBB	30	118.0		Cairns et al. 2009
Canada	PEI	North Pinette Pond	44	Pond	Fresh	2006	GBB	30	84.4		Cairns et al. 2009
Canada	PEI	Ellerslie R	47	Stream	Fresh	1993-1995	E-fish	10	0		Cairns et al. 2007
Canada	PEI	Morell R	46	Stream	Fresh	2001-2002	E-fish	10	153	10.0	Cairns et al. 2007
Canada	NL Gulf	Little Codroy R	48	Stream	Fresh	1956-1963	E-fish		1,020		Fletcher and Anderson 1973
Canada	NS Atlantic	Boars Back Lake	44	Lake	Fresh	1930s	Poisoning		12	0.2	Smith and Saunders 1955
Canada	NS Atlantic	Jesse Lake	44	Lake	Fresh	1930s	Poisoning		59	0.8	Smith and Saunders 1955
Canada	NS Atlantic	Tedford Lake	44	Lake	Fresh	1930s	Poisoning		133	2.6	Smith and Saunders 1955
Canada	NS Atlantic	Trefrys Lake	44	Lake	Fresh	1930s	Poisoning		153	2.9	Smith and Saunders 1955
Canada	NB Fundy	Potters Lake	45	Lake	Fresh	1940	Poisoning		52	9.0	Smith and Saunders 1955
Canada	NB Fundy	Bills Lake	45	Lake	Fresh	1930s	Poisoning		529	79.3	Smith and Saunders 1955
Canada	NB Fundy	Cooks Lake	45	Lake	Fresh	1930s	Poisoning		0		Smith and Saunders 1955
Canada	NB Fundy	Pollett River	46	River	Fresh	1947-1952	Seining, e-fish		1,814	38.1	Elson 1962
Canada	NB Fundy	Bennett Creek	46	Stream	Fresh	1950	E-fish	<9	24,399	170.5	Godfrey 1951
Canada	NB Fundy	Coverdale Creek	46	Stream	Fresh	1950	E-fish	<9	1,446	12.4	Godfrey 1951
Canada	NB Fundy	Nigus Creek	46	Stream	Fresh	1950	E-fish	9	13,136	106.3	Godfrey 1951
Canada	NB Fundy	Pollett River	46	Stream	Fresh	1950	E-fish	<9	1,532	22.2	Godfrey 1951
Canada	NB Fundy	Turtle Creek	46	Stream	Fresh	1950	E-fish	<9	3,133	27.2	Godfrey 1951
USA	ME	Lake Coleback	45	Lake	Fresh	1958	Poisoning	18	204	47.6	Rupp and DeRoche 1965
USA	ME	Each Machias R	45	Stream	Fresh	1996-1997	E-fish	10	2,180	67.0	Oliveira and McCleave 2000
USA	ME	Pleasant R	45	Stream	Fresh	1996-1997	E-fish	10	840	39.8	Oliveira and McCleave 2000
USA	ME	Sheepscot R	45	Stream	Fresh	1996-1997	E-fish	10	1,080	38.0	Oliveira and McCleave 2000
USA	ME	Medomak R	44	Stream	Fresh	1996-1997	E-fish	10	1,040	148.5	Oliveira and McCleave 2000
USA	MA	Falmouth	42	Salt marsh	Saline	1979	CMR	15	875		Ford and Mercer 1986
USA	RI	Annaquatucket R	42	Estuary	Saline	1990-1992	E-fish	16	3,230		Oliveira 1997
USA	RI	Narrow R	41	Stream	Fresh		CMR		300	75.0	Bianchini et al. 1982 in Nilo and Fortin 2001
USA	RI	Annaquatucket R	42	Stream	Fresh	1990-1992	E-fish	16	1,690		Oliveira 1997
USA	NY	Saw Kill	42	Stream	Fresh		CMR	13	13,100	199.0	Schmidt et al. 2006

Table 4.2.2 (continued)

Country	Prov./state/ region	Location	°N lat.	Habitat	Salinity	Years	Method	Approx. min. size counted (cm)	Eel density ^a		Source
									Number/ ha	kg/ ha	
USA	NY	Hudson R tribs below barriers	42	Stream	Fresh	2003-2004	E-fish		6,088	93.5	Machut et al. 2007
USA	NY	Hudson R estuary	42	Tidal estuary	Fresh	1997-1999	CMR	30	11		Morrison and Secor 2004
USA	NY	Hudson R estuary	41	Tidal estuary	Saline	1997-1999	CMR	30	12		Morrison and Secor 2004
USA	VA	Rivers in piedmont & mtn. region	38	Stream	Fresh	1987-1990	E-fish	6	166		Smogor et al. 1995
USA	VA	Rivers in piedmont & mtn. region	38	Stream	Fresh	1987-1990	E-fish	25	106		Smogor et al. 1995
USA	VA	Rivers on coastal plain	38	Stream	Fresh	1987-1990	E-fish	6	1,272		Smogor et al. 1995
USA	VA	Rivers on coastal plain	38	Stream	Fresh	1987-1990	E-fish	25	422		Smogor et al. 1995
USA	MD	Streams	39	Stream	Fresh		E-fish		430		Wiley et al. 2004
USA	GA	Fridaycap Creek	31	Stream	Fresh	1983	CMR	23	182	12.6	Bozeman et al. 1985

^aE-fish - electrofishing, CMR - capture-mark-recapture, GBB - glass bottom boat surveys

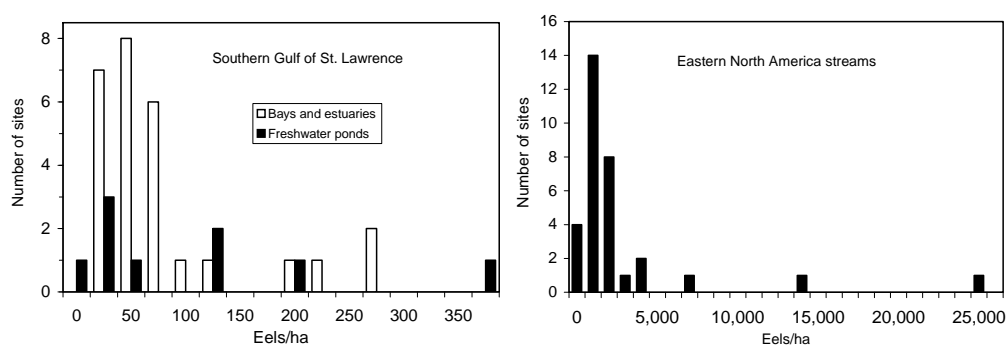


Figure 4.2.1 Frequency distributions of estimated American eel densities. Left panel: in freshwater ponds and in saline bays and estuaries in the southern Gulf of St. Lawrence, right panel: in streams in eastern North America.

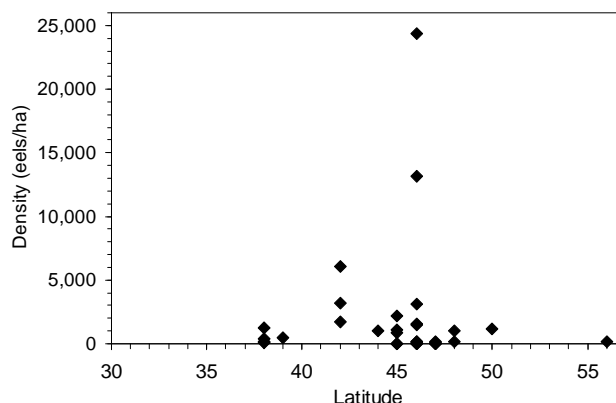


Figure 4.2.1 Estimated densities of American eels in streams in relation to latitude.

4.3 Densities, populations and movements of yellow eels in U.K. estuaries

The saline waters of estuaries, lagoons and coastal waters dominate the potentially eel-producing area of the British Isles. Recent estimates of wetted areas derived for the Water Framework Directive (WFD) suggest that the total area of saline habitats (lagoons, transitional and coastal waters) in England and Wales (excluding cross-border Solway/Tweed RBD), at about 16903 km² (2384 km² lagoons & transitional waters; 14518 km² coastal waters), is about 14 times that of rivers and lakes combined (606 km² of rivers and 585 km² of lakes). However, little is known about the characteristics of eels inhabiting this saline environment, and even less is known of their potential or actual production.

In many inland fisheries, large eels are rapidly removed by commercial fykenetting and the water has to be left for one or more seasons for small residents to grow on and for recruitment of more immigrants (Harrison 1984). Estuarine fyke netting however tends to produce higher average CPUEs, because eels in these productive habitats tend to show good growth rates (e.g. see Table 4.3.1) and numbers are maintained by immigration from adjacent coastal and freshwaters (Harrison 1984; Knights *et al.* 1996; Naismith and Knights 1990a, 1993). McKinnon and Potter (1993) found that 41% of UK commercial eel fishers fish partly or wholly in estuaries and 23% in coastal waters.

Density and biomass data for saline habitats have been principally inferred by proxy catch per unit effort (CPUE) from fyke net surveys, fisheries data and from sampling power station intake screens. Similar data for freshwaters are generally derived from fisheries and from surveys conducted using electric fishing or fyke nets. Surveys typically also collect data on individual size, age, etc., while information on in-river migrations has been collected using counts at pass-traps and mark-recapture (Naismith and Knights 1990b; Knights *et al.* 1996, 2001). Most recently, habitat use and behaviour of yellow eels in estuaries is being investigated using acoustic telemetry (see below).

Detailed studies of eels in saline waters (and associated freshwaters) have only been conducted in four estuaries across England and Wales (Severn, Thames, Mawddach estuaries and Poole Harbour). Table 4.3.1 presents a summary of the population characteristics of eels surveyed from these estuaries, along with similar data from adjacent freshwaters.

Comparison of data from surveys of the tidal reaches of the Rivers Piddle and Frome, and adjacent open waters of Poole Harbour, conducted between 1996 and 2009, suggest changes in population character which might be associated with reduced recruitment, i.e. reducing CPUE and increasing mean size of individuals.

Poole Harbour is a large coastal lagoon in on the south coast of England of ~38km² at high water, ~80% comprising intertidal areas and mudflats, connecting to the English Channel via a narrow entrance. It is relatively shallow and sheltered, has a small tidal range, low fresh water inputs from the Rivers Piddle and Frome and a relatively long flushing time (Knights 1997). Salinity is generally stable at ~18-30, falling to 5 near the river inflows. Water tends to warm quickly in spring and summer and annual temperatures range between 3 and 27°C. Primary production (of salt marsh, macroalgal and phytoplankton communities) and secondary production (based mainly on detritus) are high. Although historically supporting commercial fyke net eel fisheries, these have declined since the 1980s, and ceased altogether since 2008.

Forty-two eels from commercial fyke net catches (11 mm mesh cod end) were examined by the Environment Agency in 1996. In June 2004, 138 eels were caught during fyke net surveys (50 net-end-nights) conducted near the mouths of the Piddle and Frome, distant from the seaward entrance to the lagoon. Most recently, in June, July and August 2009, fyke net surveys (96-128 net-end-nights) using similar nets caught 505 eels in the nearby lower reaches of the River Frome and in adjacent open waters of Poole Harbour, close to the site of the 2004 surveys.

Catch per unit effort (CPUE)

No CPUE data are available for the 1996 Poole Harbour sample. CPUEs in 2004 were 2.8 eels end⁻¹ night⁻¹ and 518 g end⁻¹ night⁻¹, larger than those in the main freshwater Thames (1.4 and 387 respectively) but not dissimilar from the averages in the Thames Estuary (4.5 and 420 respectively) which were both surveyed in the early 1990s (Naismith and Knights 1993, Knights 2005). In contrast, CPUEs (1.29-1.91 eels, 276-400 g end⁻¹ night⁻¹) for Poole Harbour in 2009 were lower across June to August.

'Population' size structure

Commercial-type fyke nets (typically minimum 11 mm mesh size) do not reliably catch eels of L_T <310–320 mm (Naismith and Knights 1990a), although 54 of the 505 eels caught (10.7%) in 2009 measured <300 mm (Walker and Godard, unpublished

data). As such, the following summary size statistics relate to the population component susceptible to capture, rather than the entire local population.

In 1996, eels >450 mm (assumed female) comprised 31% of the Poole Harbour sample, up to a maximum length of 652 mm (Table 4.3.2). The low mean L_T (391 mm), and proportion of eels >450 mm (31%) imply that eel densities were relatively high. The length-class frequency distribution was similar to that of eels fykenetted in the outer and middle reaches of the Thames Estuary (Table 4.3.1).

In 2004, eels >450 mm comprised 43% of Poole Harbour catch and the mean L_T was larger at 439 mm (Table 4.3.2). Measured ages were higher, however, and the mean growth rate was estimated at 40.4 as opposed to 72.8 mm year⁻¹ in 1996. The latter value appears relatively high but age readings were carefully conducted and the majority were judged to be of high certainty (87%), with the remainder of medium certainty (13%).

The discrepancies between 1996 and 2004 may be due to differences in netting locations, timings or methods. However, the >450 mm class accounted for a higher proportion of the June to August catches (41 to 49%) in 2009, and mean lengths for the three monthly samples (441 to 450 mm) exceeded those from the 1996 and 2004 surveys of Poole Harbour (Table 4.3.2).

Growth rates

The average individual growth rate (aged by cracking and burning) in 2004 of 40.4 mm year⁻¹ was relatively high compared to those for the Rivers Piddle and Frome that discharge into Poole Harbour (20.2 and 19.3 mm year⁻¹ respectively), but similar to those in the Estuary (46.7–60.7 mm year⁻¹) and enclosed freshwater sites in the Thames catchment (61.9–66.2 mm year⁻¹) (Table 4.3.1). They are also similar to values found in warm productive estuaries/coastal lagoons in Europe (Vøllestad 1992, Moriarty and Dekker 1997, Melia *et al.* 2006) and even the Baltic Sea and Curonian Lagoon in Lithuania (Lin *et al.* 2007). No destructive sampling was conducted in 2009, and as a consequence no growth data are available for comparison with earlier years.

Comparison with local freshwater eel populations

Studies have begun recently into the level of exchange of eels between the estuary and rivers, using microchemical analysis of otoliths. The population structure of the 2004 Harbour sample was similar to that determined by electrofishing in the in-flowing River Piddle, but contemporaneous samples from Tadnoll Brook (a tributary of the in-flowing Frome) had a larger proportion of smaller eels; the mean L_T was 284 mm and only 51% were female (Bark *et al.* 2007). Mean growth rate in the 2004 Harbour samples was double that in both river samples, implying more favourable growth conditions, e.g. due to higher habitat productivity and temperature regimes.

The Piddle has shown significant declines in eel population densities over the last 25–30 years (Knights *et al.* 2001; Bark *et al.* 2006, 2007). Although these might presumably be due to reduced recruitment, the eel population in the neighbouring Frome has not shown similar changes, despite similarities in the catchments, and the fact that the mouths of the two rivers in the Harbour are only ~750 m apart. The Frome has a higher discharge and it is possible that differences in tidal currents that flow through Poole Harbour may influence the direction of upstream migration of those eels seeking freshwater.

Quantitative estimates of population size and structure

Quantifying eel populations in open and/or saline waters is complicated by difficulties in catching and representatively sampling eels in these environments, and not least by relatively low numbers of recaptures. One possibility for the latter may be that the eels are highly mobile within this environment and so only rarely susceptible to capture at fixed sampling points.

Recent acoustic tracking of 22 yellow eels in the tidal reaches of the Rivers Piddle and Frome, and adjacent open waters of Poole Harbour (Walker and Godard, submitted), suggested limited roaming during autumn and winter (Oct to Jan), with eels generally remaining within 150 m from site of original capture. In contrast, eels moved far greater distance during the summer months, with some travelling 3500 m between sites on the two rivers within a few days. Since the same eels were detected in both rivers and the open harbour often within the same 24 h period, it is assumed that the area comprises a single eel 'stock'. However, the eels certainly appear to have home ranges, since most made repeated journeys around sections of the study area, often returning to the same locations within 24–48 hours.

Most eels were detected at fixed automatic receivers on an almost daily basis, and analysis of the detection data suggests that fishing for 2 to 4 consecutive nights should offer a >90% of recapturing a high proportion of the tagged eels. However, a recapture rate of only 5.6% has been achieved during fykenetting of the same, relatively confined area in 2009, with a fishing rate of 100–130 net-ends per night per month across June, July and August (Walker and Godard, in prep). Of course, the *a priori* analysis of detection rates assumed that detection equals susceptibility to capture, but the detection range of the receivers (~100 to 200m line of sight) is presumed to be considerably larger than the effective 'hinterland' of each set of fykes. Fykes were set parallel to the flow direction and close to the shore (2–5 m). The study area is frequently used by a range of vessels and it is not possible to deploy nets in the middle. Also, tidal streams and freshwater outflow rates are considerable and it would be impossible to deploy nets perpendicular to the flow direction.

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Table 4.3.1. Summary population characteristics of eels surveyed by a range of fyke nets in English and Welsh saline habitats and associated freshwaters – a preliminary list of survey datasets. Surveys were conducted variously between the early 1990s and 2009.

	Habitat type ¹	CPUE		Mean length	Sex ratio	Growth rate	Survey method ²	Ratio B/SW: FW ¹
		eel/end/night	g/end/night	mm	% F	mm/yr		
Thames catchment ³								
Outer estuary (polyhaline)	SW	4.6	1040	490	95–100	46.7	FN	1.21
Middle estuary (mesohaline)	B	7.8	992	445	10–30	60.7	FN	1.57
Upper estuary (oligohaline)	FW	9.4	818	400	2–15	54.3	FN	1.41
Non-tidal main river/tributaries	FW	1.9	492	590	95–100	38.6	FN	[1.00]
FW reservoir & lake	FW	0.5	210	610	100	64.1	FN	1.66
B/FW migrants	B/FW	-	-	22	-	33.8	PT	0.83
Severn catchment								
Upper Severn Estuary ⁴	B	-	-	441	69	30.8	FN	1.79
Upper Severn Estuary ⁵	B	-	-	392	-	47.7	PS	2.77
R. Severn (Upper Estuary tributaries) ⁴	FW	-	-	300	9.5	18.5	EF	Mean 17.2
R. Severn (Upper Estuary tributaries) ⁶	FW	-	-	212	5	15.9	EF	[1.00]
B/FW migrants ⁷	B/FW	-	-	96	-	11.8	PT	0.72
Poole Harbour (1996) ⁸	SW/B lagoon	-	-	327	-	72.8	EF	3.67
Poole Harbour (2004) ⁶	SW/B lagoon	2.8	518	439	98	40.4	FN	2.04
Poole Harbour (2009) ⁹	SW/B lagoon	1.29 – 1.91	276 – 400	441 – 453	-	-	FN	-
R. Piddle ⁶	FW	-	-	416	94	20.2	EF	Mean 19.8
Tadnoll Brook ⁶	FW	-	-	284	51	19.3	EF	[1.00]
Mawddach Estuary ⁶	SW	1.4	131	360	31	24.5	FN	1.33
R. Wnion ⁶	FW	-	-	265	11	18.4	EF	[1.00]
Slapton Ley ⁶	FW lagoon	1.8	328	448	88	26.7	FN	1.44
Rs. Gara & Start ⁶	FW	-	-	250	58	18.6	EF	[1.00]

Key: ¹SW = marine, B = brackish waters, FW = freshwater; ²FN = fykenetting, PT = pass-trap, PS = power station filter screen, EF = electric fishing; ³Naismith and Knights (1993); ⁴M. Aprahamian (unpublished data); ⁵ Bird *et al.* (2008); ⁶ Bark *et al.* (2007); ⁷ White and Knights (1997); ⁸ Knights (1997); ⁹ A. Walker and M. Godard (unpublished data).

Table 4.3.2 Summary of Poole Harbour eel sample data, collected from fishermen by the Environment Agency in August-September 1996, and scientific surveys from 90 fyke net ends in June 2004 (Bark *et al.* 2007), and 96 to 128 fyke net ends in June to August 2009 (Walker and Godard, unpublished).

	Modal L _T mm	% of sam- ple	Mean L _T and range (mm)	Age (years)	Growth rates (mm year ⁻¹)
EA sample August-September 1996 (N = 42, all aged, modal L _T = 340 mm)					
Whole sam- ple	327	100%	391 ± 100 (244 – 652)	5.0 ± 2.8 (3 – 16)	72.8 ± 23.8 (25.5-126.7)
Females > 450 mm	-	31%	540 ± 70 (450 – 652)	8.6 ± 3.2 (2 – 16)	63.4 ± 22.0 (25.5-126.7)
Other eels (< 450 mm)	-	69%	345 ± 47 (244 – 429)	3.9 ± 1.3 (3 – 7)	75.8 ± 35.8 (26.0 – 119.7)
Survey June 2004 (N = 138, 63 aged (44 > 450 mm), modal L _T = 380 mm)					
Whole sam- ple	439	100%	439 ± 113 (149 – 805)	8.9 ± 3.0 (4 – 19)	40.4 ± 12.7 (14.1 – 74.2)
Females (> 450 mm)	-	43%	542 ± 80 (453 – 805)	9.8 ± 3.0 (6 – 16)	49.8 ± 10.7 (32.6 – 67.7)
Other eels (< 450 mm)	-	57%	398 ± 60 (149 – 448)	8.6 ± 2.9 (4 – 19)	36.4 ± 11.3 (14.1 – 74.2)
Survey June 2009 (N = 199)					
Whole sam- ple	-	100	453 (231–806)	-	-
Females (> 450 mm)	-	49	557	-	-
Other eels (< 450 mm)	-	51	354	-	-
Survey July 2009 (N = 183)					
Whole sam- ple	-	100	441 (192 – 857)	-	-
Females (> 450 mm)	-	41	566	-	-
Other eels (< 450 mm)	-	59	354	-	-
Survey August 2009 (N = 123)					
Whole sam- ple	-	100	450 (257–845)	-	-
Females (> 450 mm)	-	44	562	-	-
Other eels (< 450 mm)	-	56	363	-	-

4.4 An estimate of the standing stock of yellow eels in saline waters of the southern Gulf of St. Lawrence

Introduction

The number of American eels entering the upper St. Lawrence River and Lake Ontario has declined by >99% since 1985 (COSEWIC 2006). The collapse of recruitment to this area was a major factor that contributed to the decision by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) to assess the American eel as a species of Special Concern in Canada.

The ability to analyse strontium (Sr) and calcium (Ca) concentrations along radial transects of extracted eel otoliths has provided new insights into the movement patterns of American eel between freshwater and marine areas (Morrison *et al.* 2003, Lamson *et al.* 2006, Jessop *et al.* 2007, Thibault *et al.* 2007b). These studies have demonstrated the capability of American eels to occupy fresh, brackish, or marine areas for the duration of their growth phase, while a portion of individuals moves between freshwater and marine areas. This observation suggests that a review of traditional thinking is required about the importance of freshwater vs. marine rearing habitat for eels.

Electrofishing and mark-recapture are most common methods of estimating eel densities. In saltwater areas, possible methods of capture are limited as conventional electrofishing equipment cannot be used in areas of high salinity. To date, relatively little research has been done to estimate the densities of American eels in saltwater areas (Helfman and Bozeman 1984, Bozeman *et al.* 1985, Ford and Mercer 1986, Morrison and Secor 2004). Morrison and Secor (2004) discussed the difficulties estimating eel densities in saline areas, including variable structure habitat (i.e., depth and substrate) commonly found in these areas and the selectivity of commonly used sampling gear (i.e., seines, fyke nets, bottom trawls and eel traps). Commonly used mark-recapture surveys are typically very time-intensive and often have low recapture rates in large saline areas (Morrison and Secor 2004, Thibault *et al.* 2007a). These survey designs also do not allow eel observations to be linked to habitat parameters at a fine scale. To address these problems, a glass bottom boat methodology was developed to survey eel distributions and densities within sheltered bays and estuaries in the southern Gulf of St. Lawrence.

The glass bottom boat method is limited to the visual range of the observer, which is typically 2.5 m or less in southern Gulf of St. Lawrence waters. In comparison to other sampling methods, glass bottom boat surveys allow for measurements of environmental variables, such as water depth, substrate, vegetation type, and percent cover, in association with observations of individual eel locations. The behavioural response of individuals to the sampling gear can also be observed using the glass bottom boat method.

Methods

Glass bottom boat (GBB) surveys are conducted at night, when eels are most active, along transects that follow a zigzag pattern across a water body. GBB surveys were conducted in 2005–2008 in tidal bays and estuaries of the southern Gulf of St. Lawrence.

The glass bottom boat is 3.95 m in length and is fitted with a tempered glass viewing window at the bow (Figure 4.4.1). Six LED lights are attached to the bottom of the boat to the front and the side of the viewing window. The survey crew consisted of an observer who lies prone, looking through the glass viewing area, and a boat opera-

tor. Propulsion is supplied by a battery-powered trolling motor. At one site (Basin Head, Prince Edward Island), the GBB was rowed because motorized vessels are not permitted.

During transects, observations of depth and bottom cover were recorded on audio recording equipment at 15 s intervals. These observation times were signalled by the beep of a timer. Water depth was estimated by the observer with the aid of indicator weights suspended by cords of 100 cm and 150 cm length which were attached to the side of the viewing window. In water deeper than 2 m, depth was also recorded using an echosounder whose transducer was located adjacent to the glass viewing area. Percent cover of macrophytes was represented as the 2-dimensional cover of each vegetation type that occurred within the survey area for a given 15 s transect interval. Total percent cover could not yield greater than 100% cover in adding together all independent measures of percent cover for each vegetation type that was present.

Eel observations were recorded on audio recording systems at the time they were seen and included an estimate of total length (cm) and behaviour at the initial and at the final time of viewing, according to three categories (resting, slow swimming, fast swimming). Locations were determined with a global positioning unit (GPS) which transmitted data to an electronic recording device.

The GBB was equipped with parallel cords mounted on either side of the viewing window, and about 20 cm below the boat's hull. These strings indicated the edge of the visual field to be included in the transect. Eels seen outside the marker strings were considered to be outside the transect and were not included in calculations of eel density. Width of transect increased with water depth. The relation of transect width to water depth was calculated from observations of measuring rods placed on the seafloor under the GBB at various water depths. At 50 cm depth, the transect was 105 cm wide and at 100 cm depth, the transect was 150 cm wide. Transect width did not increase beyond 150 cm because the beam provided by the LED lights did not illuminate a broader area with depths beyond 100 cm.

Data analysis was based upon the observational information recorded for each 15 s interval. Each 15 s interval was treated as a survey quadrat, and the length of each quadrat was generated from the distance between locations of consecutive 15 s intervals. Width of quadrats were multiplied by the length to give quadrat area. Areas where the substrate could not be effectively surveyed (too deep, poor visibility, bottom obscured by vegetation) were excluded from density calculations.

Transect data had two features that precluded simple parametric estimation of mean eel densities and of confidence limits to those densities. First, the distribution of eel densities across quadrats was strongly non-normal (and non-Poisson), and second, eel densities at some sites showed significant spatial autocorrelation along transects. These problems were addressed by aggregating quadrats into larger blocks (to mitigate spatial autocorrelation) and by Monte Carlo estimation of means and confidence limits (to mitigate distributional problems). We implemented these procedures in custom software written in QuickBASIC (Microsoft Inc., Redmond, WA).

The basic approach was to combine adjacent quadrats into blocks (of length $L = 1, 2, 3, \dots$). Consider a transect which includes sets of contiguous valid quadrats, separated by quadrats for which eel density could not be assessed. Thus a stretch of $S = 11$ valid quadrats can be seen as 11 blocks of length 1, of 10 possible blocks of length 2 (of which at most 5 can be placed without overlap), and in general $S-L+1$ possible blocks of length L (of which at most the integer value of S/L can be placed without overlap).

The entire transect will include $B = \sum (S_i - L + 1)$ blocks, where there are S_i quadrats in each stretch of valid quadrats and the sum is taken over all stretches.

For any value of L , a Monte Carlo estimate of eel density can be obtained by repeatedly sampling B blocks (with replacement) from the B blocks available, and calculating an (area-weighted) mean across Monte Carlo replicates. In addition, 95% confidence limits on this estimate are given by the 2.5th and 97.5th percentiles of the distribution of Monte Carlo density estimates. For $L = 1$ this is equivalent to a bootstrap estimate of eel density directly from the raw quadrat data, and is in agreement with a parametric estimate of mean eel density, although the confidence limits are better than parametric ones because they take into account the true distribution of eel densities across quadrats.

Basing an eel density estimate on larger blocks of quadrats ($L > 1$) reduces the influence of spatial autocorrelation on the calculated confidence limits, because as L increases, adjacent blocks are less likely to suffer from non-independence in eel densities. However, as L increases, the number of usable blocks also decreases. Furthermore, quadrats located near the ends of valid stretches are increasingly under-sampled, because blocks that might include them are disallowed for overhanging the end of the stretch. (To see this, consider a quadrat at the end of a stretch. Just a single possible block of length L contains this quadrat, whereas a quadrat in the middle of a long stretch of valid quadrats belongs to L different possible blocks.) The best choice of L is the smallest value that overcomes spatial structure in the density data (no measurable autocorrelation between adjacent blocks).

To measure spatial structure remaining for data aggregated into blocks of length L , we computed two test statistics: the Pearson correlation coefficient r , and the standard χ^2 quantity for tests of independence. In each case, we identified each possible pair of adjacent blocks in a transect (these pairs overlap, because the second block of one pair can be the first block of another). For Pearson's r , we computed the correlation between eels densities in the first and second blocks of our adjacent pairs. For χ^2 , we classified each block as having eels present or absent, and computed the χ^2 value for the corresponding 2x2 contingency table. Because of the overlapping pairs of blocks, we could not use standard critical values to assess r or χ^2 values. Instead, we compared them to Monte Carlo draws of pairs of blocks, in which each block was sampled with replacement from the set of B possible blocks in the transect. These draws have no spatial structure and thus form an appropriate null hypothesis for adjacent pairs; and a P-value for r or χ^2 is simply the fraction of Monte Carlo values as extreme as or more extreme than the actual value.

The two statistics (r and χ^2) measure slightly different aspects of spatial structure, and we chose to suspect the existence of spatial structure when either measure was statistically significant ($P < 0.05$) for $L=1$. In such a case, we checked larger values of L , using the first L for which neither r nor χ^2 was significant. This procedure is slightly conservative (because the two measures do not covary perfectly, meaning that in the absence of spatial structure one measure or the other will have $P < 0.05$ more than 5% of the time), but allows us to retain sensitivity to multiple aspects of spatial structure.

Estimates of mean eel densities and confidence limits were derived from glass bottom boat surveys conducted in provincial districts (Gulf New Brunswick, Gulf Nova Scotia, Prince Edward Island). The Monte Carlo density estimates generated for each survey were sampled with replacement for 1000 bootstrap resamplings for each province. Provincial mean densities were estimated by taking the mean of all resampled Monte Carlo replicates. The mean across multiple surveys was also taken within pro-

vincial Monte Carlo replicates for sites that had multiple surveys conducted. The 2.5th and 97.5th percentiles of the distribution of the provincial mean Monte Carlo density estimates were used to generate 95% confidence limits.

In order to understand the differences among sites in each province, mean eel densities by site were generated by taking the mean eel density by survey and variance from bootstrap results for each survey. In the instance that multiple surveys were conducted at a site location, the mean eel density across surveys was generated and individual standard deviations were used to generate a pooled estimate of variance. A one-way ANOVA was then run to examine the difference between mean eel density estimates by site among the provincial districts.

Populations of yellow eels in saline waters were estimated by provincial district as the product of mean eel densities and estimated eel habitat. Eel habitat was derived from a habitat classification scheme based on degree of exposure to the open sea (see sections 2.6 and 2.7 of this report). This system classified waters as Sheltered, Semi-exposed, and Exposed. In brief, Sheltered waters were identified by moving, on a GIS map layer, a circle of 1.5 km diameter into an inlet. The points where the circle first touches the sides of the inlet are termed headlands. A straight line is drawn between the headlands. All waters upstream of this line are considered Sheltered. Semi-exposed waters are defined by a similar method, but using a 15 km circle. Semi-exposed waters are those between headland-headland lines derived from 15 km circles, and the seaward boundary of Sheltered waters. Exposed waters are all other marine waters. In this paper, Sheltered waters are considered to be eel habitat.

The proportion of Sheltered waters in various depth categories (0–2 m, 2–3 m, 3–4 m, 4–6 m, and 6–10 m) was assessed by creating depth contour lines on a GIS layer from rasterized nautical charts, and measuring area between depth contours within the Sheltered zone. At time of writing, only data for Prince Edward Island are available.

Results

Thirty-two GBB surveys were conducted at 27 sites in 2005–2008 in Gulf New Brunswick, Gulf Nova Scotia, and Prince Edward Island (Table 4.4.1, Figure 4.4.2). There were two surveys in 2005, four surveys in 2006, 12 surveys in 2007, and 14 surveys in 2008. Prince Edward Island was the only province to have multiple surveys conducted at the same site.

Eleven GBB surveys were conducted in Gulf New Brunswick in 2007–2008 (Table 4.4.1). The provincial bootstrap mean eel density estimate across all sites surveyed was 34.1 eels/ha with 95% confidence limits of 23.0–45.5 eels/ha (Table 4.4.2). In Gulf Nova Scotia, six surveys were conducted in 2007–2008, and the provincial bootstrap mean eel density was 40.9 eels/ha with 95% confidence limits of 24.8–57.3 eels/ha. On PEI, 15 surveys were conducted at 10 sites in 2005–2008, and the provincial bootstrap mean eel density was 155.7 eels/ha with 95% confidence limits of 86.3–235.9 eels/ha. These density estimates are preliminary, and will vary slightly in further analysis which will use 10,000 rather than 1,000 bootstrap iterations.

Estimated mean densities differed significantly among provincial districts (ANOVA, $F = 7.34$, $P = 0.0003$) (Tables 4.4.1 and 4.4.2). Mean eel densities in PEI sites were significantly higher than those of Gulf New Brunswick and Gulf Nova Scotia (Tukey's studentized range test, $P \leq 0.05$).

Sheltered waters, as defined by the habitat exposure classification system, were measured as 46,254, 22,505, and 57,136 ha, in Gulf New Brunswick, Gulf Nova Scotia, and Prince Edward Island, respectively (Figure 2.7.7). The majority (65.9%) of Shel-

tered water on PEI was between 0 and 2 m depth. Waters between 2–3 m, 3–4 m, 4–6 m, and 6–10 m depth accounted for 9.1%, 8.5%, 9.6%, and 6.9%, respectively, of Sheltered waters on PEI.

Based on Sheltered habitat measurements and mean densities from GBB surveys, yellow eel standing stocks were estimated to be 11,399,103 individuals in saline waters of the southern Gulf of St. Lawrence (Table 4.4.2). The population estimate for Prince Edward Island makes up 78% of the total population estimate in comparison to New Brunswick and Nova Scotia which make up 14% and 8% of the total population estimate, respectively.

Discussion

Virtually all eels seen on GBB surveys are within a few cm of the bottom (Hallett *et al.* unpubl.). Therefore GBB surveys require that the observer be able to clearly see the bottom. Factors that contribute to inability to see the bottom include turbidity due to suspended sediments, dissolved organic carbon, phytoplankton, and macrophytes. These factors also inhibit light penetration to the bottom from the LED lights. Surveys were typically conducted in spring and early summer in order to avoid dense macrophyte growth which typically occurs later in the season. Visibility conditions typically limited maximum survey depth to water depths of 2 to 2.5 m. Eel standing stocks were estimated on the assumption that densities estimated from survey data applied to all water depths in the Sheltered zone. Most (65.9%) of Sheltered habitat on PEI is shallow (≤ 2 m). The fact that densities were not generally measured in waters deeper than 2.5 m is a source of uncertainty in population estimates.

Eels typically hide in the daytime by burying themselves in the substrate. However timing and patterns of daily movements in and out of substrate have not been documented for any eel species. It is therefore possible that some eels may be buried in the substrate, and therefore not available to be counted, during GBB surveys. Densities estimated by this method are therefore considered to be minima.

Eel movements between fresh and salt water have been observed in many regions, including the Maritime Provinces (Medcof 1969, Jessop 1987, Jessop *et al.* 2002, Lamson *et al.* 2006). The proportion of the population that takes part in these movements, and the seasonality of these movements occur, will need to be factored into more detailed population estimates for eels from both fresh and saline areas in the southern Gulf of St. Lawrence.

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Table 4.4.1. American eel mean densities and confidence intervals from glass bottom boat surveys conducted in saline waters of the southern Gulf of St. Lawrence between 2005 and 2008. Estimates of the mean and 95% confidence intervals were derived from 1,000 bootstrap re-samplings at the level of survey.

Site	Province	Year	Bootstrap Block Size	Density (eels/ha)		
				Mean	95% C.I.	
					Lower	Upper
Pokemouche River Estuary	NB	2008	9	51.34	29.11	75.92
Tracadie Bay	NB	2008	1	62.45	37.53	87.35
Baie-Sainte-Anne	NB	2008	2	22.36	9.96	35.98
Tabusintac River Estuary	NB	2008	2	31.74	18.02	48.47
Kouchibouguac River Estuary	NB	2007	6	38.71	10.16	72.5
Northwest Branch Richibucto Estuary	NB	2008	1	34.72	17.18	54.06
St. Nicholas River Estuary (Richibucto)	NB	2007	1	58.85	22.07	105.25
Village Bay	NB	2008	1	31.99	16.88	51.35
Cocagne River Estuary	NB	2008	3	17.25	4.68	36.45
Shediac Bay	NB	2008	1	10.02	0	25.58
Kinnear River Estuary	NB	2008	1	19.21	5.96	32.85
Pictou Harbour	NS	2008	1	18.49	4.52	37.35
Little Harbour	NS	2008	1	47.62	26.88	71.62
Merigomish Harbour	NS	2008	1	40.69	24.65	56.7
Tracadie Harbour	NS	2008	1	14.87	2.9	29.21
Pomquet Harbour	NS	2008	2	55.03	37.33	75.16
Margaree River Estuary	NS	2007	1	67.57	44.06	92.91
Mill River Estuary	PEI	2007	1	190.95	91.88	313.74
Trout River Estuary (Roxbury)	PEI	2007	1	75.77	34.67	125.33
Grand River Estuary	PEI	2007	1	49.2	23.69	75.51
New London Bay	PEI	2007	1	53.65	22.87	87.15
Hope River Estuary	PEI	2007	1	259.88	152.42	378.3
Hunter River Estuary	PEI	2007	2	246.4	160.74	344.36
Wheatley River Estuary	PEI	2007	1	124.14	74.94	179.46
Covehead Bay	PEI	2007	1	76.72	39.65	120.03
Covehead Bay	PEI	2006	1	19.75	0	52.48
Morell River Estuary	PEI	2007	1	703.39	526.47	878.3
Morell River Estuary	PEI	2006	2	276.34	185.06	388.78
Morell River Estuary	PEI	2006	2	276.16	194.86	364.23
Basin Head Lagoon	PEI	2006	1	29.41	9.84	54.2
Basin Head Lagoon	PEI	2005	1	91.54	47.46	139.66
Basin Head Lagoon	PEI	2005	2	89.95	52.07	131.13

Table 4.4.2. American eel standing stock estimates of yellow eels in saline waters of the southern Gulf of St. Lawrence as calculated from glass bottom boat surveys. Estimates of the mean and 95% confidence intervals were derived from 1,000 bootstrap re-samplings at the level of survey and province.

Province	Sheltered area (ha)	Density (eels/ha)		Estimated eel population (# of eels)	Percent of total population estimate (%)
		Mean	±95% C.I.		
New Brunswick	46,254	34.1	23.0 - 45.5	1,579,504	14
Nova Scotia	22,505	40.9	24.8 - 57.3	920,833	8
Prince Edward Island	57,136	155.7	86.3 - 235.9	8,898,766	78

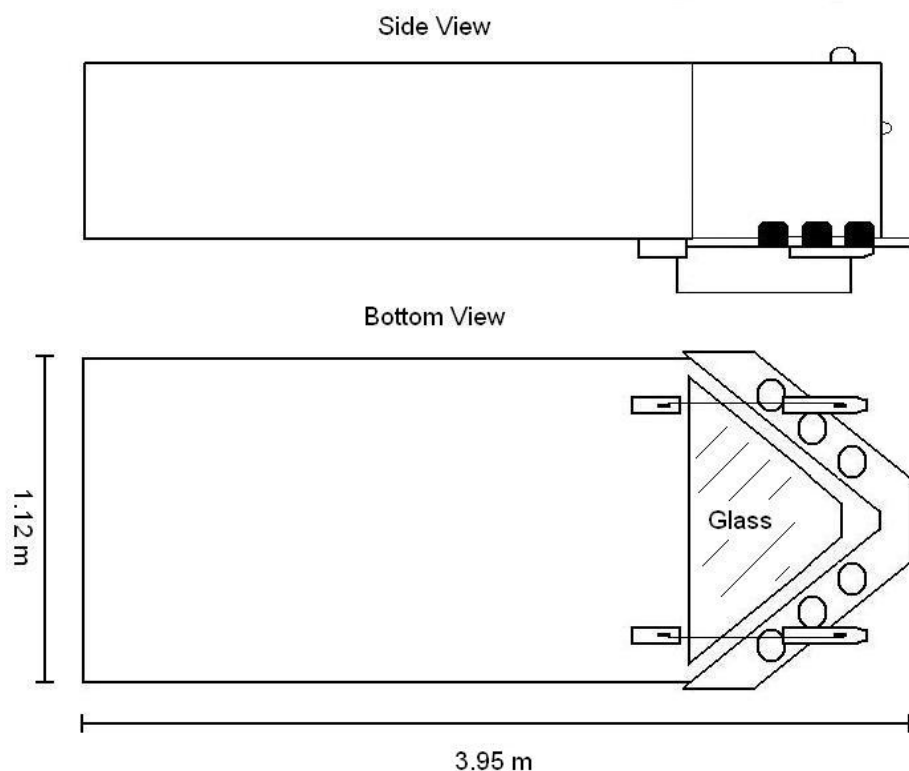


Figure 4.4.1. Schematic diagram of the glass bottom boat.

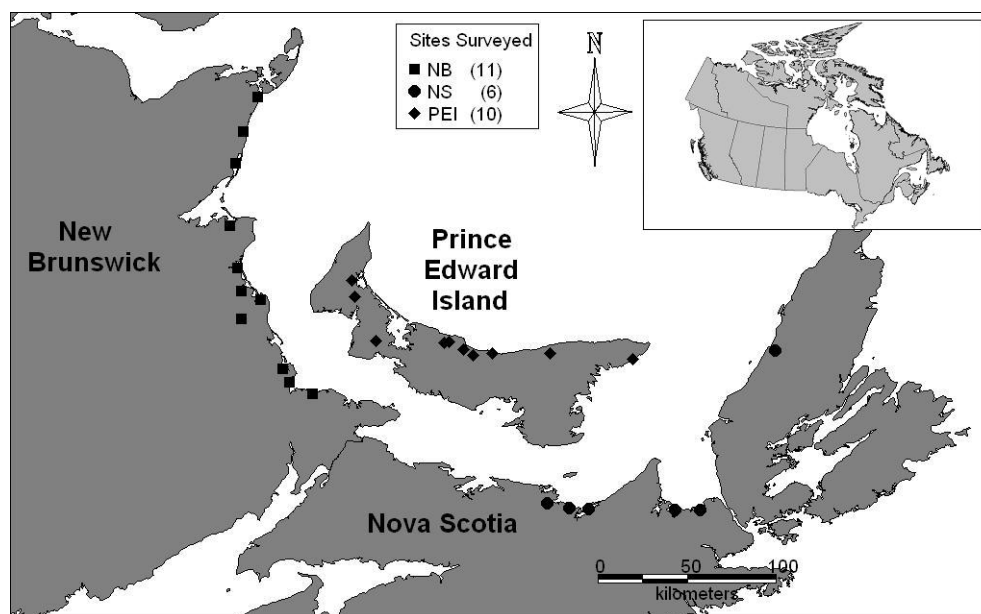


Figure 4.4.2. Location of glass bottom boat survey sites in the southern Gulf of St. Lawrence.

4.5 Fyke nets as a survey tool

Fyke nets are a common gear for capturing anguillid eels in both commercial and research fisheries. Researchers may use fyke net catches for estimating biological parameters of local populations, for tracking abundance trends, or for mark-recapture population estimates. Size selectivity of fyke nets and the relation between fyke net

catch per unit effort (CPUE) and its standard deviation were examined using data from western Ireland.

In 1987 and 1988, 2,614 eels were captured in fyke nets, marked and released. The proportion of these eels which were recaptured in fyke nets increased from nil at length 30–35 cm to over 0.2 at length 60–65 cm (Figure 4.5.1).

Based data from >20,000 net-nights, the standard deviation of CPUE increased linearly with CPUE (Figure 4.5.2). Increasing the number of fyke nets in a chain of nets from five to 10 did not decrease standard deviation of CPUE (Figure 4.5.3). This suggests that increasing chain length does not assist in achieving accurate estimates. Instead, more locations or more fishing nights may be more helpful in producing accurate estimates. A power analysis indicates that the sample size required to achieve a given precision in CPUE is strongly influenced by population density. Overall, CPUE is an insensitive tool with wide variation in numbers and weight per net. A relatively high effort is required to attain tight precision in CPUE.

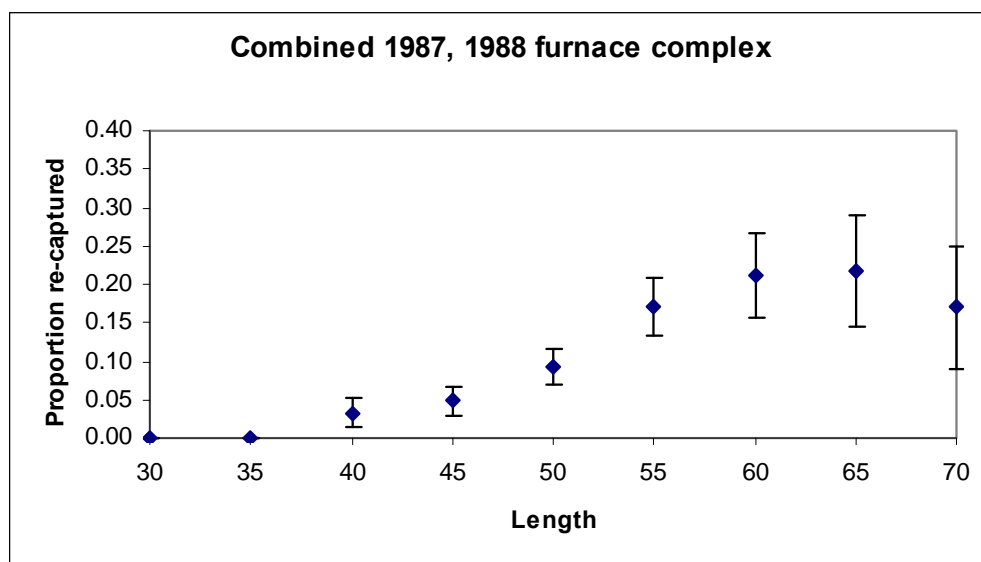


Figure 4.5.1. Proportion of European eels re-captured in fyke nets in relation to length.

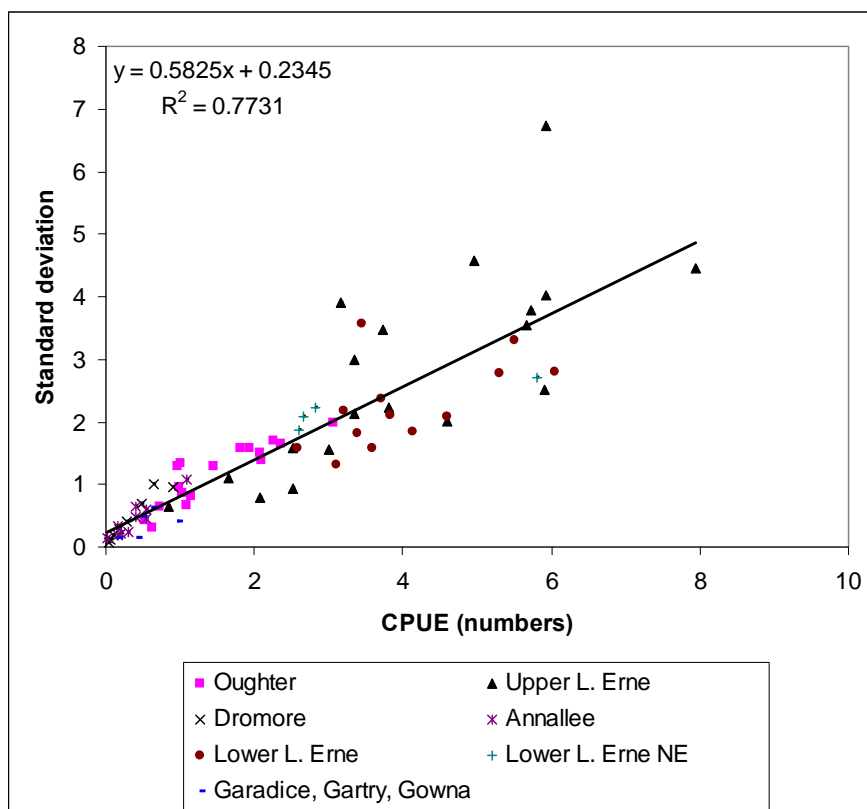


Figure 4.5.2. Relation between the standard deviation of 5 fyke chain CPUE and CPUE.

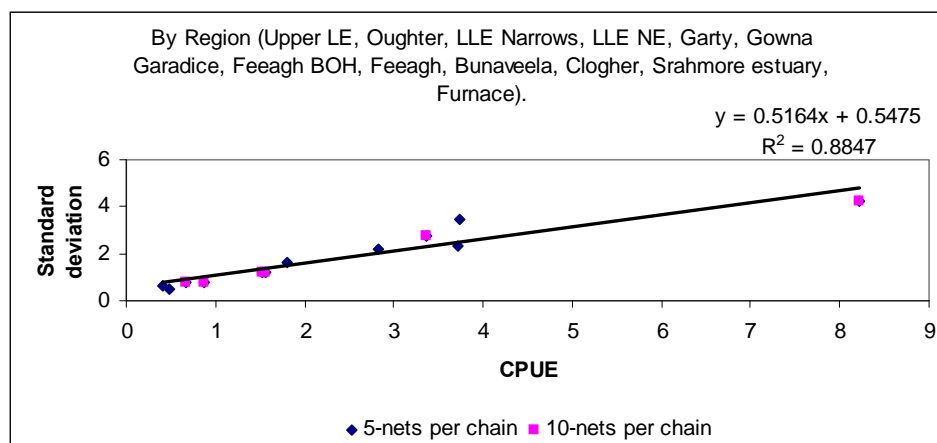


Figure 4.5.3. Relation between standard deviation and CPUE for fyke nets with 5 and 10 nets per chain.

4.6 Characterising the ecology, productivity and stability of saline eel populations in Northern Ireland

This project aims to characterise the ecological status of eels residing along salinity gradients (estuarine) and in full salinity (sea-lough) habitats in Northern Ireland. The existence of different putative migratory components will be examined using carbon and nitrogen stable isotope analysis, fatty acid analysis and Sr:Ca analysis of otolith microchemistry. A range of indices including fatty acid analysis, growth rates, sex ratios, condition indices and age structure will be used to examine inter-population

differences. Intra-population catadromy will be examined using carbon and nitrogen stable isotope analysis and a more in-depth resolution will be achieved through Sr:Ca analysis of otolith microchemistry.

Eel abundance throughout the different habitats will be assessed using mark/recapture techniques utilizing PIT (Passive Integrated Transponder) tags. Additionally, the proportion of catadromous and facultatively catadromous individuals will be examined through Sr:Ca analysis and stable isotope analysis, providing an insight both into the reliability of the abundance estimates, and as to the habitat residency profile within populations.

Samples of *A. anguilla* will be obtained from two estuaries and four sea-loughs in Northern Ireland; Rivers Foyle and Bann and Lough Foyle, Carlingford Lough, Larne Lough and Strangford Lough respectively. The habitats have been chosen based on their potential to contain populations of eel, whilst each site has unique ecological features which may contribute to the identification of factors which influence eel productivity.

Research of this nature has yet to be implemented in Northern Ireland despite the economic (Moriarty 1999, Mathews *et al.* 2001, Rosell *et al.* 2005) and conservational (Dekker *et al.* 2003) issues associated. Increasing concerns over decreasing catches by the Lough Neagh Fishermen's Co-operative Society paralleled with decreased recruitment of glass eels (Rosell *et al.* 2005) has highlighted the need for increased insight into Ireland's eel productivity and associated population distribution. The location of the eel fishery at Toomebridge, Lough Neagh, is such that a large area of putative eel habitat exists between the fishery and the sea in the River Bann. Examination of this riverine productivity, combined with examination of the tributaries to the Lough Neagh catchment, may provide an insight into the long term sustainability for the fishery whilst examining the effect of habitat shifting within the catchment.

The use of Sr:Ca ratios in otolith microchemistry (Tsukamoto *et al.* 1998, Daverat *et al.* 2006), and carbon and nitrogen stable isotope analysis (Harrod *et al.* 2005), has provided useful insight into the life history migratory components of diadromous eels. However, considering the financial expense of laboratory analytical techniques used to examine Sr:Ca ratios, the proposed research aims to simultaneously examine the use of stable isotopes analysis in relation to Sr:Ca ratios. As a result, we hope to make recommendations to a suitable cost-effective means by which to examine large numbers of individual life histories whilst retaining high experimental resolution.

Initial results from this report (Table 4.6.1.), and previous studies (Harrod *et al.* 2005) suggest that eel abundance varies in sites from western Ireland compared to those of eastern Ireland. We aim to examine this observation further through investigating and comparing a variety of sites from the east and west coasts of Ireland.

The study aims to provide insight into the ecological stability of eels along a salinity gradient and within saline waters, whilst considering the end application of the results, i.e. the provision of additional management advice for an EMU by taking into account those eels found in transitional waters.

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Table 4.6.1. Catch per unit effort ((catch/net no)/net hours) of *A. anguilla* from three Irish saline habitats; Camas Bay, Ireland (Harrod *et al.* unpublished); and Larne and Strangford Loughs, Northern Ireland (current study).

	Camas Bay (Western Ireland)	Larne Lough (Eastern Ireland)	Strangford Lough (Eastern Ireland)
CPUE	0.22	<0.01	<0.01
Standard deviation	0.1453	-	-
Salinity (psu)	34	34	34

4.7 The European eel in Portuguese brackish waters: a general overview

Introduction

This chapter presents an overview of biological and ecological aspects of eels in Portuguese brackish water systems, and reviews the effects of some anthropogenic activities on the population. The most important topics include: abundance and distribution and its relation with predation and competition, activity and condition of eels, fisheries, contamination by trace metals, and infection by the parasite *Anguillicoloides crassus*.

Biological and ecological aspects of eels in Portuguese brackish waters

- Abundance and distribution

Abundance of eels in saline waters is poorly documented, but it is possible that variation in the physiography and depth of the estuary associated with habitat complexity, similarly to what happens in freshwater (Domingos *et al.* 2006), can provide a variety of habitat conditions likely to influence ontogenetic preferences.

An analysis of eel abundance studies conducted in three Portuguese estuaries (River Mondego, River Tagus and River Mira) with different sizes and shapes, indicated

that abundance varies along the systems, possibly explained by biotic and/or abiotic conditions, as observed in freshwater habitats (Domingos *et al.* 2006).

In the Tagus estuary, eels seem to be absent from the adjacent marine waters (Cabral *et al.* 2000), rare near the river mouth (Costa 1980), abundant in the middle estuary, and declining to the upper estuary (Costa *et al.* 2008a). In the middle estuary, but at sites located at similar distances from the sea, larger eels are in the deeper stretches of the main canal, whereas smaller eels occupy shallower habitats in marginal areas (Costa *et al.* 2008a). These results are consistent with observations by Moriarty (1987) who argued that eels are almost absent from coastal areas and river mouths to avoid predation and competition for space and food.

In contrast, in the Mira estuary, eels are present close to the river mouth, rare in the middle estuary, and more abundant in the upper estuary (Costa *et al.* 2008b). These results differ from observations in the Tagus estuary, but the causes of this pattern of abundance seem to be related to predation/competition by the Lusitanian toadfish, *Halobatrachus didactylus*, a dominant and voracious predator with the same benthic habits as eels, which competes for space and food. In the river mouth, eels are absent from bare sediments (toadfish density being 80.5 ± 15.0 individuals/ha) but occur in seagrass beds, mainly in intertidal *Zostera noltii* beds, where the density is 47.0 ± 9.5 eels/ha against 1.1 ± 1.1 toadfish/ha. In subtidal *Zostera marina* beds densities were 13.5 ± 6.6 eels/ha, against 29.0 ± 8.6 toadfish/ha (Costa *et al.* 2008b). In the middle estuary, where toadfish is very abundant, the eel is rare (toadfish density is $>79.8 \pm 21.6$ individuals/ha and eel density is $< 2.2 \pm 0.1$ individuals/ha), whereas in the upper estuary, where the toadfish is rare (5.6 ± 3.9 individuals/ha), eel density starts to increase (5.1 ± 0.2 individuals/ha). These results suggest that protection from predation and competition for space may be responsible for the contrasting abundance pattern observed.

In the Mondego estuary, a microscale analysis in the middle estuary showed that abundance varied according to habitat features, namely type of substrate and cover, which are determinants of the distribution and abundance of the species. The presence of a sampling site close to slaughter house wastewater input, which can be considered an outlier because abundance was much higher (2.7 eels/fyke net/night) than in all sites sampled (< 1 eel/fyke net/night) (Domingos 2003), indicates that caution needs to be taken on sampling design to estimate eel density. The results obtained show that to be accurate, density estimates have to take the diversity of habitats into account, i.e., distance from the sea; marginal versus deep stretches; vegetated versus bare sediments, etc.

Other factors that may contribute to modify distribution and abundance of eels in Portuguese brackish water systems include predation by birds and mammals. Apart from the Lusitanian toadfish and the European eel, which can display cannibalistic behaviour, the main predators of eels in Portuguese brackish water systems include the cormorant, *Phalacrocorax carbo*, and the European otter, *Lutra lutra*. The eel is present in the diet of otters and cormorants throughout the year, but it becomes more important in spring and summer when the water level is lower (Trigo 1994, Cerqueira 2005, Dias 2007). The impact of predation on the eel population is unknown but eels represented 25.4% of the diet of otters from Ria Formosa (Cerqueira 2005), a shallow coastal lagoon, located in the south of the country, and 7% of the diet of cormorants from Minho estuary (Dias 2007).

- Activity, and condition of eels - Comparison with freshwater

Activity of eels in the Mondego estuary decreases during winter, whereas in freshwater their activity decreases not only during winter but also during summer, as high temperatures associated with low river flow contributes to reduce oxygen and habitat availability, due to the reduction in water depth and river width (Domingos 2003). In contrast, brackish water eels are more active at the beginning of spring and end of summer, when temperature becomes more favourable.

Consistent with their activity, condition of eels in the Mondego catchment is lowest in winter for brackish water systems, while for freshwater the condition is low during summer and winter. These differences in activity and condition, between freshwater and brackish water habitats, should be taken into consideration when implementing management/conservation actions for the eel population.

Anthropogenic impacts in Portuguese brackish waters

- Fisheries

Eel fisheries in brackish waters are operated by small boats (less than 9 m long) with open decks, and with the help of a variety of fishing gears whose maximum number and characteristics are set by laws regulating eel fishing, in the most important brackish water fishing areas. Fisheries are directed at yellow eels and the minimum legal size is 22 cm in all brackish waters, except in the Minho estuary where it is 20 cm. It is permitted to fish all year round and fishermen are obliged to report their catches in auction markets where landings are taken. This fishery is particularly important in coastal lagoons. Eel landings from Santo André Lagoon indicate that amongst the 14 fish species fished, *Anguilla anguilla* is the most important species both in abundance and economic value. Another example of the importance of the species in coastal lagoons is Óbidos Lagoon where total landings (1.845 kg) in 2008 represented 27% of national landings.

The glass eel fishery was prohibited in 2000, except in the River Minho where it is still permitted. Nevertheless, illegal fishing is conducted in most river basins and remains a problem despite the action of the authorities.

- Contamination by trace metals

Human pressures in estuaries may result in some negative impacts on the population, other than fishing. Concentrations of Cd, Cu, Hg, Pb and Zn in the liver of *A. anguilla* was determined in a survey conducted in five brackish water systems (Aveiro Lagoon, Óbidos Lagoon, Tagus estuary, Santo André Lagoon and Mira estuary). The results showed that eels from Portuguese brackish systems are slightly contaminated when compared to other European countries (Neto 2008, Passos 2008).

- Infection by *Anguillicoloides crassus*

Another problem resulting from anthropogenic activities (most likely the trade of live eels) is the spread of the parasite *A. crassus*. A study conducted in the same five brackish water systems mentioned above revealed that this parasite is present in all but one system, the Óbidos Lagoon (Neto 2008, Passos 2008). Prevalence ranged from 0 to 100% and intensity from 0.4 to 5.8, but there were significant differences within and among systems. The absence of the parasite in the Óbidos Lagoon as well as from the most saline site in the Tagus estuary, suggests that the infection rate (survival of the parasite) decreases with salinity (Neto *et al.* in press), implying that eels from estuarine areas are better potential spawners. As a consequence, protection of estuarine eels should be regarded as a conservation measure and management of the stock should consider protecting these eels/areas.

Conclusions

In conclusion, when compared with freshwater, eels from Portuguese brackish water systems are influenced by stronger anthropogenic impacts, namely more intense fishing pressure, predation and competition, and heavier contamination loads, despite having displayed lower trace metal concentrations than in other European catchments. However, contrary to freshwater, their activity is not reduced during summer months, which contributes to a better condition of eels in brackish water systems. Additionally, the infection by the parasite *A. crassus* seems to decrease with salinity, which implies the lower part of estuaries should be classified as protected areas. Finally, Portuguese estuaries are free from obstacles to migration, in opposition to freshwater where these obstacles increase density and competition, and lead to an artificial manipulation of sex, favouring male production, which can have negative effects on a declining population.

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4.8 Geographical and seasonal patterns in yellow eel CPUE in Sweden

Monitoring of coastal fish communities in Sweden has a history going back to the 1960s. It was initiated mainly to monitor potential effects of the nuclear power plants established on the east and west coasts of Sweden. A number of reference areas, with a low degree of human impact, were also monitored for purposes of comparison. Some of these reference areas were eventually integrated into a system of national reference areas for coastal fish monitoring, with a focus on fish communities in shallow coastal habitats. Fyke nets of the same type used in the commercial eel fishery were selected as the standard fishing gear for monitoring in the Öresund, Kattegat and Skagerrak reference areas. Consequently, the abundance of yellow eel has been, and continues to be, well monitored in these areas since a long time back.

On the other hand, fishery independent data for yellow eel in the Baltic Sea are scarce. Other net types are used as the standard gear for monitoring in the Baltic Sea reference areas. Some data are available however. Since the late 1990s sampling for length and age of eel was combined with collecting data on effort and unsorted catches of yellow eel in the commercial fyke net fishery. Although not independent, these data indicate relative densities in Swedish Baltic Sea coastal areas.

This document gives a brief overview of the geographical distribution of yellow eel in Swedish coastal habitats. Existing data on seasonal, vertical, as well as open sea abundance are also presented, and possible reasons behind a mismatch between trends in recruitment and yellow eel abundance are suggested.

Materials and Methods

Test fishing with fyke nets following a standard protocol (Andersson 2009) has been performed annually since the late 1970s in April and August in Barsebäck in Öresund and Vendelsö in Kattegat. Monitoring started at Fjällbacka in Skagerrak in 1998, and has since been performed annually in August and October–November. In these areas fixed stations are fished repeatedly during a period of 6–12 days in each season. In the reference areas Lysekil, Älgöfjorden and Kullen, a larger number of stations are selected randomly, although stratified by depth within specified geographical boundaries. In this case, each station is normally fished one single night in each survey and surveys are normally carried out in August and October. The major part of the data presented represent shallow coastal waters, from a depth range of 2–5 m. Coastal survey data from deeper bottoms (20–30 m) exist for the areas Fjällbacka and Vinga and the offshore shallow banks Fladen and Lilla Middelgrund in Kattegat were surveyed in 2003–2004 (Table 4.8.1, Figure 4.8.1). Stratified random sampling was applied also in these surveys.

Each station is fished with two or more fyke nets linked together. The number used is dependent on the depth and the local topography, and the fyke nets may be set perpendicular to the shoreline, as well as in chains in open and deeper water. The catch per unit effort (CPUE) is always defined as numbers per single fykenet-night. The fyke net is 0.55–0.60 m high at the entrance with a 10–11 mm bar length in the finest meshes of the cod end. A 5 m leader is fixed in front of the entrance of each fyke net.

Length and age data has been collected annually from Swedish commercial landings of yellow eel in the Baltic Proper. As the legal size limit for landing was 60 cm in the Baltic Sea, sampling covered all sizes big enough to be caught by the fishing gear. Along with this sampling the total effort spent to retrieve the sample was collected. Thus the relative abundance could be estimated in the same way as in the fishery independent survey data from the west coast. This estimate may be positively biased however, as the yellow eel is the single target species in this fishery.

The average CPUE from existing fishery independent surveys during 2002–2006 is presented here from sites on the Swedish west coast, separated according to depth, season, and distance from shore. Commercial data from 2002–2005 were used to estimate relative abundance in the Baltic Proper.

Results and discussion

Average relative abundance (from here onwards referred to as CPUE) of yellow eel in six different shallow sites on the Swedish west coast was estimated to 0.6–1.4 individuals during the warm season of the year. CPUE in spring or fall was 0.1 individuals or less in the same areas. CPUE was similarly low in coastal sites deeper than 20m, in summer as well as in late autumn. Two data sets from the spring season and one from summer revealed a similar seasonal pattern for yellow eel CPUE on open sea banks in the Kattegat area as in the shallow coastal zone. CPUE of yellow eels in one single survey of the Fladen area in the Kattegat in late summer of 2003 was estimated to 0.4.

Commercial CPUE ranged from 0.06 to 0.30 in ICES subdivisions 25 and 27. In contrast to survey data from the west coast, the estimates were highest in the early season and decreased with time during the season. The highest CPUE estimate from the Baltic Proper was well below the range observed on the west coast. Survey data from a single sheltered bay in the archipelago area of the northern Baltic Proper present a CPUE of 0.03 eels in spring, corresponding to 1.8 kg/ha biomass, estimated from a mark-recapture experiment (Adill and Andersson 2005).

Data on the habitat preference of yellow eels from one site in the Öresund area indicated a preference for mosaic gravel and vegetation bottom types, in favour of sandy areas with a low degree of vegetation cover. With the exception of this data, information on the habitat preferences of eels is scarce from marine areas in Sweden. General observations made during coastal fish monitoring indicate a preference for shallow habitats, rich in vegetation, but this needs to be confirmed.

The general picture of decreasing yellow eel recruitment all over Europe is reflected also in the recruitment index from Ringhals in the Kattegat (Anon. 2008). In contrast to this negative trend in recruitment, relative abundance of yellow eel adults increased significantly in the nearby reference area Vendelsö over the period 1976–2008. A warmer climate and probably also a reduced fishing pressure are suggested as drivers of this process.

Conclusions

- Marine yellow eel CPUE is higher in shallow coastal habitats on the Swedish west coast than in similar habitats of the Baltic Proper
- Offshore shallow banks are also inhabited by yellow eel
- A preference by yellow eel for habitats with vegetation is indicated
- There is no evident relationship between recruitment and yellow eel CPUE on the Swedish west coast

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Table 4.8.1. Yellow eel CPUE in survey sites on the Swedish west coast 2002-2006.

Period	Area	Coastal shallow (2-5 m)		Coastal deep (20-30 m)		Open sea banks 10-20 m	
		summer	spring/fall	summer	fall	spring	summer
2002-2006	Fjällbacka	1,15	0,12		0,01		
2002-2005	Lysekil	1,41	0,18				
2002-2006	Älgöfjorden	0,71	0,21				
2002-2006	Vendelsö	1,43	0,09				
2002-2006	Kullen	0,72	0,14				
2002-2006	Barsebäck	0,62	0,05				
2004-2006	Vinga			0,07	0,03		
2003-2004	Fladen					0,02	0,42
2004	Lilla Middelgrund					0,01	

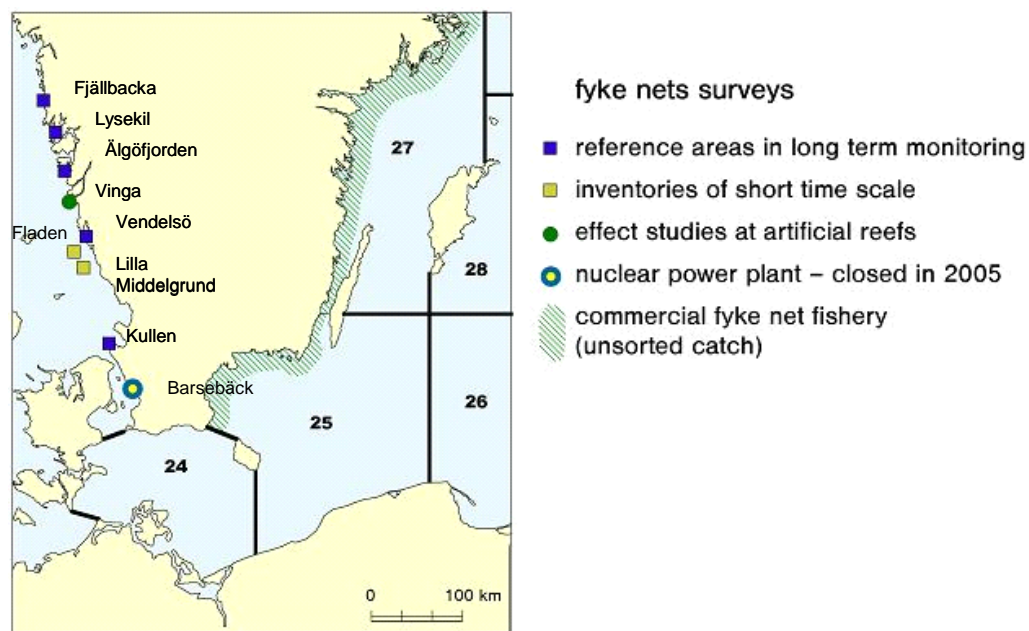


Figure 4.8.1. Sites with data on CPUE from fyke net surveys on the Swedish west coast (rings and boxes). Commercial CPUE is obtained from the hatched area on the Baltic coast.

4.9 The unexpected lack of a freshwater origin in most silver eels leaving the Baltic Sea

The European eel has decreased all over Europe since the late 1970s. Stocking programs have been implemented in Sweden to enhance the eel populations and to support an eel fishery as well. The pigmented elvers used were imported from France

and the UK. In addition, domestic yellow eels of medium size were used for stocking in both freshwater lakes and in brackish coastal waters. Recently and in accordance with the Council Regulation (EC) No 1100/2007, "Establishing measures for the recovery of the stock of European eel" Swedish authorities are trying to improve the eel stock through stocking with the final aim of increasing the escapement of spawners.

Previous work (Wickström 2001) indicated that stocked eels do survive, grow and become migrating silver eels at predicted rates. Stocked eels are now quite common and dominate eel populations in many lakes where natural recruitment is low. But do stocked eels contribute to the spawning stock? This was questioned in a series of papers by Westin (cf. Westin 2003) based on tagging experiments with silver eels from a stocked population. A few case studies indicate that silver eels with a probable stocked origin are present among eels caught in or near the main outlet from the Baltic Sea, such as in the Sound (Öresund) between Sweden and Denmark (Limburg *et al.* 2003). Approximately 27% of the analysed eels were stocked, (20% were stocked in freshwater and 7% in brackish water), and 31% were from freshwater. That study was based on small sample sizes and it is therefore desirable to obtain more robust data on this important issue.

Recent data suggest that the proportion of stocked and freshwater origin silver eels in the Öresund area is lower than was reported by Limburg *et al.* (2003). In 2003 a total of 800 silver eels was collected from the commercial fishery for silver eels on both sides of the Öresund. Four hundred fifty silver eels were also sampled from the commercial fishery from nine sites representing seven Swedish lakes and 125 eels were collected from the commercial catch at five sites along the Swedish Baltic coast (Figure 4.9.1). After dissection, sexing and ageing, the fat content in muscle was analysed and otoliths were prepared for Sr/Ca analysis with WDS (wave-length dispersive x-ray spectrophotometry) in collaboration with Uppsala University (Clevestam and Wickström 2008). The eels were then classified into six life history types according to the temporal changes in the Sr/Ca-ratios in their otoliths, to evaluate the contribution of stocked eels to the silver eel run out of the Baltic Sea. The ratio between fresh- and brackish water grown eels was also of interest.

Approximately 800 silver eels from Öresund were analysed. It was found that 95% of the eels were females and no males were found in the 450 freshwater eels. Eels sampled from freshwater were larger and in most cases older than those caught in Öresund. The mean length and age in the Öresund sample were 650 mm and 12.0 years, respectively. The largest eels (874 mm in average) were found in Lake Ymsen. The oldest eels (18.6 years on average) came from one site in Lake Vänern.

Stocked and non-stocked eels from Öresund with some freshwater experience were on average 32 mm larger than those from brackish water. The eels from brackish environments were on average fatter than those from freshwater, with fat content approximately 32% (w/w) from one site in the Baltic Sea and about 25% (w/w) in Lake Ringsjön as the extremes. However, fat content was variable among individuals and was not significantly different among sites ($p > 0.05$).

The different types of life histories were classified according to the temporal changes in Sr/Ca ratios beyond the metamorphosis check (Figure 4.9.2). Six major types were found for the eels collected from Öresund. Brackish water eels dominated (>65 %) the samples (Figure 4.9.3). True catadromous eels (freshwater residents) constituted only 8% of the total eels examined, while 3% must have been stocked to freshwater as elvers. It was also found that eels stocked as medium sized yellow eels coming directly from the marine environment to freshwater could be readily distinguished.

These eels constituted less than 2% of the sample. More than 7% of the eels were stocked as elvers in freshwater but then left for brackish water. “True interhabitat shifters” between fresh and brackish water constituted almost 5% of the eels analysed. However, both elvers and yellow eels stocked in the brackish Baltic Sea were difficult to distinguish from natural recruits using Sr/Ca transects with 30 spots only (Figure 4.9.2).

Age, size and fat content differed among the six life history types. The catadromous eels were the largest, fattest and oldest, while eels stocked in freshwater were the leanest, the smallest but one and sexually not as well developed as the catadromous ones. Eels from brackish water were often quite small and not that well-advanced in their sexual maturation (small eyes, high “digestive tract index” etc.).

Despite all uncertainties we tried to estimate the minimum proportion of stocked eels in the material from Öresund. In total 21% originated from stocked eels, i.e. a figure that corresponds quite well with the findings of Limburg et al (2003). Eight percent were natural recruits and the remaining 70% were of unknown, mostly brackish water origin.

As about 1 000 000 elvers are successfully stocked annually in Sweden it was assumed and hoped more of them subsequently would show up among the silver eels trying to leave the Baltic Sea through Öresund. In many lakes most eels originate from stocked eels and fairly large numbers have been stocked also in the brackish environment. Still the proportions of stocked eels in general (21%) and of eels from freshwater in particular (20%) were unexpectedly low.

There are several alternative interpretations to these results:

- Stocked eels (mainly from freshwater) are fished before arriving in the Öresund area
- Stocked eels do not migrate and behave as expected and are therefore not fished efficiently
- Eels from freshwater in general do not migrate and behave as expected and are therefore not fished efficiently
- Naturally recruited eels are more common than expected in comparison with stocked eels

This study will be continued to shed further light on the above possible interpretations. In one ongoing field experiment, eels with a known proportion of stocked eels were tagged with external tags in Lake Mälaren (Sjöberg *et al.* 2008). Some of the stocked eels were also tagged with DST (data storage tags) to obtain more detailed information about their migration. So far, very few of these eels have been recaptured outside the lake along the Swedish East Coast. Instead they seem to roam around in the lake, often migrating in the wrong direction. However, all of the eels recaptured along the coast will be analysed by otolith microchemistry to understand their habitat use and migratory behaviour. In the future more elements will be analysed by ICPMS or PIXE and if required also using stable isotopes to better understand detailed migratory environmental history and to increase the discrimination, precision and accuracy among life history groups.

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Figure 4.9.1. The sites from where silver eels were sampled for this study. The five coastal sites along the Baltic coast are not shown.

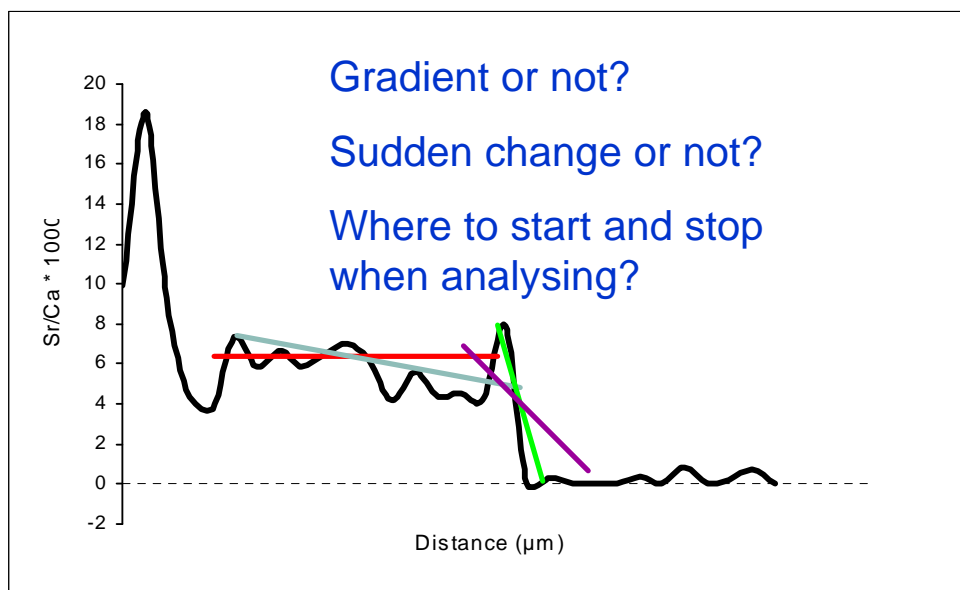


Figure 4.9.2. Hypothetical temporal changes in Sr/Ca in the otolith from an eel caught in freshwater. The difficulties in interpreting the conceivable environmental life history are illustrated. (The metamorphosis check is the first peak of the curve and the elver check is the first trough. Both are referred to in the text).

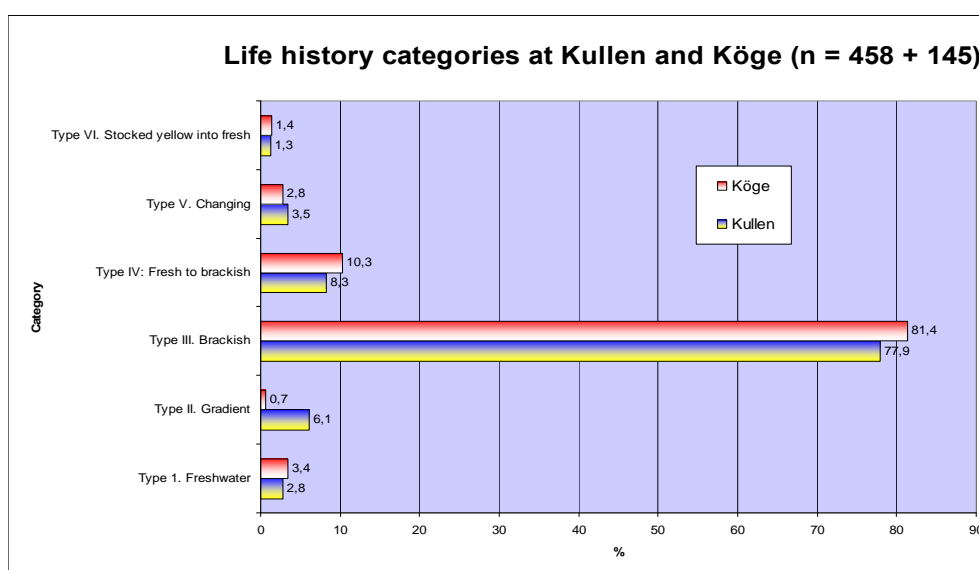


Figure 4.9.3. The composition of the different life history types of eels leaving the Baltic Sea as classified by otolith Sr/Ca ratios. (The total numbers of eels examined are approximately 800).

4.10 Historic eel surveys in the German Bight of the North Sea

As indicated by high commercial eel landings and high glass eel recruitment, European eel stocks appeared to be in good condition in the 1960s and 1970s.

Beginning in 1964, a trawl fishery on eel was conducted in the German Bight. The eels were fished as alternative to cod and flatfishes depending on season and economic yields possible. By intensifying fishing pressure, the eel catches from coastal waters increased by about 100% from approximately 160 tons to more than 300 tons per year

(Aker and Koops 1979). This eel trawl fishery lasted for about 15–20 years and was stopped in the 1980s.

The sizes of the fishing vessels were mainly between 16–24 meters with 150–250 hp engines (Aker and Koops 1974). Eel was mainly fished at water depths between 10–50m. Eel trawl fishing was usually operated between the mid-May and mid-November. More than 50% of the annual catches were realized during August and September (Aker and Koops 1974).

In the late 1960s and the 1970s several scientific surveys were conducted in the German Bight and in the lower reaches of relevant river systems. The purpose of these surveys was to support the eel fishery by finding new fishing grounds and to develop new fishing gears. Further, different studies dealt with biological aspects of eels in this area. Unfortunately, most of the results have never been published in the international literature and are thus not available to a broader readership. Therefore, the results of the most relevant studies are summarized in this abstract (Aker and Koops 1973, 1974, 1979; Löwenberg 1979).

Scientific trawl surveys conducted in different water depths indicated that the number of smaller eels varied with the water depth with higher numbers of small eels present in depths of 11–18 m than in deeper areas (20–24 m). The absolute number of bigger eels in the catches was similar but about twice as many smaller eels were caught in the shallower areas compared to deeper areas (Löwenberg 1979).

The population was dominated by yellow eels, indicating that the German Bight was used by eels as a feeding habitat during that time. The proportion of silver eels in the catches varied throughout the fishing season, reaching a maximum with 25% in November (Löwenberg 1979).

Population estimates

Löwenberg (1979) estimated the population density of eels in the part of the German Bight where the eel trawl fishery was concentrated (south-east of the isle of Helgoland), with two different methods.

The first estimate was simply based on the catches of eels by trawling, which were related to the area fished (distance fished multiplied by width of trawl net). By using the simplistic assumption of a 100% gear efficiency this method resulted in a population estimate of about 2.57 million eels with a biomass of 424 tons (20 ind./ha, 3.3 kg/ha).

The second estimate was based on a more indirect calculation. The catches of the commercial fishery were combined with the size distribution from scientific trawls. A comparison between commercial eel landings and scientific trawl surveys had shown that the eel size distribution was similar for commercial and scientific catches. The combination of catch statistics (biomass) and size distribution was used to calculate the numbers of eels in each size group, which were caught by the commercial fishery. Further, tagging studies had shown a gear efficiency of about 30% (Aker and Koops 1973). By integrating this rate as a correction factor the population size was estimated as 1.85 million eels with a biomass of 323 tons (14 ind./ha, 2.5 kg/ha).

Both results must be considered as more or less rough estimates. These estimates could only be applied to the study area (south-east of the isle of Helgoland), since eels seemed to prefer these areas and the commercial fishery favoured this area because of the higher eel harvest compared to other parts of the German Bight. The methods obviously had some weaknesses (e. g. the assumption of 100% gear efficiency of the

scientific trawls). However, both approaches resulted in similar population size estimates and may provide an idea about the order of magnitude of the eel population size in the German Bight in the 1970s. This could be of particular interest, since the pre-1980s period can potentially be used to estimate the reference status in the frame of Eel Management Plans.

Tagging experiments – habitat use

From 1968 to 1973, nearly 15 000 eels were tagged in the North Sea and in the lower reaches of rivers draining into the North Sea. Depending on the aims of the respective experiments, the fishes were either released at the original place of capture or they were transplanted to another habitat. Data on recaptures were recorded from scientific trawls as well as from the commercial fishery. The main results of the tagging experiments (Aker and Koops 1973) can be summarized as follows:

- For eels living upstream of the tidal limit, no migration to the coastal waters was observed.
- Eels in the tidal area of rivers (studied river: Eider) mainly stayed in the river; only a few were recaptured in coastal waters.
- Rivers were preferred for overwintering by those eels which live nearer to the coast during summer, whereas eels living more off-shore tend to overwinter in deeper areas near the isle of Helgoland.
- Eels transplanted from rivers into the sea returned to freshwater (but not necessarily to the same river). No such homing was observed for eels transplanted from the sea to freshwater.
- Part of those eels being found in the shallow parts of the sea at Büsum during summer were moving towards deeper and more distant areas in late autumn; others entered rivers. Rivers located southward were preferred.
- In autumn, the Büsum-fishing-grounds were passed by eels migrating northward to the river Eider.
- It was obvious that eels in the German Bight were more or less vagabonding; yet a homing tendency could be observed when transplanting eels from shallow areas near the coast to more distant areas and vice versa.

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4.11 Eels in bottom trawl surveys in the North Sea

Introduction

The stock of the European eel is in decline: in the past six decades, fishing yield has gradually shrunk to below 20% of former levels; since 1980, recruitment has declined to a few percent (Dekker 2004a, FAO/ICES 2008). The European Union has established a management plan (EU 2007), aiming at protection and recovery of the stock.

According to this plan, each Member State must develop a management plan for the part of the eel stock on its territory, aiming at a uniform restoration target (Dekker 2008a, 2009a). These management plans cover inland waters, and may or may not cover the coastal waters; the latter are also covered by the Common Fishery Policy, but inclusion in national plans will integrate the management of coastal and inland waters.

Interest in eel in the Netherlands has been restricted almost exclusively to fresh water habitats, though it is well known that eel and eel fisheries occur in marine waters too. The Dutch Eel Management Plan (Min LNV 2008) refers to encompassing the eel stock in coastal waters, but it does not provide any detail and does not include coastal waters in habitat estimates. Tien and Dekker (2004) quantified the habitat available for eel, but ignored all marine waters.

The objective of this paper is to quantify the abundance of eel in the southern North Sea on the basis of research surveys, to describe its distribution and historical trend in abundance, and to relate that to the inland stock.

Material and methods

The Demersal Fish Survey (DFS) is an ICES-coordinated beam trawl survey in the coastal areas of the southern North Sea, held annually in (Aug) - Sept-Oct, with records spanning the years 1970–present (2008). A data set of eel catches was kindly supplied by ICES working group Beam (chair Ingeborg de Boois, pers. comm.). Figure 4.11.1 presents the spatial distribution of eel catches.

The fishing gear is a beam trawl of either 3-m (in sheltered areas) or 6-m width (in exposed areas), equipped with a single tickler chain and a bobbin rope. Mesh size scales down from 35 mm in the front of the net to 20 mm in the cod-end. Hauls of 15 minutes duration are made at 2–3 knots; fished surface is $\frac{1}{3}$ ha and $\frac{2}{3}$ ha for the two gear types, respectively. The sampling protocol is fixed, essentially since 1970. The Belgian and (most) UK data do not contain any eel; assuming that eels caught have not been recorded, all data from these countries have been excluded. The remaining data set comprises nearly 20.000 hauls, a total number of 5.472 eels, with a mean length of 34 cm and a mode at 28 cm.

In order to analyse the spatial distribution and temporal trend in the abundance of eels in the DFS, a generalised linear model of the abundance (catch per haul) of eel was designed, taking year, region (Belgian coast, Dutch coast, German Bight, Scheldt estuary, Dutch Waddensea and German/Danish Waddensea), water depth and distance to the coast as explanatory variables. Note that only Dutch (not Belgian) data were used for the Belgian coast region.

Results

From 1970 to 1980, abundance fluctuated without trend (Figure 4.11.2); in the years 1980–1985 abundance peaked, to decline subsequently to an all-time low in 2008.

The spatial distribution of the predicted abundance shows a steep gradient in abundance going off the coast, exacerbated by water depth and the difference between regions (Figure 4.11.3). The range of abundances within the map spans nearly two orders of magnitude (1:93), which is about the same as that between the highest and the lowest year (1:60). That is: the best location in 2008 has a roughly equal abundance as the worst location in 1982. On the basis of this analysis, and knowing the surface area swept by the fishing gear, the total number of eels in the sampling area is estimated at 222 ton in 1982, sloping down to approx. 3 t in 2008.

Conclusions

The time trend in abundance found in the DFS data corresponds reasonably well to the trend in glass eel abundance (Dekker 2004a, 2008b), taking into account that the eels sampled by DFS are a few years older. It does not correspond well to the trend in landings for Europe (Dekker 2003) and for Lake IJsselmeer (Dekker 2004a), or to the trend in stock abundance found in Lake IJsselmeer surveys (Dekker 2004b). The declines observed prior to 1980 are not reflected in the DFS data.

The eel in the southern North Sea is distributed in a small coastal fringe, extending less than 20 km offshore. Since abundance declines rapidly with distance offshore, and sampling extended a few kilometres beyond the furthest observation, it seems highly unlikely that major concentrations have been missed, though Aker and Koops (1974) describe an offshore eel fishery in deeper waters south of Helgoland, with a total annual yield of approx 300 t, which ceased after a few years.

The estimate of the total stock in the survey area based on areas swept by the 20 mm (cod-end) trawl is in the same order of magnitude as the commercial landings of eel from marine areas in the Netherlands (Dekker 2009b). For Lake IJsselmeer, however, the catch per surface area of a 20-mm meshed beam trawl is approx. 15 times lower than that of a 2-mm meshed, electrified beam trawl (see Dekker 2004b for a description of these gears). Tentatively assuming that a 20-mm meshed trawl (as applied in the DFS) underestimates the true eel stock abundance by a factor of at least 15, the total coastal stock is estimated at >3.250 t in 1982 and >44 t in 2008, which is in reasonable agreement with the reported fishing yield.

Reported landings from inland waters in the Netherlands are currently estimated at approx. 800 t (Dekker 2009b), while landings from marine waters are only 19 t. The current analysis suggests that the eel stock in marine waters is in the order of >44 t standing stock, that is: the 19 t landing is probably not a great underrating of the true catch. It is therefore concluded, that the eel stock in marine waters constitutes a minor fraction of the total stock around the Southern North Sea.

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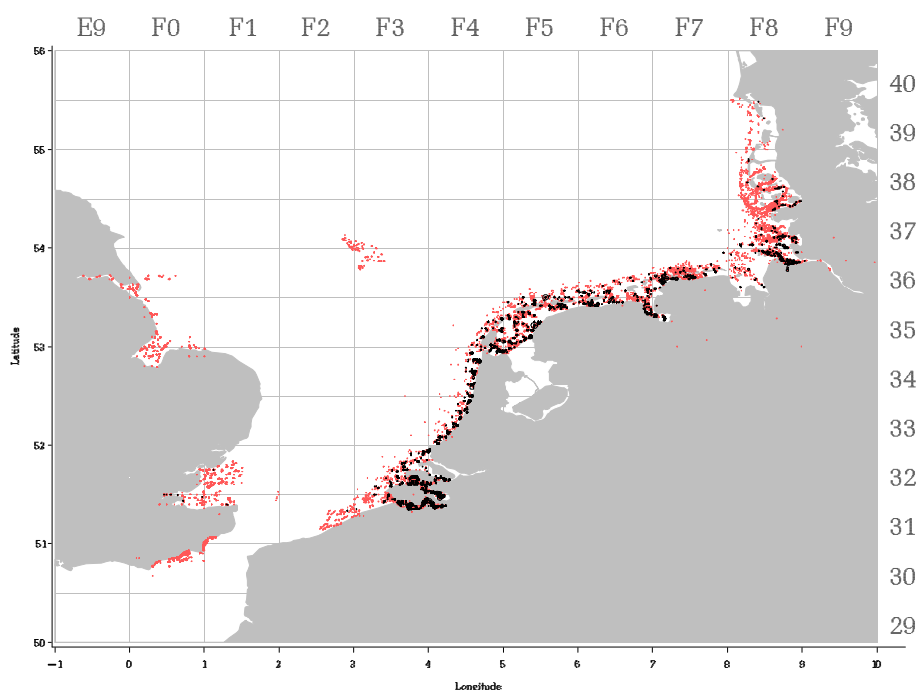


Figure 4.11.1. The distribution of the Dermersal Fish Survey sampling in the southern North Sea since 1970. Red dots indicate a zero observation; black circles are proportional to the number of eels recorded. The all-zero records from Doggerbank and English coasts, and records from Belgian research vessels on the Belgian coast, were excluded from further analysis.

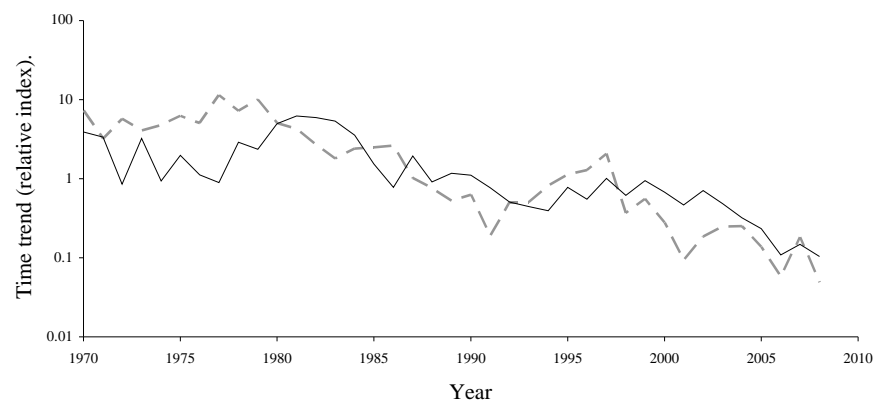


Figure 4.11.2. Time trend in eel catches in the DFS (solid), after correction for region, water depth and distance to the coast. For reference, the trend in the Den Oever glass eel index has been added (dashed, data from Dekker 2009b). Note that the vertical axis is on a log scale for both series.

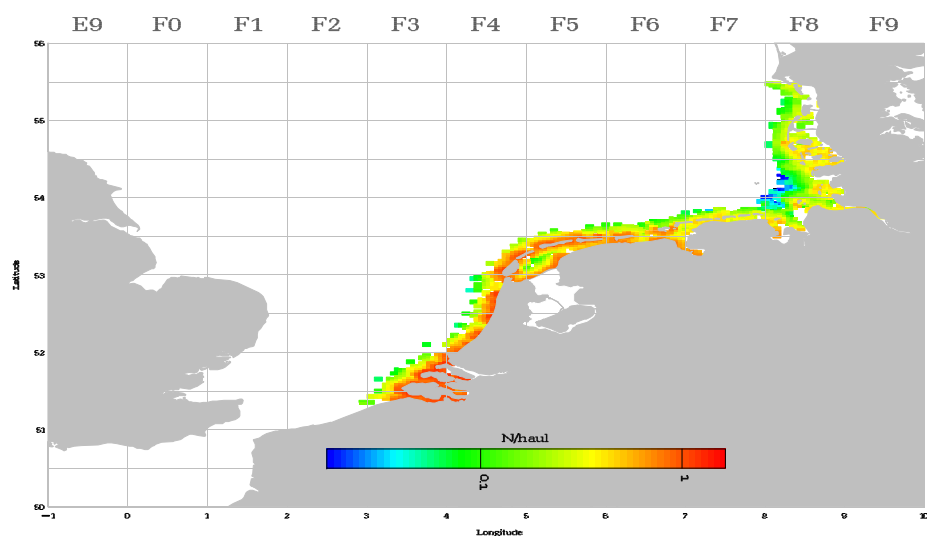


Figure 4.11.3. Predicted abundance per standard haul in 1982. Each grid cell measures $0.025^{\circ}\text{N} \times 0.05^{\circ}\text{E}$ and has a surface area of nearly 10 km^2 .

4.12 Trying to estimate the density of the European eel stock in coastal areas - a survey approach in the Baltic Sea of Northern Germany

Although the member states of the European Union have to implement eel management plans, which consider freshwater and coastal areas (EC 2007), little is known about the eel stock in coastal areas. However, recent studies using otolith analysis have shown that saline waters are important eel habitats (Tsukamoto *et al.* 1998, Tzeng *et al.* 2000). Thus there is an urgent need for more detailed data on the eel stock in coastal waters.

To assess eel density along the Baltic Sea coastline of Mecklenburg-West Pomerania (M-V, northeast Germany), an eel monitoring program was established in 2008. The coastline of M-V can be mainly classified into an external part with a total length of around 350 km and an internal coastal part with a shoreline of 1.358 km. Along the coastline a salinity gradient from west to east exists with higher PSU-values in the

western parts. Furthermore, the coast of M-V is characterized by a high diversity of different habitat types ranging from exposed sand-silt habitats with a PSU of 11 to sheltered highly eutrophic internal coastal zones with submerged vegetation and a salinity of 1-2 PSU. Eel occurs in all habitat types along the coast of M-V (Winkler *et al.* 2007).

As a first step, a detailed habitat characterisation was conducted to identify different habitat types which are representative of the external and internal coastal waters of M-V. Based on the habitat characterisation 72 sampling points were identified covering all different habitat types. After the evaluation of possible eel monitoring approaches, which should allow the sampling of the different habitat types, a transportable fyke net system was developed. The fyke net system consists of a square external leader net weir with a fyke net chamber in each corner. The net square encloses a total fished area of 1 ha (Figure 4.12.1). In addition, six chains of customary eel traps (4 double chamber fyke nets with 8 m leader net) were deployed in the square fished area to increase the likelihood of catching all eel above a certain size that are within the net weir. In the optimal case, this system catches all eels above a certain total length that are enclosed by the net weir and no eels migrate from outside into the fyke net system. To test this monitoring system, 43 different stations were sampled in 2008, with each station being fished for 48 h.

During the test phase of the fyke net system in 2008, 139 eel were caught resulting in a relative mean eel density of 3.2 eel/ha (± 4.8 SD). The average eel length was 45.7 cm (± 10.6 cm SD). The length distribution ranged from 25 cm to 81 cm. The harvested eel were mainly identified as yellow eel (96%). This preliminary result may indicate that there were many more yellow eels than silver eels present in the enclosed areas.

Based on this experience the new fyke net system was judged to be a suitable approach for sampling eel in different habitat types with a standardised method. According to the positive results of 2008 the monitoring program will be continued till the end of 2010. Additional investigations concerning the size selectivity of the fyke net systems and the proportion of eel leaving the bordered fished area will be conducted to model the eel density in the coastal area of M-V by taking the effect of different habitat types into account.

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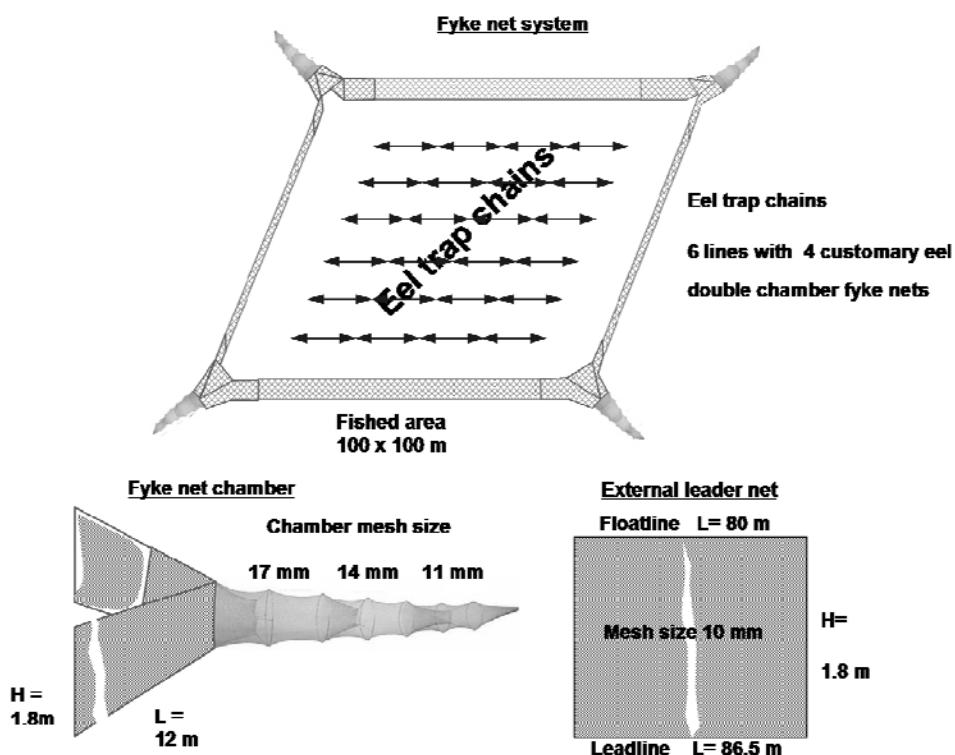


Figure 4.12.1. A newly developed fyke net system with an external fyke net weir with 4 corner chambers and 6 internal eel trap chains for monitoring the eel density in different habitat types along the Baltic coast of Mecklenburg-West Pomerania (North-eastern Germany).

4.13 Eel catches in France in relation to salinity of the habitat

Introduction

The eel stock has declined all over Europe (FAO and ICES 2008), and the European Union has accepted an eel recovery regulation (EU 2007). This regulation requires the quantification of eel stocks by Eel Management Unit (EMU).

The distribution of eels in relation to the distance upstream of tidal limits has been described by various authors using different indicators: density or occurrence of >150mm eels, 150–300mm eels or all sizes combined. It has been related to explanatory variables such as distance to the tidal limit in absolute (km) or relative terms (Ibbotson *et al.* 2002, Laffaille *et al.* 2003, Imbert *et al.* 2008, Lasne and Laffaille 2008). However, the distribution of the river stock in total (in numbers or weight) and the distribution downstream of the tidal limit has never been analysed in detail.

The objective here is to describe the distribution of eel in France, including the areas downstream of the tidal limit, on the basis of catch data, with special reference to salinity parameters.

Material and methods

Data on catches of yellow and silver eels were used as a proxy for stock abundance. In France, five categories of fishers are authorised to fish for eel, as characterised by professional/amateur and marine/riverine, with a separate category for angling. Marine and riverine professional fishers and riverine amateur fishers have to fill in compulsory logbooks, and thus, these are the categories for which most data are available. Here we present data for these three categories from various sources (com-

pulsory logbooks collected by Ifremer and Onema; scientific surveys by Cemagref and Ifremer; expert estimates by scientists, administrations and fisher organisation). More detail is provided in Beaulaton *et al.* (2009). Here, only data for the period since 1999 are considered, most often focusing on averages over the period 1999–2007. Fishing sectors were classified as non-tidal freshwater, tidal freshwater ($<0.5\text{g.L}^{-1}$), brackish water or marine water ($>30\text{g.L}^{-1}$). Where possible, silver eel catches were separated from yellow catches, but an unknown part of the supposedly “yellow” eel may in fact be silver eel.

Results are presented at the national scale and EMU scale. The Loire and Rhone EMUs are presented as examples.

Results

The average reported annual catch in France is 1127 t, of which 270 t (24%) is silver eel. This breaks down into 130 t (12%) for freshwater, 15 t (1%) for tidal freshwater, 406 t (36%) for brackish water and 575 t (51%) for marine water.

Figure 4.13.1 shows average annual documented catches by EMU and salinity. Great variability is found among EMUs, both in overall documented catches (ranging from 2 t to 883 t) and in salinity profile (3 EMUs are freshwater-dominated and 5 EMUs are dominated by brackish and marine water catches). The two EMUs yielding the highest documented catches are the Loire (freshwater catches dominate) and the Rhône (brackish and marine water catches dominate).

Figure 4.13.2 shows documented catches in the Loire and Rhône EMUs broken down by basin, salinity, and distance to the tidal limit. The pattern in freshwater (Loire and Rhône basins) is correlated with distance to the tidal limit, the most downstream reaches yielding highest catches. In the Rhône (including Vaccarès and les Impériaux lagoons) and Vendée basin, documented catches increase from freshwater to brackish and marine areas. In the Languedoc-Roussillon, which is part of the Rhône EMU, documented catches occur only in brackish and marine lagoons, the latter producing highest catches. In the “other PACA” area (also part of the Rhône EMU), documented catches occur only in brackish lagoons (in Berre). However, the pattern seems more complicated in the Loire basin, where the highest production is found in the downstream freshwater area. This high productivity is dominated by the silver eel fishery in the Loire River (24 t) and yellow and silver eel fisheries in the Grand Lieu Lake (28 t), but this lake is atypical in the French context. Without those two fisheries, the pattern in the Loire River would be quite similar to that in the Rhône.

Discussion and conclusions

First of all, data on angling in freshwater and amateur fishing in marine water are lacking. Angling is scattered throughout France and it can be found also in rivers smaller than where amateur and professional fisheries occurs. Briand *et al.* (2008) estimated angling catches to be between 500 t and 2000 t. The catches of marine amateur fishers are unknown, but probably non-negligible. For the categories covered here, underreporting might have occurred and some fisheries may have been missed completely. Some of the marine fisheries described by Aubrun (1986 and 1987) don't appear here, and it is unclear whether they still exist or not. Summarising all information (including the undocumented but apparently large angling catch in freshwater), fresh and saline waters probably contribute roughly equally to total French eel landings.

Assuming that fisheries are well spread over the available habitats and that exploitation rate is (spatially) homogeneous, the eel stock above and below the saline limit is of the same size. The former assumption seems reasonable, considering that each habitat has its specific group of fishers. The latter assumption, however, is less evident since gears are not equal and some fisheries in enclosed areas might have a higher impact.

The current study analyses catch weight. It is noted that mean individual weight differs between areas, e.g. small yellow eels (<100 g) from Mediterranean lagoons versus big silver eels (~900 g) from the Loire river.

In conclusion: the catch data indicate that the eel stock in brackish and marine waters in France is substantial, with a catch of approximately 1 000 t of yellow and silver eel (about 50% of total French catches, including undocumented angling catches).

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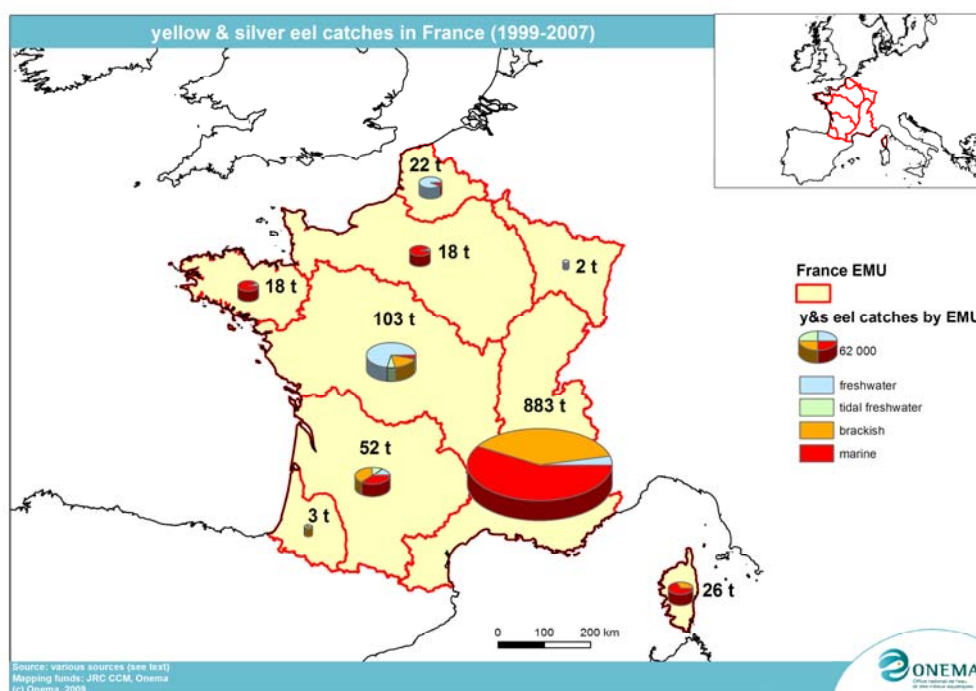


Figure 4.13.1. Yellow and silver eel catches by marine and river professional fishers and amateur river fishers in France, broken down by eel management unit (EMU) and salinity.

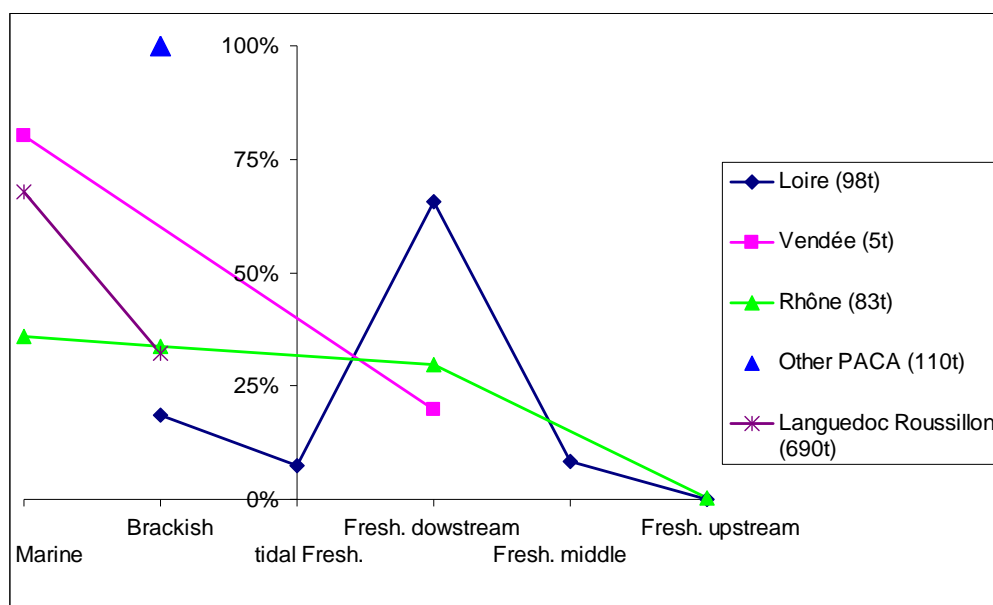


Figure 4.13.2. Catch profile for the Loire (Loire and Vendée) and Rhône (Rhône, other PACA, and Languedoc Roussillon) EMU.

4.14 The effect of stocking the shallow Roskilde Fjord

To enhance eel populations in Denmark a national stocking program has been ongoing since 1987 covering both inland and marine waters. The stocking program is financially based on a fish licence which is obligatory for sport and recreational fishermen. Because most recreational fishermen operate in saline waters, about 75%

of the stocked eel is released in marine waters. Since 1987 between 0.5 million and 8 million eel per year has been stocked in shallow marine waters. The stocking material is glass eel imported mostly from France by Danish eel farmers and further grown in heated culture to a weight of 2–5 g before they are stocked.

Knowledge of the outcome of stocking marine waters using cultured eel as seed material is limited. Previous work indicated, however, that stocked eels do survive, grow and become migrating silver eels (Pedersen 1998). In 1998 a new study was initiated with the aim of gaining more knowledge on the population dynamics of stocked eel in a marine area.

The study site, Roskilde Fjord, has a water surface of 123 km² and the fjord is shallow with mean and maximum depths of 3 m and 32 m, respectively. The salinity is 12 ppt in the bottom of the fjord due to freshwater supply from several streams and a salinity of 18 ppt where the fjord meets the Kattegat Sea. A professional and recreational fishery traditionally targets eel in the fjord.

Glass eels grown 3–6 month in heated culture were tagged with coded wire tags (CWT) (Thomassen *et al.* 2000) and released in the inner part of the fjord during the summers of 1998 and 1999. In total 50 603, small eel of 3 g and 50 268, large eel of 9 g were stocked. Fisheries landings were checked for tagged eel in 2000–2006, using a CWT tunnel detector (North West Marine Technology). Spatial distribution of the tagged eel was studied by examining catches in adjacent areas to the stocking area.

CWT captured eels were sexed and the CWT was removed from the eel and the code read using a microscope. Sagittal otoliths were removed and sent to Uppsala University, Sweden and analysed for Ca/Sr + content by Wavelength Dispersive Electron Microprobe as described by Limburg *et al.* (2003).

To study the behaviour of stocked eel in the silver eel stage silver eels of wild and stocked origin (CWT) were captured in the professional fishery during September, Carlin-tagged, and released in the inner part of the fjord in 2004 and 2005. A reward was given the fisherman for returning the Carlin tag together with information on capture site and date of capture.

During the period 2000–2006 a total of 84 047 captured eels were examined for CWTs and 1834 CWTs were recovered corresponding to an overall recapture rate of 1.8% of the stocked fish. The spatial distribution of the stocked eel gradually decreased with distance from the stocking site suggesting that the eels generally stayed in and near to the stocking site but one eel was recaptured outside the fjord. Sr/Ca analyses in otoliths of 28 specimens indicated that the stocked eels did not enter freshwater during the 6–7 years that passed between stocking and recapture.

Growth increment was between 30 and 75 mm per annum. The sex ratio of stocked eel is ca 1:2 (M:F) in yellow eels but 50:1 (M:F) in silver eels. This paradox of different sex ratios between yellow and silver eel is possibly a result of a high fishing mortality in Roskilde Fjord implicating that an eel is caught before it grows large.

At stocking the same number of large and small eels was used. At recapture (N = 1678) 60.3% were identified as small 3 g eel and 39.7% were identified as 9 g eel, thus suggesting that the small eel was more valuable as stocking material than the larger eels.

In autumn 2004 and 2005 silver eels of stocked and wild origin were Carlin-tagged and released in the bottom of the fjord. The result was a higher recapture rate of wild eels (28%) compared to stocked eels (19%) but the difference is not statistically differ-

ent (χ^2 test, $P=0.12$). Independent of eel origin (wild and stocked), both eel types were caught in the same proportion in the southern part of the fjord (56%) and in the northern part of the fjord (44%), indicating that the stocked eels migrate toward the outlet of the fjord together with the wild silver eels (χ^2 test, $P=0.94$).

The total number of recaptured tagged fish was estimated using the official catch data multiplied by the frequency of recaptures. From this conservative estimate it was found that 10.3% of the 3 g and 6.8% of the 9 g eels were recaptured by the professional fishermen. The stocked eel is also captured by recreational fishermen, but these catches are not registered and are therefore unknown. The catch of recreational fishermen was in 1997 estimated to be 26% relative to the registered professional catch in the whole country and was probably even more than 26% in Roskilde fjord. Stocking saline Roskilde fjord with 3 g eel provides a possible catch to fishermen of at least 13% (professional and recreational) of a stocked cohort. Another 5% was estimated to leave the fjord as silver eels. In conclusion, the effect of stocking Roskilde Fjord is that at least 18% of a cohort of 3 g eel are captured or escaped as silver eels, the remaining 82% is the accumulated natural mortality in the fjord.

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4.15 Discussion - densities, populations and relative abundance

Implications for stock assessment and management

It is difficult to say that we should give any area higher protection than any other area. However, this is already being done in Germany, where fishing above hydro dams is banned to compensate for turbine mortality.

Research needs

Densities, abundances, and productivities of eels in saline waters and contribution to the spawning stock; patterns of movement and exchange across salinity boundaries; the contribution of stocked eels to silver eel escapement; the value of stocking in fresh vs. saline waters; how population and demographic factors vary across space and time, what areas should be priority for stocking. We need not just observations, but understanding of processes.

Research methods

Capture methods (fyke nets, trawls, pots, vacuum pump, rotary screw traps, stow nets, trammel nets); observation methods (scuba, glass bottom boat, cameras); mark-recapture; acoustic tracking; otolith strontium:calcium ratios; stable isotopes; fatty acid analysis; the German 1 ha corral trap; fishery data, reporting and taking into account its reliability; extraction of historical data where available; phenotypic and genetic differences; differences in gene expression. It would be useful to establish standardized sampling methods that work across habitats.

5 Choice of salinity zone in growth-phase anguillid eels

5.1 Consequences of facultative catadromy in American eel

Temperate eels (*A. rostrata*, *A. anguilla*, *A. japonica*) show what has been termed facultative catadromy, where some but not all eels invade freshwater from natal saltwater habitats (Tsukamoto *et al.* 1998, Limburg *et al.* 2003, Jessop *et al.* 2004). The previous long-held view held that yellow eels occurring in coastal waters, such as the Baltic Sea, were only temporary occupants and were destined for freshwater later in their lives (Harden Jones 1968). Otolith microchemistry studies have changed that view – some juveniles persist in marine or estuarine waters until maturity, while other juveniles do indeed migrate into fresh water. The discovery of these two contingents (terminology after Elsdon *et al.* 2008) has generated controversy on the relative importance of freshwater v. saltwater habitats in the population dynamics of temperate eels. Indeed, a central justification by U.S. Fish and Wildlife Service not to list American eel was centred on the eel's ability to complete its life cycle outside of freshwater: "The status of the American eel and the effects of freshwater loss must be examined in light of the American eel's habitation in fresh, estuarine, and marine habitats" (USFWS 2007).

What do saltwater and freshwater eel habitats represent?

In interpreting patterns of habitat use from otolith microchemistry and inferred freshwater and saltwater eel contingent structure, we should be wary of a false dichotomy. The otolith strontium:calcium ratio, which is most frequently used to identify contingents, is functionally related to salinity in a non-linear manner (Kraus and Secor 2004), which allows confident separation between freshwater and brackish water habitats, but does not clearly separate habitats within freshwater or saltwater environments. Thus, one could ask whether contingents separated 20 km distant between tidal brackish or fresh water were demographically and functionally different. Other examples of similar habitats across freshwater-saltwater classifications include saltwater v. freshwater ponds; fjords v. estuaries; and freshwater v. saltwater marshes. In contrast, one would expect large differences in vital rates and ecological function between two eels of the same contingent, one resident in freshwater tidal and the other in a pool-riffle habitat in nontidal fluvial waters. As such, contingent structure is a very coarse indicator of the diversity in habitat use among eels. Still, the freshwater-saltwater dichotomy can permit quantitative assessment of spatial demographics in temperate eels, and permit informed perspectives on how diverse habitat use affects population stability and recovery (Secor 2004). Also, one can look at systems that likely function as important freshwater and saltwater growth habitats for yellow eels at the population level (e.g. the St. Lawrence Estuary v. Lake Ontario; tidal v. fluvial Chesapeake Bay watershed) and generalize that these differ fundamentally in faunal assemblage, water quality and flow, proximity to natal oceanic habitats, intensity of exploitation, and degree of anthropogenic alteration.

Because it is likely that most environmental stresses to eels occur in freshwater habitats, a precautionary approach would emphasize this habitat in terms of its contribution to eel population dynamics. These include loss of historical habitats due to dams and impoundments, disease and contaminants, water quality, and fish passage (reviewed in USFWS 2007; see also Machut *et al.* 2007). Further, freshwater eel habitats are arguably much more diverse and distributed than saltwater habitats. Varying estimates indicate that 25% (USFWS 2007) to 84% (Busch *et al.* 1998) of the American eel's freshwater habitat has been lost during the past century. The less conservative

estimate depended on the assumption that eels could efficiently negotiate barriers <8 m, which was refuted in a recent directed study of Hudson River tributaries where dams <3 m substantially impeded upstream migrations (Machut *et al.* 2007). In any event the historical freshwater abundances of American eels must have represented a massive reservoir of potential spawning biomass. Therefore, the remainder of this essay responds to the questions: (1) Why should eels occur in freshwater habitats? and, (2) What role do freshwater habitats play in regulating population dynamics?

Why do eels invade freshwater?

Saltwater habitats tend to be more productive than freshwater ones as growth habitats (Helfman *et al.* 1987; Morrison and Secor 2003; Jessop *et al.* 2004; Machut *et al.* 2007); why then would individual juveniles elect to continue to migrate to up-estuary or upstream freshwater habitats? Various theories have been advanced related to this aspect of facultative catadromy and are briefly reviewed here. These theories should not be viewed as mutually exclusive.

Growth-Survivorship Trade-off

Cairns *et al.* (2009) used a demographic model to test the idea that individual local fitness, the balance of growth and survival rates as they influence reproductive rate, might be equivalent between freshwater and saltwater habitats. Systems that support such comparisons are currently limited to the Canadian Maritimes and the Hudson River. This analysis indicated that survivorship would have to be enhanced ~2-fold in freshwater over saltwater habitats to compensate for the growth advantage in saltwater habitats. Because no such survivorship differences were detected in the Hudson River, evidence would not support that selection for either habitat would constitute an evolutionary stable strategy in this system. Still, for many systems predation mortality is believed to be substantially higher in estuarine and saltwater habitats than in freshwater habitats (Helfman *et al.* 1987).

Mating System

Helfman *et al.* (1987) and more recently Oliveira (1999) suggested that sexes may differentially use freshwater and saltwater habitats, where females are risk-averse and trade off growth for reduced mortality to attain large sizes in freshwater, albeit at a much reduced growth rate. Males, which mature and emigrate at much smaller sizes than females, opt for a time-minimization strategy, where higher growth rates are traded against higher mortality risk in saltwater habitats. Large females frequently dominate in nontidal freshwater habitats, but are well known to occur throughout estuarine and marine habitats as well. Thus, evidence only partially supports this hypothesis. Further, recent evidence supports a negative association between female sex determination and density, which would confound a simple explanation for sex differences between freshwater and saltwater habitat classifications. Finally, sexes may show certain gear affinities, which could bias sex ratios in saltwater habitats where multiple gear types are used (e.g., pots, weirs, fyke-nets, trawls).

Colonization

Tsukamoto and Aoyama (1998) presented facultative catadromy as a corollary to the unique invasiveness by temperate eels within the family Anguillidae. Colonization of originally tropical Indo-Pacific species into temperate waters depended upon their use of freshwater habitats, which permitted stair-step colonization through the Tethys Sea into the Atlantic Ocean. Facultative catadromy arose presumably because saltwater habitats could support overall higher productivity and stabilize recruitment

variability in temperate latitude environments. If freshwater invasion is evolutionarily hardwired, then facultative catadromy could occasionally lead to ecological traps over the history of the species (Tsukamoto *et al.* 1998; Cairns *et al.* 2009).

Entrainment

The entrainment hypothesis stems from the view that juveniles learn migration routes from adults, rather than juveniles responding to some innate cue in their adoption of migration patterns (Corten 2002). Though no evidence exists for this hypothesis, the gregarious nature of yellow eels and evidence of acuity in chemical communication (Huertas *et al.* 2008) could support the idea that shoaling and schooling behaviors by yellow eels could lead to entrainment. Seasonal migrations to brackish/marine waters during spring by freshwater contingent yellow eels (Jessop *et al.* 2008) could entrain younger eels to freshwater habitats. Such a behaviour would result in an up-estuary progression of age structure, which is suggested by age and size structure differences between brackish (younger) and freshwater (older) regions of the same estuaries (Helfman *et al.* 1987, Morrison and Secor 2003). Entrainment during seasonal migrations could also explain sudden shifts in freshwater/saltwater water habitat use across the yellow eel stage, which has been frequently reported (Morrison *et al.* 2003, Davaret *et al.* 2006, Jessop *et al.* 2008).

Partial Migration

Lifetime patterns of residency or migration within populations of birds, salmon, and white perch, termed partial migration, are the result of early life developmental switch points (Berthold 1996, Kerr and Secor in press). Dedicated research on the propensity of glass eels either to disperse into brackish water or continue up-stream migrations into nontidal freshwater habitats provides evidence for partial migration in European eel (Edeline *et al.* 2007). Edeline (2007) argued that greater physiological condition and thyroid hormone levels were associated with those glass eels that immigrated into nontidal fluvial habitats in comparison to those that dispersed into freshwater and saltwater tidal habitats. He hypothesized that this represents a conditional strategy, cued by the physiological status of an individual glass eel upon arrival at the fall line. Edeline's concept for partial migration could have strong explanatory value as it integrates ocean conditions, which will influence the glass eel's physiological status. Thus poor ocean conditions might result in diminished use of freshwater habitats during the yellow eel period. Further, he proposed that the freshwater tactic was a mechanism of competitive release, the consequence of which will be influenced by the overall number of glass eels moving up an estuary.

Consequences of freshwater invasion

- The Storage Effect

The storage effect applies to complex life cycles where part of the life cycle, the longer part, is buffered against environmental variability, and the other, typically shorter phase is more tightly coupled to periodic environmental variations that only occasionally favour survival (Frank and Brickman 2001; Secor 2007). The storage phase of life cycles include the dormant seed phase of many plants, the diapausing stages of cladoceran zooplankton, the pupa phase of cicadas, and the adult stage of condors - all of which serve to stabilize populations and match them to cycles of the environment that favour persistence and growth. For eels, the early life oceanic phase varies in concert with oceanic conditions, whereas the relatively long juvenile continental growth phase is insulated from environmental variations. Fluctuations of glass eels are coupled to oceanic conditions (NAO Index, temperature, primary productivity)

experienced during the leptocephalus stage (Bonhommeau *et al.* 2008). In contrast, the relatively long yellow eel stage is buffered from the environment to a greater extent due to its larger size and behavioural and physiological attributes that adapt to seasonal and spatial changes in the environment. For eels, the storage effect is determined by the length of the yellow eel phase and how well it is matched with intervals between oceanic conditions that favour recruitments.

Consider a hypothetical case where all silver eels mature at the same age. Here, the storage effect would not operate because leptocephalus production would occur as discrete episodic events with a period matched to generation time, similar to some populations of sockeye salmon. Rather, overlapping generations of eels are critical for the operation of the storage effect. Multiple year-classes of silver eels buffer population responses to oceanic conditions as they overlap long-term environmental oscillations. The degree of overlapping year-classes depends upon a diversity of maturation rates in the population, which in turn is related to the variable growth conditions that yellow eel contingents experience.

One can measure an aspect of the storage effect by simply examining how multiple age-classes of silver eels increasingly spread a generation's egg production over many years, and thereby dampen variability. Consider a mean level of annual variability in oceanic survival. That annual variability is then sampled over a range of years, matched by the underlying diversity of age structure of silver eels emigrating from diverse continental growth conditions. A simple plot of coefficient of variation shows that with increasing number of age-classes of silver eels (annual sampling), recruitment variability diminishes in geometric proportion (Figure 5.1.1).

- The Portfolio Effect

Due to their relatively high longevity, high individual fecundity and small egg size, temperate eels represent periodic strategists (Winemiller and Rose 1992). Temporally, eels match inter-annual variations in recruitment with their reproductive schedule and longevity. Spatially, the broadcast of lots of small offspring permit adults effectively to sample nursery environments that are patchy at a regional scale. If we extend this logic further, glass eels may be sampling diverse freshwater and saltwater regions that vary as growth habitats on inter-annual and inter-generational time scales.

Using stability again as a population end-point, one can measure how asynchronous responses in different entities (e.g., habitat types, contingents) result in reduced variance in overall production, a.k.a. the portfolio effect (Doak *et al.* 1998; Tilman *et al.* 1998; Secor *et al.* in press). Here, I define the portfolio effect as the degree of variance dampening imparted by asynchronous freshwater and saltwater eel contingents when faced with climate and other environmental forcing. Below, I develop an approach to measure the portfolio effect by comparing contingent and population coefficients of variation.

The approach is to compare coefficients of variation (CV) at each contingent (C) scale to that observed at the population (M) scale (Secor *et al.* in press). First, CV_C and CV_M were modelled for a 10-year time frame (related to a hypothetical generation time for American eel) for abundance (S) of each contingent and the overall population. Then, by weighting the individual CV_C according to their respective abundances (in terms of population abundance, SC), one estimates the population CV_M^* , a measure of variance at the aggregate level if the two contingents were responding in complete synchrony to environmental forcing:

$$CV_M^* = \sum_{C=1}^{C=k} \left(\frac{S_C}{S_M} CV_C \right)$$

where k is the number of contingents.

A comparison of the CV_M with CV_M^* provides an estimate of what has been termed the portfolio effect (PE; Doak *et al.*, 1998), the degree of to which variance is dampened due to independence between contingents in their contributions to an aggregate population biomass:

$$PE = 1 - (CV_M / CV_M^*)$$

The PE positively scales with population stability, but also indexes how contingent independence contributes to this stability. For instance, what additional stability is conferred by considering contingents as part of a population versus considering contingent stabilities on an individual basis? For a two contingent system with no correlation between contingents ($r = 0$), the portfolio effect would be 30% according to the modified formula from Doak *et al.* (1998):

$$CV_M = CV_C \frac{(1 + r(k-1))^{0.5}}{k^{0.5}}$$

One can consider a series of types of covariance between contingents. The first scenario is that the same set of environmental conditions favours one but not the other contingent; in fact the two contingents show negative correlation in their response to the environment: when one is up, the other is down. In this special instance, there is nearly complete damping of the population variance due to the negative covariance between contingents. In a modelled scenario, mean contingent abundances and variances were the same but $r = -1$, and recruitment was allowed to vary randomly about the mean. Here, the estimated portfolio effect is 93%. Thus, variance is nearly completely dampened (Figure 5.1.2, top panel). Now consider two contingents that have the same overall abundance and variance levels, but are allowed to vary completely independently of each other ($r = 0$; Figure 5.1.2, middle panel). In this scenario, we approach the theoretical prediction of a 30% portfolio effect for two contingents. Finally, consider a structured independence scenario where one contingent is much lower in abundance and variability respective to the other (Figure 5.1.2, bottom panel). Here a reduced portfolio effect is expected, but the asynchronous behaviours of the two contingents still gives evidence of contributing to overall population stability.

Summary

Facultative catadromy in temperate eels may have evolved to support population colonization, growth and stability where past populations were exposed to periodic variations in climate and oceanic regimes. In ecological time, the storage effect can be sustained by allowing escapement of silver eels from both freshwater and saltwater habitats, which will contribute to overlapping generations and diverse age structure by silver eels. Independence between freshwater and saltwater juvenile habitats should also contribute to population stability and persistence through the portfolio effect. Management priority on only a saltwater juvenile contingent for maintenance or recovery is a risky strategy in that (1) we lack historical perspective on the relative importance of freshwater habitats; (2) current information on the relative ranking of saltwater versus freshwater habitats is likely influenced by impoundments, which curtail freshwater habitat immigration by glass eels; (3) although relative silver eel

production between freshwater and saltwater habitats are unknown for American eels, for other temperate eels, freshwater habitats can produce a substantial (although a minority) fraction of silver eels (Limburg *et al.* 2003; Chino and Arai 2009). Exciting new research is underway to better understand mechanisms underlying facultative catadromy by temperate eels (Edeline 2007; Edeline *et al.* 2007; Imbert *et al.* 2008; Bureau du Colombier *et al.* 2008). But for now, our understanding of partial migration remains incomplete. From a precautionary perspective, we should focus on the consequences of partial migration as it relates to population dynamics and stability. To this end, due to their likely independence in habitat production rates in comparison to saltwater, freshwater habitats play a key role in enhancing population stability and persistence through the storage (diverse age structure) and portfolio (independent growth habitats) effects.

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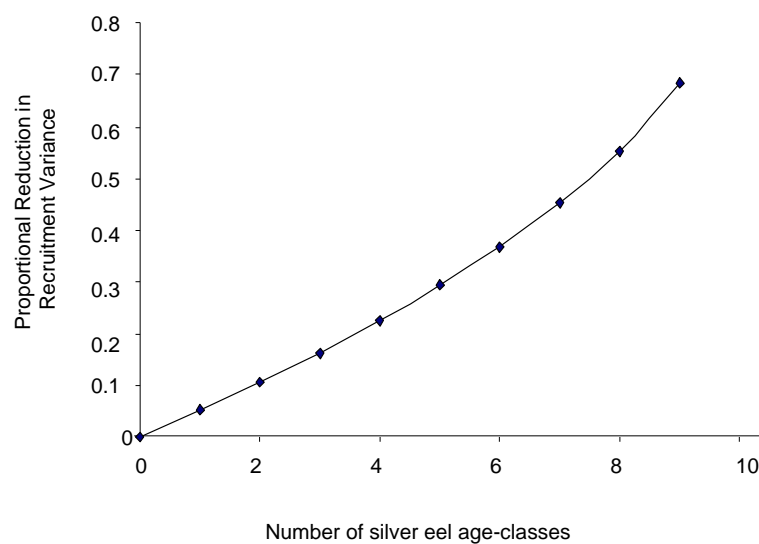


Figure 5.1.1. Proportional reduction in coefficient of variation in annual recruitment versus number of silver eel age classes (baseline is single age-class). The form of the function is dependent upon formulation of the coefficient of variation ($SD/(\sqrt{n})/\text{mean}$) and is independent of the stipulated value of variance.

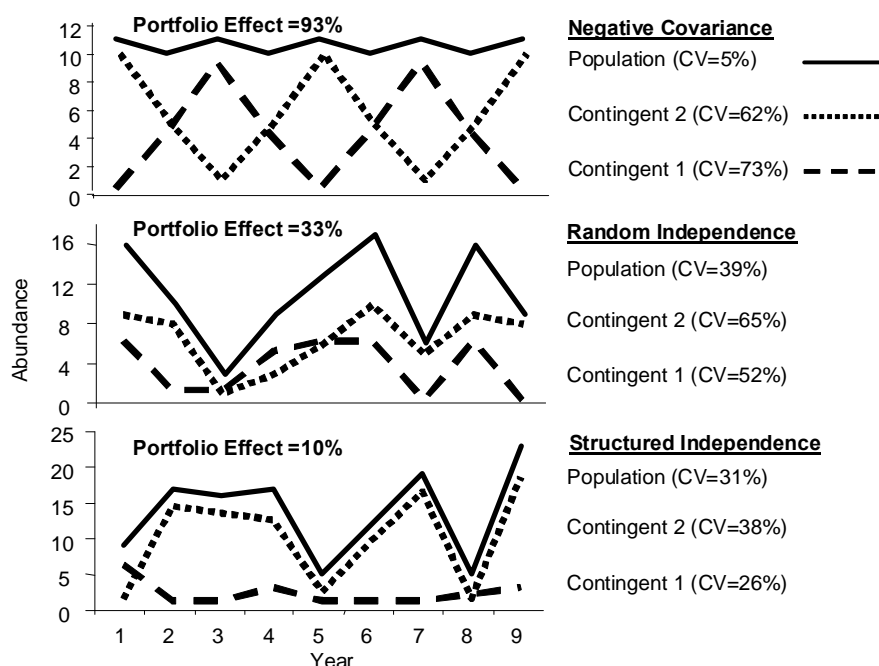


Figure 5.1.2. Scenarios of covariance between saltwater (contingent 1) and freshwater (contingent 2) contingents of American eel. In the negative covariance ($r=-1$) and random independence scenarios ($r=0$), variance and abundances were stipulated at the same mean (but allowed to vary randomly about the mean). In the structured independence scenario ($r=0$), the freshwater contingent is 10-fold less abundant than the saltwater contingent.

5.2 Review of behavioural experiments and theories on habitat choice by recruiting glass eel

Introduction

Many behavioural experiments have been performed on glass eels. The first attempts were made around 1930 (cited by Fontaine and Callamand 1941), signalling an early interest in identifying the factors that trigger the passage from saline water to fresh water.

This brief review summarizes results of behavioural experiments on glass eel swimming capacity and perception ability, and describes migratory behaviour and individual characteristics after behaviour-based sorting. This knowledge leads to a current conceptual model that seeks to explain the behaviour variability of glass eels.

Swimming capacity of glass eels

Glass eels can be considered as classical swimmers with cruising speed equal to $0.10\text{--}0.15\text{ m s}^{-1}$ ($1\text{--}2$ body length (BL) s^{-1}) and burst speed equal to $0.25\text{--}0.40\text{ m s}^{-1}$ ($4\text{--}6$ BL s^{-1}) (Tsukamoto *et al.* 1975, McCleave 1980, Barbin and Krueger 1994, Langdon and Collins 2000). But glass eels encounter currents more rapid than their swimming capacity, especially during ebb tide in estuaries. They therefore need to adapt their behaviours to overcome these conditions and to save energy.

Perception abilities of glass eels

Behavioural experiments give information on what glass eels can perceive. Glass eels can detect and orientate (i) toward salinity differences at least as low as 5 ppt (Tosi *et al.* 1988, Tosi *et al.* 1989), (ii) towards temperature differences at least as small as 2°C

(Tongiorgi *et al.* 1986, Tosi *et al.* 1988) with sensitivity thresholds varying with acclimatization, and (iii) between different odours in the water (Sorensen 1986). In particular they are highly sensitive to very diluted (as low as 10–13 mg L⁻¹) concentrations of geosmin (Tosi and Sola 1993) or amino acid (Sola *et al.* 1993). Salinity is the most important factor guiding movement choice. Preference for fresh water is affected more by temperature than by odour (Tosi *et al.* 1990).

Glass eels can also react to light (Bardonnnet *et al.* 2003) with a very low threshold (Bardonnnet *et al.* 2005) and to current. In binary choice experiments a positive rheotaxis (swimming against the current) is observed. In a large flume, most of the glass eels are caught in the downstream trap (Bardonnnet *et al.* 2003, Bureau du Colombier *et al.* 2007b). In an annular (donut-shaped) flume where swimming is less constrained, both positive and negative rheotaxis are observed (Creutzberg 1961, Wippelhauser and McCleave 1988, Bolliet *et al.* 2007). They respond to rapid current by sheltering in bottom gravel where available (Creutzberg 1959, Barbin and Krueger 1994). They are also sensitive to the presence of conspecifics (Miles 1968, Sorensen 1986). Overall, glass eels are well equipped to perceive relevant conditions in coastal and estuarine waters.

Description of migratory behaviour

Behavioural experiments were also used to clarify how glass eels move in zones subject to tides (coastal zone and estuary). The behaviour work of Creutzberg (1958) was the starting point of productive investigations on selective tidal stream transport (STST) which proved to be a common behaviour in fish, specially for early stages (Forward and Tankersley 2001). As a first description, glass eels swim in the water column during the flood tide and remain on or near bottom during ebb tide (McCleave and Kleckner 1982). However, this migration is not as efficient as it might be since the ratio of the observed migration speed to the potential speed (flood tide current speed and swimming speed) in the Gironde basin, France, ranges between 0.15 and 0.19 (Beaulaton and Castelnaud 2005).

STST is triggered by an endogenous biological clock (Wippelhauser and McCleave 1988) which is likely synchronized through an interaction of environmental and/or social cues (Bolliet *et al.* 2007). The maximum duration of glass eel activity per tidal cycle is estimated to about 190 min (McCleave and Wippelhauser 1987, Bardonnnet *et al.* 2003). Recent experiments have revealed two patterns, i.e. positive and negative rheotaxis, of rhythmic activity in opposing phases, both with a tidal period (Bolliet *et al.* 2007). There is a very low probability that an individual fish exhibits both behaviours (Bolliet and Labonne 2008).

Characteristics of individuals within behavioural groups

The current trend in glass eel behavioural research is to use experiments to sort glass eels by behavioural pattern in order to highlight biometric, energetic or hormonal differences between groups exhibiting different behaviours. This information is used to try to identify which glass eels are destined to settle in the estuary and which will settle in the river.

Sorting has been based on salinity (Edeline and Elie 2004, Edeline *et al.* 2005, Edeline *et al.* 2006), on the dusk signal (Bardonnnet *et al.* 2003, Bureau du Colombier *et al.* 2007a, Bureau du Colombier *et al.* 2007b), and on current direction (Bolliet and Labonne 2008). The sorting techniques have limits: very small experimental devices and short duration of experimentation, response to a single factor, and inconsistency of behaviour (see multiple choice in Edeline *et al.* 2005, Imbert *et al.* 2008). Furthermore,

experiments typically use glass eels captured in the estuary; these fish may be a non-random sample of recruits. Because of these limits any extrapolation to behaviour in nature must be made carefully. As per the terminology of Bureau du Colombier (2008), fish that prefer fresh water, that are active during dusk, or that swim with current, are considered to present a high propensity to migrate (M+). Other fish are considered to have a low propensity to migrate (M-).

These experiments indicate that M+ glass eels are characterized by (i) a high level of thyroid hormone T4 (Edeline *et al.* 2004) which is consistent with field data in the tidal zone (Edeline *et al.* 2004) and with experiments with river glass eels (Imbert *et al.* 2008), (ii) a high weight (Bardonnet *et al.* 2003, Bureau du Colombier *et al.* 2007b, Bolland and Labonne 2008), (iii) a high condition factor (Edeline *et al.* 2006), and (iv) a high energetic state as indicated by percentage of dry weight (Bureau du Colombier *et al.* 2007b). Moreover these M+ glass eels present a low Pb and Zn load (Bureau du Colombier *et al.* 2007a). Results concerning growth are contradictory. Edeline *et al.* (2005) found superior length growth in M- fish, but Bureau du Colombier *et al.* (2008) concluded that feeding rate and weight gain were higher in M+ fish. No difference in mortality was found between M+ and M- fish when they are fed (Edeline *et al.* 2005, Bureau du Colombier *et al.* 2008). There appears to be no relation between propensity to migrate and energetic cost of osmoregulation (Bureau du Colombier 2008).

Conceptual models to explain behavioural responses

Edeline (2007) viewed diadromy in temperate-zone eels as a threshold reaction norm (Gross 1996) to an individual's energetic status: individual eels choose the migratory tactic (catadromy/freshwater residence vs. non-catadromy/brackish residence) that maximizes fitness depending on the level of energy stores. Catadromy is considered to be the most advantageous tactic for individuals with high energetic status because it allows competition avoidance.

This model, albeit appealing, poses several problems. It is based on an extrapolation of the behaviour of M+ and M- groups to catadromous and non-catadromous fish. It simplifies the migration to a one-time decision (settle or migrate) although the glass eel faces many choices (burrow or swim) which modify its energetic status. The model is based on short-term fitness, but other factors also influence fitness over the eel's life (foraging, sex determinism, maturation). In particular, the role of mortality in shaping lifetime fitness of catadromous and non-catadromous eels is not clear (Cairns *et al.* 2009).

Recently, Cairns *et al.* (2009) noted that facultative catadromy increases the diversity of occupied habitat and might therefore lower fitness variance caused by environmental fluctuations. In this case, anguillid eel strategy flows from the paradigm of adaptive population resilience and can be viewed as a mechanism that hedges against unforeseen adverse circumstances in any one habitat (Secor and Rooker 2005). This model also leaves many questions open. In this context, it is difficult to explain which fish will settle in the estuary or in the river. The proportion of settlement in one habitat should be clarified according to habitat suitability differences and the frequency of adverse conditions in each habitat. To date, this point of view should be considered as the consequence of the previous model.

Conclusions

Based on present knowledge of glass eel behaviour and ecology, the final settlement destination can be viewed as a consequence of the reasonably well-synchronized in-

ternal clock, the animal's energy budget, and environmental conditions. The causal scheme is summarized in 3 points:

- 1) Locomotor activity of a glass eel responds to its energy state (threshold reaction norm) and its internal clock state.
- 2) Energy cost varies among individuals (physiological status). Locomotor activity costs energy and reduces energy state, which limits the ability to migrate.
- 3) Synchronization of the internal clock is achieved by environmental cues (especially prior to reaching the freshwater estuary) and by social cues. This last component explains glass eel and elver schooling behaviour in freshwater estuaries and rivers. It introduces a density-dependent component which could explain the greater reduction of the freshwater contingent compared to the marine one (Briand 2009).

Efforts to integrate these rules into an individual-based model (Lambert 2005, Bureau du Colombier 2008) should continue until all the main components of glass eel behaviour are represented. Then alternative behaviours could be tested to evaluate the fitness of actual glass eel behaviour.

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5.3 Speculations on the selective advantages and evolution of facultative catadromy in eels

Introduction

This presentation is largely speculative because of the lack of specific evidence, but it is suggested that facultative catadromy arose in the early evolution of tropical Anguillidae and has subsequently been retained as an Evolutionary Stable Strategy (ESS), even by temperate-zone species. It is suggested that key selective advantages of ESSs accrue from enhanced habitat utilisation and bet-hedging strategies in the face of major environmentally-driven fluctuations in recruitment, associated with the unique anguillid life history, periodic strategies and physiological, anatomical and behavioural adaptations.

Evolution of facultative catadromy

The superorder Elopomorpha arose from primitive teleost ancestors, and the Anguilliformes possibly evolved some 52 Mya in what is now the Indo-Malaysian region of the Pacific Ocean, the North Atlantic species speciating perhaps 6–10 Mya. Elopomorphs are unique in having a planktonic leptocephalus that uses ocean currents to migrate from oligotrophic deep ocean spawning areas to growth habitats. In tropical anguillids, spawning and recruitment to continental waters might be possible all year round because of relatively constant environmental conditions and short migration distances. Conversely, in temperate species with very long migration distances and durations, spawning and migrations need to be synchronised with seasonal climatic factors to maximise survival.

Amongst extant elopomorphs, only the Anguillidae show facultative catadromy. They are fitted to life in a wide range of habitats because they are physiologically robust and can utilise a wide range of prey. They use daytime cryptic behaviours which conserve energy and help avoid predation, agonistic encounters and cannibalism. Their euryhaline abilities possibly originated in ancestral tropical elopomorphs in order to utilise productive brackish waters as nursery grounds, as shown by present-day tarpon and ladyfish 'whitebait' larvae and bonefish juveniles. Fuller use of brack-

ish and shallower coastal waters would have been encouraged by the higher net primary productivities (NPPs) commonly found in such habitats (Table 5.3.1). Allochthonous detrital secondary production and slow flushing times can also add significantly to overall productivity and hence prey availability in habitats such as estuaries, coastal lagoons and some freshwater lakes (Dobson and Frid 1998). Another selective advantage of catadromy could have been avoidance of competition with other stenohaline marine elopomorphs (and other early teleosts) (Table 5.3.1). In addition, numbers of potential fish predators tend to be lower in brackish and freshwaters compared to the sea, especially in temperate regions (Jonsson and Jonsson 1993, Limburg 1996).

Life in brackish waters has energetic advantages as eels are in approximate osmotic equilibrium in intermediate salinities, and maintaining hydromineral balance in fresh or fully saline waters could increase standard metabolic rates by ~8–10% (Knights 1984). Such extra energy costs could have been offset in early tropical anguillids because of the higher net primary productivity (NPP) and hence prey availability in freshwaters compared to marine habitats (Gross *et al.* 1988). This advantage is however lost at higher latitudes, and growth rates in freshwaters (except productive stillwaters) tend to be lower than those saline waters (e.g. Cairns *et al.* 2009). Eels are also warm-water species and growth seasons with temperatures >10°C shorten with increasing latitude, resulting in clines of slower growth rates and hence increases in age- and size-at-maturity and relative fecundity (Vøllestad 1992, Yalcin-Ozdilek *et al.* 2006). Such delays in maturation and emigration mean that yellow eels are exposed for longer to natural and anthropogenic mortality factors. However, high spatio-temporal variability in growth rates and spawner escapement can also help offset potentially very high variability in recruitment success. This is associated with the periodic life strategy characteristics shown by anguillids.

Anguillids, like other Elopomorpha, are periodic life strategists, characterised by relatively long generation times and high size-related fecundity to compensate for potentially high planktonic oceanic larval mortality (Winemiller and Rose 1992, King and McFarlane 2003, Winemiller 2005). Bonhommeau *et al.* (2009), for example, estimate typical mortality for *A. anguilla* leptocephali + glass eels during a typical 21 month Atlantic migration period to be ~99.88%. Anguillids appear to be well adapted as this mortality, considering the long duration, is relatively low compared to estimates for other teleosts. Due to the effects of stochastic fluctuations in climate-ocean conditions on larval transport currents and food availability, periodic strategists commonly exhibit large inter-annual and decadal-scale fluctuations and regime shifts in larval survival, and hence in recruitment (King and McFarlane 2003). Such fluctuations have been evidenced in *A. anguilla* and other Northern Hemisphere species (Bonhommeau *et al.* 2008, Bonhommeau and Rivot 2008, Miller *et al.* 2009; B. Knights, unpublished data presented to ICES WGEEL in 2007 and 2008). Variability in recruitment would be further exacerbated by longer migration distances and durations, and also by near-continent local conditions (e.g. variations in water temperatures). The sum of these effects would be greater towards the edges of species' ranges (e.g. B. Knights, op.cit.). It also appears that spawner emigration can be influenced by continental climate-environmental factors, e.g. geographical differences in precipitation and river discharges associated with the NAO (Kettle *et al.* 2008a; B. Knights, op. cit.). However, spatio-temporal variations in reproductive output by periodic strategists spread over relatively long periods promotes reproductive success in the long term and hence species survival, despite long intervals when environmental conditions are unsuitable for early life stages (King and McFarlane 2003, Winemiller 2005).

From the preceding discussions, facultative catadromy in anguillids could be interpreted as an ESS bet-hedging strategy in that any growth rate penalties imposed in freshwaters are offset by extensions in habitat utilisation and smoothing of stock-recruitment relationships. Colonisation of freshwaters may actually be dependent on critical densities, biomasses and carrying capacities being exceeded in saline habitats. This would correlate with the tendency for the numbers of recruits and hence stock densities in rivers to decline with distance from the spawning areas and oceanic migration pathways, such effects being most significant at the geographical extremes of species' distribution ranges (Bark *et al.* 2007, Knights *et al.* 2009). Dispersal upstream may also be density-dependent, driven by agonistic interactions and/or poor feeding. Evidence that inadequate feeding may stimulate local ranging behaviours comes from studies of juvenile eels caught in pass-traps. At the tidal head of the Severn Estuary, for example, mean growth rates of samples of such eels were only 30% and 72% of rates in samples from the Upper Estuary and nearby freshwater tributaries respectively (E.M. White, unpublished results). Similarly, growth rates of samples from pass-traps in the Thames catchment were 56% and 88% of nearby brackish and freshwater samples (derived from Naismith and Knights 1993). Growth rates may then recover when such eels reach low density sites further upstream. Also, declines in stock densities with distance from tidal limits (possibly exacerbated by barriers such as weirs and dams) tend to be offset by increases in individual size and hence biomasses. The proportion of (larger) females then tends to increase due to density-dependence of sex determination, leading to compensatory increases in spawner escapement biomass and relative fecundity. It must also be noted that lower densities in outer estuary, coastal lagoon and lake habitats also tend to produce relatively more females, e.g. as in the Thames catchment (Naismith and Knights 1993).

Another reason for the retention of facultative catadromy by anguillids is probably that, coupled to the potentially wide dispersal of larvae and the mobility of continental life stages, they are able to rapidly colonise new brackish and freshwater habitats and to recolonise disturbed or defaunated ones over wide geographical ranges. For example, after being restricted to the Iberian Peninsula and North Africa during the last Ice Age, European eels would have been amongst the earliest recolonisers of brackish and freshwaters as glaciers retreated and temperatures rose (Kettle *et al.* 2008b). They would also, for example, have been early entrants to the present-day brackish Baltic Sea when it fully connected to the North Sea ~8000 years ago. On more local scales they are early recolonisers of rivers after monsoonal and cyclonic wash-out, droughts, major pollution kills, etc.

Temperate-zone anguillids appear to be panmictic and it is possible that the main contributions to successful recruitment overall are made by relatively few females or that many females contribute only a relatively small number each (Pujolar *et al.* 2009). This would result in high genetic heterogeneity over broad spatio-temporal scales, helping to ensure the retention of ESS traits via gene flow over long time scales.

Conclusions

On the basis of current knowledge, many of the suggestions made above must be considered speculative. However, they suggest how and why facultative catadromy evolved in anguillids and why this life style has been successful over millions of years. From management viewpoints, the ideas proposed point out the need to use holistic approaches, including consideration of possible impacts of oceanic and continental climate factors in both saline and freshwaters over long time-scales as well as anthropogenic factors.

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Table 5.3.1. Mean net primary productivity (mgC m⁻² y⁻¹) estimated for different aquatic habitats and the distribution of various elopomorph families adapted to such habitats. In habitats marked with an asterisk, NPP is commonly supplemented by autochthonous detrital secondary production. Data from Koblenz-Mishke *et al.* (1970) and Lieth and Whittaker (1975).

Ecosystem	Mean net primary productivity (mg C m ⁻² yr ⁻¹)	Examples of elopomorph families in different habitats (~720 species)
Subtropical gyres	25	Serrivomeridae
Open oceans	125	Nemichthyidae
Continental shelves	360	Muraenidae
Inshore coastal waters	1240	Congriidae, Opichthidae
Coral reefs/algal beds	2500	Synaphobranchidae
Mangroves/marshes	2000*	Anguillidae
Estuaries	1500*	
Rivers	250	
Lakes	600*	

5.4 Searching for an adaptive understanding of anguillid eel migrations and life history

Introduction

Rapid growth in fish is commonly associated with enhanced fitness, because larger fish are less vulnerable to predation, and because rapid growth shortens the time to attainment of reproductive maturity. In Anguillid eels of the temperate zone, growth is generally faster in saline waters than in fresh (Cairns *et al.* 2009). The fact that many eels nevertheless undertake catadromous migrations to fresh water has been termed a paradox by Edeline (2007). This paradox is the more acute because glass eels that have the best body condition, and which are therefore best equipped to choose the habitat where they will settle, tend to preferentially move toward fresh water (European eel: Edeline *et al.* 2006 Bureau du Colombier *et al.* 2009, American eel: Sullivan *et al.* 2009).

Recent literature on fish diadromy emphasizes the diversity of diadromous movement patterns (Secor and Kerr 2009), historic pathways under which diadromy could have arisen (McDowall 2008, 2009; Tsukamoto *et al.* 2009), and the demographic consequences of diadromy (Secor 2007). This paper focuses on the adaptive nature of fish diadromy, and more specifically on anguillid eel catadromy in the temperate zone. Three approaches are used. First, it reviews the application to eels of the model of latitudinal inversion in productivity and food availability ratios proposed by Gross *et al.* (1988). Second, it looks at arithmetic mean fitness, geometric mean fitness, and non-adaptiveness as ways to examine the adaptive bases of eel fresh-salt migratory decisions. Finally, it reviews whole life-cycle adaptations of anguillid eels, for the purpose of finding consistent or recurring patterns that might shed light on the adaptive bases of eel migratory patterns.

Does latitudinal inversion of food availability ratios explain patterns of eel catadromy?

Most current thinking about the adaptive nature of anguillid eel migratory patterns is based on a paper published by Gross *et al.* in 1988. In this chapter, the ideas of Gross *et al.* (1988), and their modern interpretations, are collectively referred to as the latitudinal inversion of food availability ratios (LIFAR) model. This model is outlined below.

Gross *et al.* (1988) employs the analysis of McDowall (1987), which showed that in temperate latitudes, anadromous fish species outnumber catadromous fish species, while in the tropics, catadromous species outnumber anadromous species (Figure 5.4.1). Gross *et al.* (1988) reported that in temperate latitudes, ocean primary productivity is higher than freshwater productivity, while at low latitudes freshwater productivity is higher than ocean productivity (Figure 5.4.2). Gross *et al.* (1988) explained the latitudinal shift in the catadromous:anadromous species richness ratio by saying that the preponderance of anadromous species at temperate latitudes is due to greater food availability in the sea at such latitudes as indicated by higher primary productivity there. Similarly, the preponderance of catadromous species at low latitudes was said to be due to greater food availability in freshwater because of higher primary productivity there.

Temperate-zone anguillid eels are traditionally regarded as catadromous, but it is now known that many temperate-zone eels never enter fresh water. Edeline (2007), Aoyama (2009), McCleave and Edeline (2009), and others have interpreted lifetime marine residence in many temperate eels as due to higher productivity in the sea than in fresh water at temperate latitudes.

Several questions can be posed about the data, assumptions, and implications of the LIFAR model.

Under the LIFAR model it is expected that growth is controlled by food supply, which in turn is controlled by aquatic productivity. However Edeline *et al.* (2005) found that European glass eels fed *ad lib* in tanks had higher growth rates in saline water than in fresh. Cote *et al.* (2009) monitored growth in captive American eels for seven months from the glass eel to the post-elver stages, and found that animals grew faster in saline than in fresh water during this period, when both groups had equal food availability. Growth hormone promotes growth in teleost fishes, but has also been found to facilitate osmotic adaptation to seawater in a number of species, including European eels (Sakamoto and MacCormick 2006, Kalujnaia *et al.* 2007). These findings suggest that higher growth of eels in saline waters could be a direct conse-

quence of habitat salinity, and could come about even if food supply is not higher in saline than in fresh water.

The Gross *et al.* (1988) analysis of latitudinal productivity patterns is based on the ocean productivity data of Bunt (1975) (Figure 5.4.2). Bunt (1975) estimated productivity within cells of equal size, along latitudinal bands across the ocean. Since most of the world's oceans consist of deep waters beyond the continental shelf, productivities in the deep ocean drive the mean productivities used by Gross *et al.* (1988). The productivity of deep oceanic water is typically much lower than that of continental shelves and of bays and estuaries (Table 5.3.1). Hence the productivity of deep oceanic water cannot be relied upon to indicate the productivity of continental shelves, bays, and estuaries at the same latitude. The habitat choice that a diadromous fish may plausibly make is typically between fresh water and bay/estuary/continental shelf habitat, rather than between fresh water and deep oceanic habitat. Therefore the latitudinal productivity analysis used by Gross *et al.* (1988) has limited relevance to the migratory choices of diadromous fish.

Under the LIFAR model it is expected that temperate zone eels will grow faster in saline water than in fresh. Cairns *et al.* (2009) calculated ratios of saline: fresh growth rates in eels whose salinity histories had been measured by otolith strontium:calcium analysis. Saline-water growth was indeed faster than freshwater growth, although the saline: fresh growth ratio varied among species, with the American eel showing much higher saline: fresh growth ratios than other species.

Under the LIFAR it is expected that the ratio of growth in saline waters to growth in fresh water will increase with latitude. Figure 5.4.3 plots growth rate ratios of eels reared in saline water vs. eels reared in fresh water in the same water systems, against latitude (data from Cairns *et al.* 2009). These values were not significantly correlated ($r=0.479$, $P=0.229$, $n=8$). The upward but non-significant trend shown in Figure 5.4.3 is due to the *A. rostrata* saline: fresh growth ratios, which are much higher than those of other species. Without the *A. rostrata* data, the plot shows a non-significant downward trend ($r=-0.620$, $P=0.264$, $n=5$).

Under the LIFAR model it is expected that eels in the tropical zone will grow more rapidly in fresh than in saline water, and that marine residence should be uncommon because fresh water offers better feeding opportunities. The only tropical study which has used Sr:Ca to measure habitat history is that of Briones *et al.* (2007) in the Philippines. This study reported that eels sampled in the lower part of the river were *Anguilla bicolor*, most of which had marine experience during their growth phase. All of the eels at an upstream sampling point were *A. marmorata*, most of which had used fresh water exclusively during their growth phase. Robinet *et al.* (2007) found that *A. bicolor* was confined to lower altitude reaches in rivers of Reunion Island, Indian Ocean, while *A. marmorata* occupied all altitude zones. Growth rates calculated from data reported by Briones *et al.* (2007) suggest that *A. bicolor*, which commonly used saline habitats, had similar or higher growth rates than *A. marmorata*, which generally did not use saline habitats (Table 5.4.1). These growth comparisons must be viewed with caution because the comparisons are between species, and growth may be influenced by species, and also because growth rates were calculated from group means, rather than from data on individual fish.

The LIFAR model implicitly assumes that the need to maximize feeding opportunities drives eel migratory patterns during the growth phase. This assumption is widely accepted (Edeline 2007, Aoyama 2009, McCleave and Edeline 2009), although

neither this assumption nor possible alternatives have been critically evaluated by Gross *et al.* (1988) or by subsequent literature.

Finally, the LIFAR model assumes that food availability determines, or at least strongly influences, species richness. In 2008, McDowall rejected the conclusions of the Gross *et al.* (1988) paper which he co-authored 20 years earlier, and argued that there is no basis for the view that food availability controls species richness. Geographic variation in genotype is commonly a precursor to speciation, and therefore favours species richness. It would seem particularly difficult to support a general relation in diadromous fishes between species richness and food availability given that the leading anadromous family (Salmonidae) has a migration pattern that favours geographic heterogeneity of genotype, while the leading catadromous family (Anguillidae) has a migration pattern that favours geographic homogeneity of genotype (McDowall 1987, Minegishi *et al.* 2009).

The above considerations suggest that the LIFAR model does not fully or reliably explain migratory patterns in anguillid eels. It therefore seems appropriate to look for alternate approaches that might help clarify the adaptive basis of eel migratory patterns. The following sections propose two such approaches.

Alternate views of fitness optimization

Eels in the temperate zone commonly grow faster in saline water than in adjacent fresh waters, with mean saline:fresh growth ratios of 2.07 for American eels in north-eastern North America, and between 1.12 and 1.14 for European, Japanese, and short-finned eels (Cairns *et al.* 2009). The use by many eels of fresh water, despite higher growth in saline water, is paradoxical (Edeline 2007). This section discusses three types of adaptive explanation to this phenomenon.

First, the use of slow-growth fresh water habitat might be explained by arithmetic mean fitness. This is the traditional view of fitness, which holds that natural selection shapes an animal's behaviour so that it will maximize its individual fitness. This view excludes arguments based on good of the population or good of the species. If fitness is measured several times, the overall fitness level will be a simple arithmetic mean. The idea that natural selection favours the maximization of individual fitness does not necessarily mean that the population will be pushed towards a single pattern. As Edeline (2007) has pointed out, it is possible that two migratory contingents of eels can co-exist which have equal fitness.

One possible basis for fitness equality between catadromous and marine-resident eels would be that slow growth in fresh water is offset by low mortality there. Demographic data in the saline and fresh reaches of the tidal Hudson River estuary in New York State, USA (Morrison and Secor 2004), offer a test of this idea. In this system growth rates are about twice as high in saline water as in fresh, but, estimated loss rates (a proxy for mortality) are similar between the brackish and fresh zones (Cairns *et al.* 2009). This test thus fails to support the notion that low freshwater mortality offsets slow growth there. However, it must be emphasized that this is a single study in a tidal system and may not be representative of other areas, especially non-tidal fresh waters.

Second, the use of slow-growth freshwater habitat might be explained by considerations of geometric mean fitness. Theoretical and empirical tests have confirmed that the geometric mean, rather than the arithmetic mean, indicates true fitness of a lineage, and that individuals may act in a way that improves their geometric mean fit-

ness, even at the expense of lowering their arithmetic fitness (Yoshimura and Jansen 1996, Fox and Rauter 2003, Orr 2007).

The geometric mean of a series of numbers is defined as the product of the series raised to the power of $1/n$, where n is the number of numbers in the series. If all numbers in the series are the same, the geometric mean and the arithmetic mean are the same. However, if the numbers in the series vary, the geometric mean will be lower than the arithmetic mean, and the depression of the geometric mean relative to the arithmetic mean will increase with increasing variance of the series.

In a simple population with discrete and non-overlapping generations, fitness may be operationally defined as the ratio of population at generation $g+1$ divided by the population at generation t (see Yoshimura *et al.* 2009). Consider the following scenarios of fitness values over five generations:

1, 1, 1, 1, 1: Arithmetic mean fitness = $(1+1+1+1+1)/5 = 1$

Geometric mean fitness = $(1 \times 1 \times 1 \times 1 \times 1)^{(1/5)} = 1$

1, 1, 1, 1, 0.5: Arithmetic mean fitness = $(1+1+1+1+0.5)/5 = 0.9$

Geometric mean fitness = $(1 \times 1 \times 1 \times 1 \times 0.5)^{(1/5)} = 0.87$

1, 1, 1, 1, 0: Arithmetic mean fitness = $(1+1+1+1+0)/5 = 0.8$

Geometric mean fitness = $(1 \times 1 \times 1 \times 1 \times 0)^{(1/5)} = 0$

In the second scenario the presence of a low fitness value causes the geometric mean fitness to be lower than the arithmetic mean fitness. In the third scenario the presence of a zero value causes only a moderate depression in the arithmetic mean fitness, but the geometric mean fitness falls to zero. The biological interpretation of this is that if all animals in a generation fail to reproduce, the lineage becomes extinct.

Because variance in fitness depresses geometric mean fitness, behaviours which lower fitness variance will improve geometric mean fitness. Use of a variety of habitats spreads risk and may lower fitness variance and optimize geometric mean fitness, because random environmental fluctuations that disrupt fitness in some habitats are unlikely to have the same negative effects on all habitats. Facultative diadromy, in which eels use both saline and freshwater habitats, might therefore be an adaptive response to the need to maximize geometric mean fitness. In this view, facultative diadromy increases resilience of eel populations, and the resilience itself is adaptive. However, bet-hedging behaviour to maximize geometric mean fitness has been shown to be adaptive only in specific ecological and demographic circumstances (Yoshimura and Jansen 1996, Fox and Rauter 2003, Orr 2007, Yoshimura *et al.* 2009). To determine whether geometric mean fitness considerations can explain catadromous migrations in anguillid eels would require detailed analyses that have yet to be conducted.

The third type of explanation proposes that the catadromous behaviour is maladaptive, under either or both arithmetic and geometric mean fitness. In this view, eels that enter freshwater suffer fitness costs, with no offsetting advantages. Battin (2004) pointed out that anthropogenic impacts commonly reduce the fitness value of habitats, but that animals sometimes have no way of knowing this. Hence animals that respond to cues which formerly indicated good habitat may be unwittingly led into poor habitat.

Recurring themes in eel life-cycle patterns

The choice of growth habitat that temperate-zone eels make is one of many choices they make during their life cycle. In this section, the eel's life cycle is examined in holistic fashion, to look for overall or recurring adaptive strategies. The premise is that such recurring patterns might suggest perspectives or offer insight into the adaptive basis of the eel's choice of salinity zone during the growth phase.

Figure 5.4.4 shows the main features of the anguillid eel life cycle, and that of typical teleost fish. Many of the major traits of eels differ from those of most other teleosts. Traits where the eel diverges from the common or typical teleost pattern include elongate body, nocturnality, burrowing behaviour, use of very low productivity spawning grounds, and prolonged transparency of the larval phase, and exceptionally low resting metabolic rate (Clarke and Johnston 1999) (Figure 5.4.4). In financial investment, the practice of doing things in a manner opposite to most other investors is termed contrarianism. Likewise, a fish that does things in a different or opposite way to most other fish may be termed a contrarian. None of the features of the anguillid eel life cycle is unique, but overall eels appear to show a broad and repeated pattern of divergence from the teleost norm, such that the label "contrarian" is warranted.

Figure 5.4.5 shows some major adaptive features of anguillid eels. This figure shows the interconnectedness of these features, where a single trait may enable diverse ecological functions. For example, the eel's elongate body facilitates creeping up vertical walls at the elver stage to colonize upriver habitat (Legault 1988), burrowing in the substrate for daytime and winter hiding (Atkinson and Taylor 1991), and long-distance migration to the spawning grounds with remarkably low energy expenditure (van Ginneken *et al.* 2005). The eel's elongate body is poorly adapted to burst swimming (van Ginneken *et al.* 2002), which increases vulnerability to predatory attack. However, use of daytime and winter burrows (facilitated by the elongate body form) mitigates this predation risk. Natural mortalities estimated for European eels during the growth phase are much lower than those estimated for fish in general, when natural mortalities are controlled for body size (Bevacqua *et al.* unpubl. ms.).

Adaptations which are oriented towards slow growth and low mortality risk occur repeatedly in the anguillid life cycle. These include use by larvae of barren waters with few predators, prolonged larval transparency, nocturnality in the yellow stage, use of burrow refuges, and slow burst speed.

This section has proposed that the eel life cycle is characterized by contrarian adaptations, slow growth, and low natural mortality. This characterization is preliminary; a firmer characterisation of the eel life cycle requires a more complete and rigorous evaluation of eel traits. In the meantime, it may be speculated that these characteristics are central pillars of the life history strategy which has enabled anguillid eels' remarkable success. Eels are typically present and active at times and places (e.g. at night, or in barren oceanic waters) where most other fish are absent or inactive. This behaviour can be viewed as a broadly-based niche differentiation which reduces competition with other species and provides enhanced access to resources.

Gross *et al.* (1988) and most other authors view eel life history as being primarily driven by the need for feeding opportunities. The perspective of eel life history offered in this section suggests that eel choice of habitat during the growth phase may instead be guided by avoidance of competition with other fish, and towards slow growth and minimization of predation risk.

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Table 5.4.1. Salinity history and growth rate of eels in a Philippine river, from Briones *et al.* 2007. Growth rates are based on mean length and age data from Briones *et al.* 2007 and glass eel lengths from Marui *et al.* 2001.

Species	Distance from river mouth (km)	N	Percent with saline history	Growth (cm/yr)
<i>A marmorata</i>	100	9	11.1	4.1
<i>A bicolor bicolor</i>	13	11	62.5	4.2
<i>A bicolor pacifica</i>	3	11	100	4.0
<i>A bicolor pacifica</i>	9	10	100	7.3

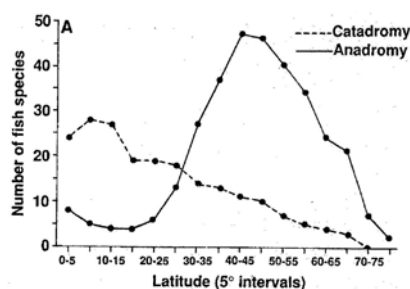


Figure 5.4.1. Number of catadromous and diadromous species in relation to latitude, from Gross *et al.* 1988.

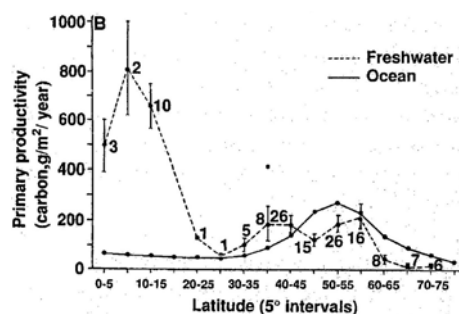


Figure 5.4.2. Primary productivity in freshwater and the oceans in relation to latitude, from Gross *et al.* 1988.

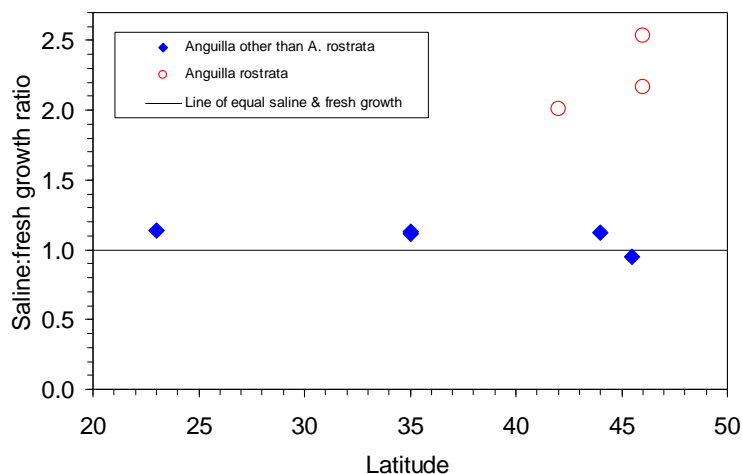


Figure 5.4.3. Relation between the ratio of mean annual length increments in eels reared in saline water vs. fresh water, and latitude. The plot is based on data in which otolith strontium:calcium ratios indicate that eels used only a single salinity zone during their continental phase (Cairns *et al.* 2009). Where data within a study were reported separately for males and females and for brackish:fresh growth ratio and for salt:fresh growth ratio, the mean of the various values was used.

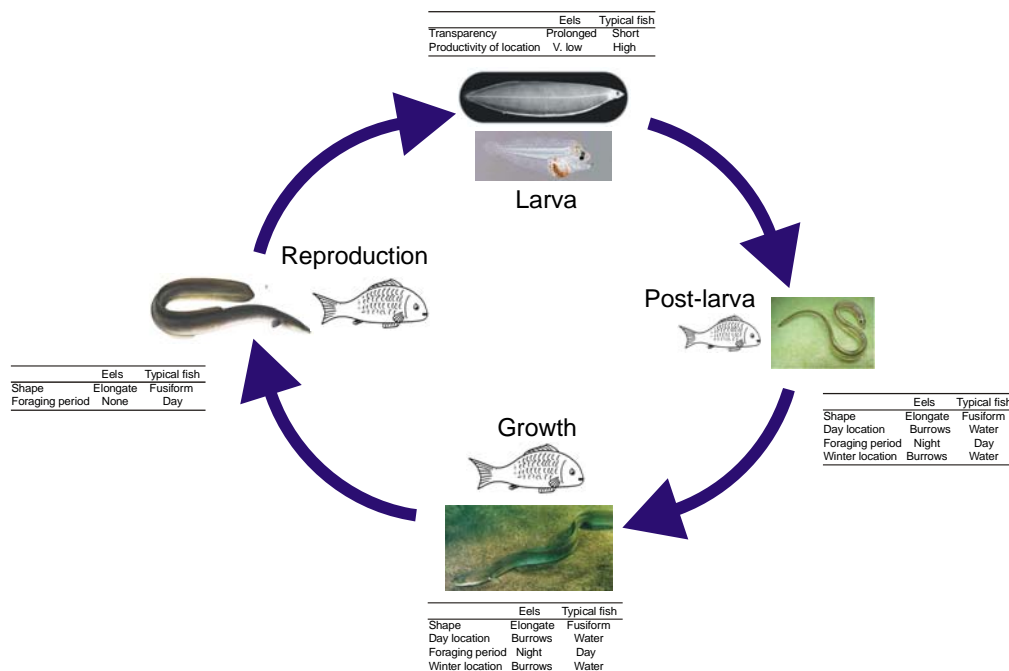


Figure 5.4.4. Life cycles of anguillid eels and typical teleost fish.

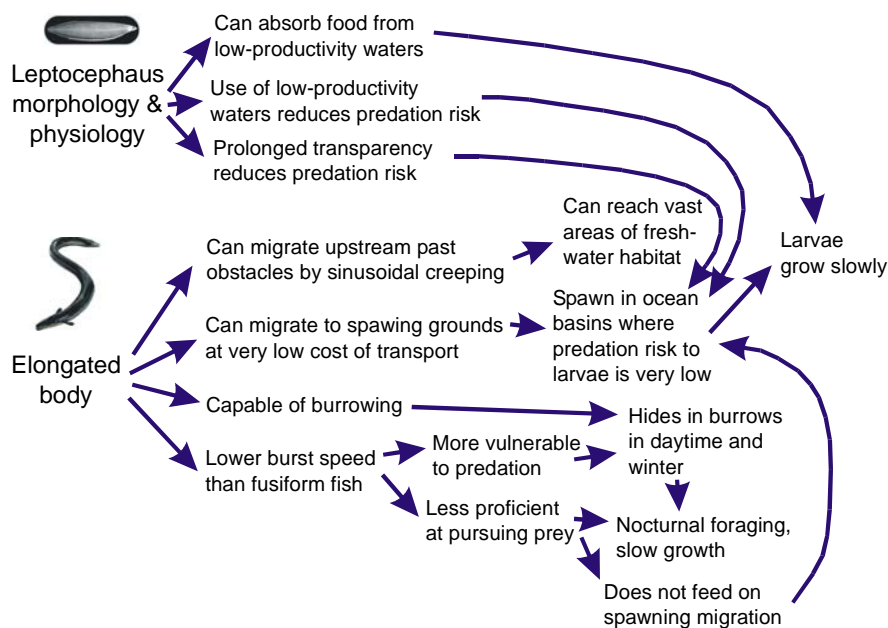


Figure 5.4.5. Some adaptive traits of anguillid eels, behaviours they enable, and their ecological consequences.

5.5 Discussion - choice of salinity zone

Implications for stock assessment and management

We lack knowledge on spawner production on a regional and global scale, but we do know that management practices in saline waters may affect populations in fresh waters.

Research needs

Clarify whether the various contingents represent genetic differences or phenotypic plasticity; clarify how the relation between salinity and otolith strontium:calcium ratios varies with species and location; establish the life history parameters for each contingent; because temperate eels are considered panmictic, establish international data collection systems; work towards understanding the evolution of different contingents.

Annex 1: SGAESAW Terms of Reference for the meeting in 2009

2008/2/DFC06 A Study Group on Anguillid Eels in Saline Waters [SGAESAW] (Chair: David Cairns*, Canada) will be established and will meet in Gothenburg, Sweden on 3–5 September 2009 to:

- a) review and synthesize knowledge about habitat use, demographic characteristics and stock assessment methods in anguillid eels in saline waters in comparison with these features in fresh waters, and to review and evaluate available information on the relative importance of eel production from saline vs. fresh rearing areas;
- b) review and synthesize knowledge about factors which influence eels to settle in saline vs. fresh rearing areas, especially in the context of changing overall recruitment levels;
- c) make recommendations on the use of habitat-specific demographic characteristics in population models (e.g. SPR, biomass targets, silver eel escapement rates), and on overall conservation approaches that embrace salinity-based differences; and
- d) define research and analytic approaches for anguillid eels in saline waters that will advance progress towards the ability to construct robust stock-wide management models.

SGAESAW will report by 31 October 2009 for the attention of the WGEEL, ACOM TGRECORDS and SCICOM.

Supporting Information

Priority:	The work of the Group is essential if ICES is to be appropriately placed to advise on the development of recovery plans for eels in Europe and North America, and particularly the Eel Management Plans required under EU Regulation 1100/2007.
Scientific justification and relation to action plan:	European and American eel stocks are currently in a severely depleted state. ICES has proposed that biological reference points for eels could be derived from spawner-per-recruit (SPR) analysis and the EU Regulation for the Recovery of the Eel Stock requires biomass estimates of current silver eel escapement. For this approach to provide meaningful results at the local and stock (species) scale, biologists need to know the relative importance of the habitat types used by eels and what demographic characteristics they exhibit in these habitats. One key habitat distinction is between fresh and saline (brackish/salt) waters. While recent research has increasingly revealed the importance of brackish and sheltered salt water habitats for eel, little remains known about eels in estuarine and particularly coastal waters, and most assessments currently take little or no account of the importance of these habitats in the production of potential spawners. The Study Group will inform the future development of assessment methods.
Resource requirements:	None.
Participants:	Members of WGEEL and invited experts from areas of the North Atlantic and elsewhere with eel populations.
Secretariat facilities:	None.
Financial:	None. It has been proposed that a preliminary meeting will be held in USA or Canada to co-ordinate inputs from North America.
Linkages to advisory committees:	The proposal originates from DFC but is of direct relevance to ACOM and review group activities in relation to the development of appropriate assessment methods for eel.

Linkages to other committees or groups:	WGEEEL and SciCom, other Working Groups on inshore fisheries, Canadian Eel Science Working Group, U.S. Atlantic States Marine Fisheries Commission Eel Technical Committee
Linkages to other organizations:	Institutes participating in EU FP7 EELIAD, Organisations developing EU Eel Management Plans

Annex 2: Meeting agendas

First meeting, 16-18 March 2009, Sackville, New Brunswick, Canada.

The meeting was held at the Marshlands Inn.

Monday 16 March

8:30 Start of the meeting

Introductions

Role of Study Groups in ICES

Review of the Terms of Reference and meeting agenda

Gaps and limitations in knowledge of inter-habitat movements in eels

A brief summary of otolith strontium:calcium studies in anguillid eels - David Cairns

Cautions in the use of otolith microchemistry to infer anguillid eel migration patterns - Brian Jessop

Do strontium-calcium measurements fail to detect wintering migrations to fresh-water of eels that summer in saline waters? - Marie Clément

What are the migratory patterns of small eels in the Hudson River system? - Karin Limburg

Migration and habitat choice in small eels - David Cairns

Preparation of an atlas of American eel habitat and fisheries on the east coast of North America

Mapping and measuring eel habitat in the Gulf of St. Lawrence by depth zone and by exposure category - Jean-Denis Dutil and Serge Proulx

Mapping eel fishing areas in eastern North America - Joshua Mailhiot

Locations of eel fishing in Delaware - John Clark

Locations of eel fishing in Virginia - Laura Lee

Discussion - How to obtain, compile, analyze, and map the further information that is necessary to complete the Atlas.

Survey data sets which could be explored for presence/absence or relative abundance of eels in estuarine, bay, inshore, and offshore waters

A preliminary list of survey data sets - David Cairns

Discussion

Tuesday 17 March

Review of draft report from yesterday's session.

Ecology, movements, populations, and demographic characteristics of American eels in saline and fresh waters

American eel landings and densities, by habitat salinity - David Cairns

Eel movements and growth in the Saint-Jean River system, Gaspé Peninsula, Quebec - Mélanie Dionne

Eel densities and regional populations in saline and fresh waters of the southern Gulf of St. Lawrence - Jason Hallett

Eel distribution and depth preferences in Delaware Bay and its tidal tributaries - John Clark

Eel ecology, movements, and growth in St. Jones River, Delaware - Dewayne Fox
Discussion

Catadromy vs. marine residence in eels

A re-examination of the Gross *et al.* model of latitudinal variation in diadromy patterns - David Cairns

Explanations of eel catadromy based on individual fitness, on population resilience, and on non-adaptiveness - David Cairns

Consequences of diadromy to anguillid eels - Dave Secor
Discussion

Moving forward to the meeting in Sweden

Discussion.

Wednesday 18 March

Review and completion of draft reports.

Discussion of the implications of facultative diadromy on conservation and management

- Are anthropogenic impacts changing the relative importance of fresh vs. saline habitat use, and if so, what are the implications for population monitoring and conservation management?
- How can management approaches embrace and use salinity-based differences in eel ecology?
- How can knowledge of the proportion of total American eel habitat that is fished vs. unfished be used in conservation management?
- Are we within striking distance of obtaining an estimate of the total standing stock of American eels, and if so, how could such knowledge be used in conservation management?
- What research and analytic approaches are most likely to advance understanding of fresh-saline dynamics in eel ecology, and lead us to effective conservation models?

Second meeting, 3-5 September 2009, Gothenburg, Sweden.

The meeting was held at the Agren Residence, University of Gothenburg, on 3-4 September, and at the Swedish Board of Fisheries on 5 September.

Thursday, 3 September

Welcome

Opening remarks from the Director of Research, Swedish Board of Fisheries - Ingemar Berglund

Terms of Reference and meeting objectives

Introductions

Local arrangements - Hakan Westerberg

Anguillid eel habitat use in saline and fresh water

Review of Sackville presentations - David Cairns

Behaviour difference between silver eel migration in lakes and marine waters - Hakan Westerberg

Migratory behaviour and habitat use of Japanese eel in the estuary as revealed by both conventional mark-recapture method and otolith elemental signature (by Shih-Huan Lin and Wann-Nian Tzeng) - Wann-Nian Tzeng

European eel movements during continental life in the Rhône river delta (South of France): high level of sedentarity revealed by otolith microchemistry (by Jacques Panfili, Audrey Darnaude, Yu-Chia Lin, Mikael Chevalley, Yoshiyuki Iizuka, Wann-Nian Tzeng, and Alain Crivelli) - Wann-Nian Tzeng

Using stable isotopes and fatty acids to examine salinity habitat use in European eels - Chris Harrod

Discussion - habitat use in saline and fresh water

Implications for stock assessment and management - Chris Harrod

Key research needs - Hakan Wickstrom

Key research methods - Alan Walker

Anguillid eel demographic characteristics in saline and fresh water

Characteristics of yellow eel along a North Sea-Baltic gradient (by Ann-Britt Florin) - Jan Andersson

Naturally-recruited and restocked eels in Latvia: discrimination and growth comparison (by Yu-Jia Lin, Jen-Chieh Shiao, Maris Plikshs, Artis Minde, Yoshiyuki Iizuka, and Isaak Rashal) - Wann-Nian Tzeng

Friday, 4 September

Naturally-recruited and restocked eels in Latvia: discrimination and growth comparison (continued) - Wann-Nian Tzeng

The effects of ambient salinity on eel spawner quality - Reinhold Hanel

Demographic differences between freshwater and estuarine eels in the Severn, England - Miran Aprahamian

Population dynamics of European eel in a Mediterranean lagoon - Daniele Bevacqua

Eel growth and quality issues from Mediterranean lagoons - Fabrizio Capoccioni

Discussion - demographic characteristics in saline and fresh water

Implications for stock assessment and management - Willem Dekker

Key research needs - Miran Aprahamian

Key research methods - Patrick Lambert

Anguillid eel densities, populations, and relative abundance in saline and fresh water

Review of Sackville presentations - Mélanie Dionne

Synthesis of American eel monitoring work on the Saint-Jean water system, Québec, Canada, 2001-2007 - Mélanie Dionne

American eel landings and densities, by habitat salinity - David Cairns

Densities, populations and movements of yellow eels in U.K. estuaries - Alan Walker

Yellow eel standing stocks in saline waters of the southern Gulf of St. Lawrence, Canada - Jason Hallett

Estimating estuarine yellow eel density using spatially explicit mark-recapture - a case study and preliminary evaluation - Russell Poole

Characterizing the ecology, productivity and stability of saline eel populations in Northern Ireland - Kenny Bodles

The European eel in Portuguese brackish waters: a general overview - Isabel Domingos

Geographical patterns in yellow eel CPUE in Sweden - Jan Andersson

The unexpected lack of a freshwater origin in most silver eels leaving the Baltic Sea - Hakan Wickstrom

Historic eel surveys in the German Bight of the North Sea - Klaus Wysujack

Eels in bottom trawl surveys in the North Sea - Willem Dekker

Trying to estimate the density of the European eel stock in coastal areas - a survey approach in the Baltic Sea of Northern Germany - Malte Dorow

Saturday, 5 September

Review of productivity in areas with different salinities in France - Laurent Beaulaton

The effect of stocking shallow marine waters compared to freshwater - Michael Pedersen

Discussion - densities, populations and relative abundance

Implications for stock assessment and management - Malte Dorow

Key research needs - Mélanie Dionne

Key research methods - Klaus Wysujack

Choice of salinity zone in growth-phase anguillid eels

Review of Sackville presentations - David Cairns

Consequences of facultative catadromy in American eel - Dave Secor

Review of behavioural experiments and theories on habitat choice by recruiting glass eel - Patrick Lambert

Speculations on the selective advantages and evolution of facultative - Brian Knights

Searching for an adaptive understanding of Anguillid eel migrations and life history - David Cairns

Discussion - choice of salinity zone

Implications for stock assessment and management - Jan Anderssen

Key research needs - Wann-Nian Tzeng

Key research methods - Michael Pedersen

Recommendations

On use of habitat-specific demographic characteristics in population models.

On overall conservation approaches that embrace salinity-based differences

On research and analytic approaches that will enhance ability to construct robust management models

Housekeeping

Plans for finalization of report

Appointment of a person to report Study Group recommendations to the meeting of the Transition Group on the Science Requirements to Support Conservation, Restoration and Management of Diadromous Species, during the ICES ASC in Berlin, 22 September 2009.

Annex 3: List of meeting participants

NAME	ADDRESS	PHONE/FAX	E-MAIL	MEETINGS ATTENDED
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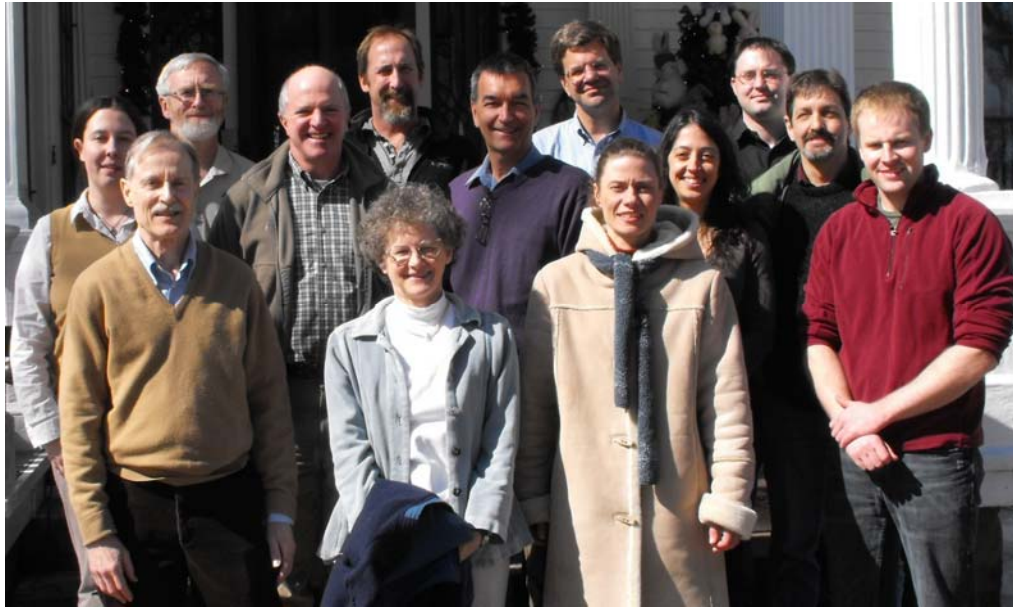
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*Did not attend either meeting, but delivered a presentation by audio link

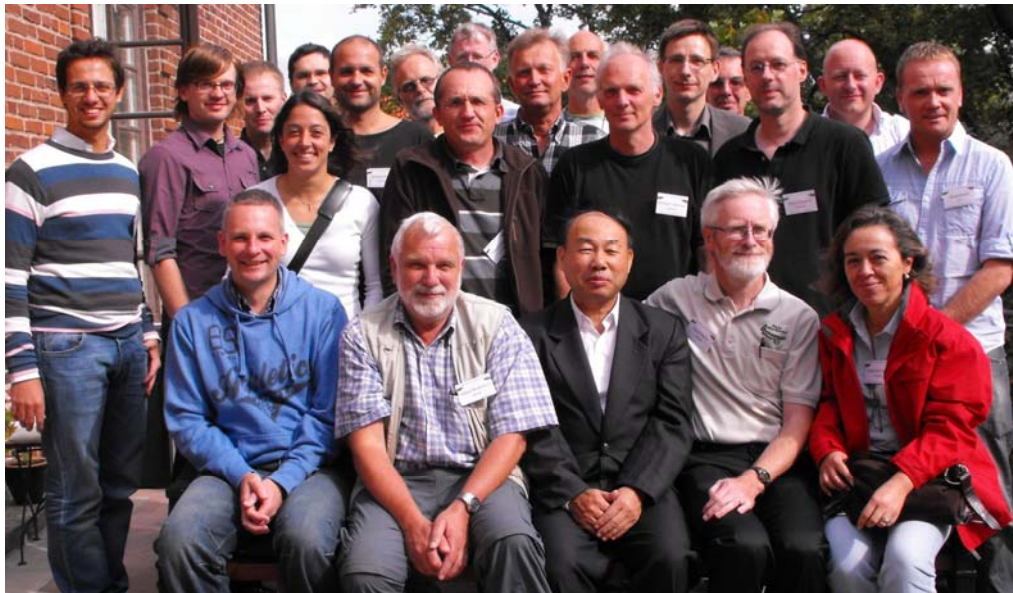
**Did not attend either meeting, but prepared material which was presented by Jan Andersson

***Did not attend either meeting, but prepared material which was presented by Wann-Nian Tzeng

Annex 4: Photographs of meeting participants



Sackville meeting: Front row - Brian Jessop, Karin Limburg, Marie Clément, Jason Hallett; second row - Laura Lee, John Clark, Jean-Denis Dutil, Mélanie Dionne, Serge Proulx; third row - David Cairns, Dewayne Fox, Dave Secor, Joshua Mailhiot.



Gothenburg meeting: Front row - Alan Walker, Håkan Westerberg, Wann-Nian Tzeng, David Cairns, Isabel Domingos; second row - Fabrizio Capoccioni, Kenny Bodles, Mélanie Dionne, Patrick Lambert, Michael Pedersen, Klaus Wysujack, Derek Evans; third row - Jason Hallett, Laurent Beaulaton, Reinhold Hanel, Håkan Wickström, Russell Poole, Jan Andersson, Willem Dekker, Malte Dorow, Miran Aprahamian, Chris Harrod.

Annex 5: Report to the ICES Steering Group on Ecosystem Function

Introduction

The ICES Study Group on Anguillid Eels in Saline Waters (SGAESAW) met on 16–18 March 2009 in Sackville, Canada, and on 3–5 September in Gothenburg, Sweden. The chair was David Cairns (Canada). Thirty-two participants representing 12 nations attended one or both of the meetings.

Saline waters are important growth habitats for European and American eels, but receive little attention in most current assessments. To address this, SGAESAW was asked to review knowledge of saline-fresh differences in ecological parameters and stock assessment methods, and recommend approaches that will embrace salinity-based differences in management models.

The approach taken at the meetings was to hear presentations on topics pertinent to the SGAESAW mandate, discuss reported findings, and generate recommendations for research and management.

In this report, the term “saline” refers to brackish and salt waters which may be used by anguillid eels as growth habitat.

Findings

European and American eels are traditionally viewed as catadromous, meaning they migrate to fresh water during their growth period. The use of otolith strontium:calcium ratios to infer history of habitat use has revealed that eels adopt one of three movement patterns: a) exclusive saline-water residency, b) exclusive freshwater residency, or c) shifts between saline and fresh waters.

Eel densities may vary widely among sites, even within the same geographical area. Small juvenile eels appear to differ from larger eels in their fine-scale distribution, presumably to reduce risk predation, including cannibalism.

Eel growth increases with temperature, and eels generally grow faster in saline water than in fresh water. Eels produced in saline waters have lower loads than those grown in fresh water of the swim-bladder nematode *Anguillicoloides crassus*, which may improve their chances of reaching the spawning grounds.

An estimated 11 million yellow eels occupy saline waters of the southern Gulf of St. Lawrence, Canada. Elsewhere, local and regional populations of anguillid eels in saline waters are generally unknown. In North America, eels appear to be rare or absent in exposed marine waters. In Europe, eels are presently found in exposed waters of the southern North Sea close to the Dutch, German, and Swedish coasts. Most silver eels exiting the Baltic Sea have grown in brackish water, and in France, the great majority of eel landings are from saline water. In other regions, there is little information from which to infer the ratio of saline to fresh origin among migrating silver eels.

Catadromous migrations of temperate-zone anguillid eels are paradoxical, because these eels experience slower growth in fresh water, and slow growth is commonly associated with lower fitness.

Implications and perspectives

European and American eels are widespread and common in estuaries and sheltered bays, and in at least one exposed marine region (the southern and eastern edges of the North Sea). However the overall ratio of saline to fresh habitat in production of successful spawners remains unknown. The superior growth in saline vis-à-vis fresh habitats has also been confirmed, but salinity-specific demographic data cannot be used in population models in a comprehensive way due to the absence of comparative data on natural mortality in the two habitats. Given current limits to understanding, it is not presently possible to formulate management recommendations that are specific to salinity zones.

SGAESAW was formed because saline habitats are almost certainly of major importance to the conservation of European and American eels, but in general we do not properly treat, and we do not know how to properly treat, these habitats in conservation models. SGAESAW has made only a small beginning to solve this large and complex problem.

Future progress towards understanding and properly treating eel conservation in saline waters will require broad-scale efforts which draw best advantage from emerging research approaches, including the following. The loading of multiple investigations on a single field sampling campaign has the potential to improve efficiencies and ecological insights. Studies of stable isotope and fatty acid composition, and otolith profiling of elements in addition to strontium and calcium, may offer further insights into saline-fresh migrations. Densities of small juvenile eels can be measured by lowering an open-bottomed aluminum box to the substrate and extracting surface material by hand or by vacuum-pump. Densities of larger yellow eels may be measured by night-time surveys with a glass-bottom boat, or (potentially) by a corral trap with fyke net cones placed in each corner and with additional fyke nets inside the corral. An atlas of potential eel habitat on the east coast of North America is under development.

Recommendations

SGAESAW recommends:

That existing data be collated and new data be collected, on the quantity, demographic characteristics, distribution, potential habitat, and quality of eels in saline waters of Europe and North America, and that such data be assembled into an overview report.

That analyses be undertaken of eel demographic processes in relation to habitat characteristics in saline environments.

That the precautionary approach be applied to European and American eels at all locations where they occur.

That work be undertaken to calibrate and validate sampling methods to ensure their comparability and to facilitate robust assessments of eel production.

That results of the data collation, demographic process analysis, and sampling comparability exercises be reported to appropriate subgroups of the ICES/EIFAC Eel Working Group.

That an ICES Study Group on Anguillid Eel Stock Assessment Methodology in Saline Waters be struck, with a mandate to meet before or during autumn 2010.

Linkage with the ICES Science Plan

The work of SGAESAW is linked to the following elements of the ICES Science Plan:

4. High priority research topics

4.1. Understanding Ecosystem Functioning.

Fish life history information in support of Ecosystem Approach to Management (EAM);

Biodiversity and the health of marine ecosystems;

The role of coastal-zone habitat in population dynamics of commercially exploited species.

4.2. Understanding Interactions of Human Activities

Impacts of fishing on marine ecosystems;

Population and community level impacts of contaminants, eutrophication, and habitat changes in the coastal zone.

4.3. Development of options for sustainable use of ecosystems.

Marine living resource management tools.

Annex 6: Recommendations

RECOMMENDATION	FOR FOLLOW UP BY:
1. That existing data be collated and new data be collected, on the quantity, demographic characteristics, distribution, potential habitat, and quality of eels in saline waters of Europe and North America, and that such data be assembled into an overview report.	ICES/EIFAC Working Group on Eel (WGEEL), Canadian Eel Science Working Group, American Eel Technical Committee of the U.S. Atlantic States Marine Fisheries Commission.
2. That analyses be undertaken of eel demographic processes in relation to habitat characteristics in saline environments.	ICES Study Group on Anguillid Eels in Saline Waters (SGAESAW)
3. That the precautionary approach be applied to European and American eels at all locations where they occur.	ICES, Canadian Eel Working Group, U.S. Atlantic States Marine Fisheries Commission
4. That work be undertaken to calibrate and validate sampling methods to ensure their comparability and to facilitate robust assessments of eel production.	ICES Study Group on Anguillid Eels in Saline Waters (SGAESAW)
5. That results of the data collation, demographic process analysis, and sampling comparability exercises be reported to appropriate subgroups of the ICES/EIFAC Eel Working Group..	ICES/EIFAC Working Group on Eel (WGEEL)
6. That an ICES Study Group on Anguillid Eel Stock Assessment Methodology in Saline Waters be struck, with a mandate to meet before or during autumn 2010.	WGRECORDS, SCICOM Steering Group on Ecosystems Function (SSGEF)

Annex 7: SGAESAW Terms of reference for the meeting in 2010

2009/2/SSGEF22 The Study Group on Anguillid Eels in Saline Waters (SGAESAW), chaired by [to be announced] will meet in VENUE, DATE [to be announced] to:

- a) Extract and examine eel data from general fish stock surveys in open marine waters;
- b) Review and develop local stock assessment methods in anguillid eels in saline waters with reference to habitat use, demographic characteristics and sampling techniques and in comparison with these features in fresh waters;
- c) Make recommendations on the use of habitat-specific demographic characteristics in population models (e.g. SPR, biomass targets, silver eel escape rates), and on overall conservation approaches that embrace salinity-based differences;
- d) Define research and analytic approaches for anguillid eels in saline waters that will advance progress towards constructing robust stock-wide management models.

SGAESAW will report by 31 December 2010 (via SSGEF) for the attention of WGEEL, SGIPEE, ACOM, WGRECORDS and SCICOM.

Supporting Information

Priority	The work of the Group is essential if ICES is to be appropriately placed to advise on the development of recovery plans for eels in Europe and North America, and particularly the Eel Management Plans required under EU Regulation 1100/2007.
Scientific justification	European and American eel stocks are currently in a severely depleted state. ICES has proposed that biological reference points for eels could be derived from spawner-per-recruit (SPR) analysis and the EU Regulation for the Recovery of the Eel Stock requires biomass estimates of current silver eel escapement. For this approach to provide meaningful results at the local and stock (species) scale, biologists need to know the relative importance of the habitat types used by eels and what demographic characteristics they exhibit in these habitats. One key habitat distinction is between fresh and saline (brackish/salt) waters. While recent research has increasingly revealed the importance of brackish and sheltered salt water habitats for eel, little remains known about eels in estuarine and particularly coastal waters, and most assessments currently take little or no account of the importance of these habitats in the production of potential spawners. The Study Group will inform the future development of assessment methods. A major gap identified by SGAESAW 2009 was the lack integrated assessment methods to determine the density and biomass of the local stocks.
Resource requirements	None.
Participants	Members of WGEEL and invited experts from areas of the North Atlantic and elsewhere with eel populations.
Secretariat facilities	None.
Financial:	Covering the expenses of travel & meetings would be appropriate
Linkages to advisory	The group is of direct relevance to ACOM in relation to the development of appropriate assessment methods for eel.

committees	
Linkages to other committees or groups	WGEEL, SGIPEE and SCICOM, other Working Groups on inshore fisheries, Canadian Eel Science Working Group, U.S. Atlantic States Marine Fisheries Commission Eel Technical Committee
Linkages to other organizations	Institutes participating in EU FP7 EELIAD, Organisations developing EU Eel Management Plans, DGMARE Pilot study on estimating silver eel biomass