

Demographic attributes of yellow-phase American eels (*Anguilla rostrata*) in the Hudson River estuary

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Abstract: Management of American eels (*Anguilla rostrata*) requires an understanding of how demographic attributes vary within large estuaries. Yellow-phase American eel length and age structure, growth, dispersal, nematode infestation rates, loss rate (natural mortality and emigration), and production were measured at six sites throughout the tidal portion of the Hudson River. Short-term dispersal was low, with >70% of eels at all sites captured <1 km from their original tagging area. Length was similar among sites (total length = 45.7 ± 0.3 cm), whereas age was substantially lower for brackish-water sites (8 ± 4 years) than for freshwater sites (17 ± 4 years). Growth was higher for brackish-water sites than for freshwater sites ($8.0 \text{ cm}\cdot\text{year}^{-1}$ and $3.4 \text{ cm}\cdot\text{year}^{-1}$, respectively). From 1997 to 2000, infestation by the exotic nematode *Anguillicola crassus* increased dramatically in mean intensity as well as prevalence. Annual loss rates measured for the six sites varied between 9% and 24%, with no statistical difference between freshwater and brackish-water sites. Estimated eel production was higher in a brackish-water habitat ($1.10\text{--}1.77 \text{ kg}\cdot\text{ha}^{-1}\cdot\text{year}^{-1}$) than in a freshwater location ($0.21\text{--}0.58 \text{ kg}\cdot\text{ha}^{-1}\cdot\text{year}^{-1}$). The results of this study support a recent proposal to establish freshwater areas as exploitation reserves.

Résumé : La gestion des anguilles d'Amérique (*Anguilla rostrata*) exige une compréhension de la variation des caractéristiques démographiques à l'intérieur des grands estuaires. Nous avons mesuré la structure en longueur et en âge, la croissance, la dispersion, le taux d'infection par les nématodes, les taux de perte par mortalité naturelle et par émigration, ainsi que la production chez des anguilles jaunes à six sites situés dans la section du fleuve Hudson affectée par les marées. La dispersion à court terme est réduite et >70 % des anguilles à tous les sites sont recapturées à <1 km de leur point original de marquage. La longueur est la même à tous les sites (longueur totale = $45,7 \pm 0,3$ cm), alors que l'âge est considérablement plus bas aux sites d'eau saumâtre (8 ± 4 ans) qu'aux sites d'eau douce (17 ± 4 ans). La croissance est plus forte en eau saumâtre qu'en eau douce, respectivement de $8,0 \text{ cm/an}$ et de $3,4 \text{ cm/an}$. De 1997 à 2000, l'infection par le nématode exotique *Anguillicola crassus* a augmenté de façon spectaculaire, tant en intensité qu'en prévalence. Les taux de pertes annuelles aux six sites varient de 9 à 24 %, sans qu'il n'y ait de différence statistique entre les sites d'eau douce et d'eau saumâtre. La production estimée des anguilles est plus forte dans l'habitat d'eau saumâtre ($1,10\text{--}1,77 \text{ kg}\cdot\text{ha}^{-1}\cdot\text{an}^{-1}$) qu'en eau douce ($0,21\text{--}0,58 \text{ kg}\cdot\text{ha}^{-1}\cdot\text{an}^{-1}$). Les résultats de notre étude appuient la suggestion récente de l'établissement des zones d'eau douce comme réserves d'exploitation.

[Traduit par la Rédaction]

Introduction

Estuaries are very productive habitats for yellow-phase American eels (*Anguilla rostrata*) (Helfman et al. 1987), but the ecology and stock dynamics of American eels in estuarine waters is not well understood. During the past 20 years, U.S. landings of American eels, which mostly occur from estuarine waters, have declined from 1500 to 400 tons during the period 1980 to 2001 (NMFS 2002). To evaluate regional and species-wide sustainability, managers and scientists have placed priority on conducting stock assessments for American eels, focusing particularly on the estuarine yellow-phase eel (Anonymous 2001).

In estuarine habitats, a principal hypothesis is that growth, abundance, and productivity of yellow-phase eels is higher in downstream brackish-water habitats than in upstream freshwater locations (Helfman et al. 1987). This hypothesis was drawn from diverse monitoring and research projects but is also a corollary to the general observation that large coastal estuaries support higher fishery yields (Houde and Rutherford 1993). Despite the recognized importance of estuaries as productive habitats, few studies have investigated eel production in estuaries (Helfman and Bozeman 1984; Bozeman et al. 1985) or compared differences in age, length, and growth between eels in freshwater and brackish-water habitats in the same estuary (Helfman and Bozeman

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1984). No single study has investigated demographic trends throughout an entire large estuary.

To compare demographic attributes between different regions within the Hudson River, it was necessary to determine the degree of dispersal of eels. A recent otolith microchemistry investigation in the Hudson River suggested that yellow-phase (~5–25 years old) eels showed three migration behaviors: freshwater residency, brackish-water residency, and a single habitat shift during the yellow-phase from fresh water to brackish water (Morrison et al. 2003). At seasonal and annual time scales, past tagging studies indicate that eels occupy a limited home range and suggest that home ranges are larger in freshwater than in brackish-water areas (Helfman et al. 1987; Table 1). Here, we evaluated home range at six sites within the Hudson River estuary to support demographic comparisons among regions represented by these sites.

Because of PCB (polychlorinated biphenyl) contamination, the Hudson River eel fishery has been closed (except for a small bait fishery) since 1976. This long-term closure provided an opportunity to study eels in an unexploited state, allowing for isolation of growth and losses without the effects of fishing. Losses of yellow-phase eels in the Hudson River include both natural mortality and silver eel emigration, when eels return to the Sargasso Sea to spawn. In *Anguilla* species, researchers have found that maturity and the resultant emigration as silver eels was dependent more on length and fat content than age (Helfman et al. 1987; De Leo and Gatto 1996; Oliveira 1999).

This investigation measured dispersal, age and length structure, growth, mortality, and other demographic attributes of yellow-phase eels across freshwater and brackish-water regions of the Hudson River estuary during the period 1997–1999. The presence of the introduced parasitic nematode *Anguillicola crassus* (Barse and Secor 1999) was monitored to evaluate the rate at which infection is spreading. Finally, total production was estimated for 1998 and 1999, at one upriver and one downriver site, to evaluate possible productivity differences between freshwater and brackish-water zones within the Hudson River estuary.

Methods

The Hudson River estuary (Fig. 1) occupies a long, straight, and relatively deep basin formed by glaciers during the Pleistocene. The estuary is well mixed, with tidal influence from New York City Harbor to Troy Dam, 255 km upriver. The salt wedge is usually found near Yonkers (river kilometre (river km) 25) in high-flow months (late winter to early spring) and moves upriver to Newburgh (river km 100) when water flow decreases during summer (Dovel et al. 1992). For this study, sites below Newburgh (George Washington Bridge (GWB) and Haverstraw (HAV)) were designated brackish-water sites and Newburgh and the sites north (Newburgh (NEW), Kingston (KIN), Athens (ATH), and Albany (ALB)) were considered freshwater sites. These designations were based on past longitudinal studies (e.g., Dovel et al. 1992) and were corroborated by salinity measurements collected during this study.

Mark-recapture experiments were conducted at the six sites during summers 1997–1999. Sites were distributed through the entire length of the estuary but also were chosen to represent similar depths and bottom characteristics. All sites were located in shoal habitats 2–10 m deep. Bottom sediments were fine-grained clay and silt at all sites. Yellow-phase eels were captured in standard 100 cm long \times 25 cm diameter double funnel eel pots (1.3 cm \times 1.3 cm mesh), which were baited with a single large (>25 cm total length) menhaden *Brevoortia tyrannus* and soaked overnight. The use of bait to attract eels removes the possibility of collecting silver eels, which do not feed (Tesch 1977). A grid of 36 pots was deployed in either a 12 \times 3 (HAV, NEW, and KIN sites), 18 \times 2 (ATH and ALB sites), or 36 \times 1 (GWB site) configuration, depending on the dimensions of the river at each site. Pots were deployed approximately 200 m apart at all sites. The pots efficiently captured eels between 30 and 75 cm long. In earthen ponds, Hornberger (1977) found that 1.3 cm \times 1.3 cm mesh pots captured eels of a similar length distribution (total length range = 30–70 cm) as that of eels released into the ponds. Helfman and Bozeman (1984) poisoned a section of the stream after potting and found that 1.3 cm \times 1.3 cm mesh pots effectively captured eels between 20 cm and 80 cm. Based on these studies and size distributions of eels captured during this study, we have assumed unbiased sampling of eels \geq 30 cm.

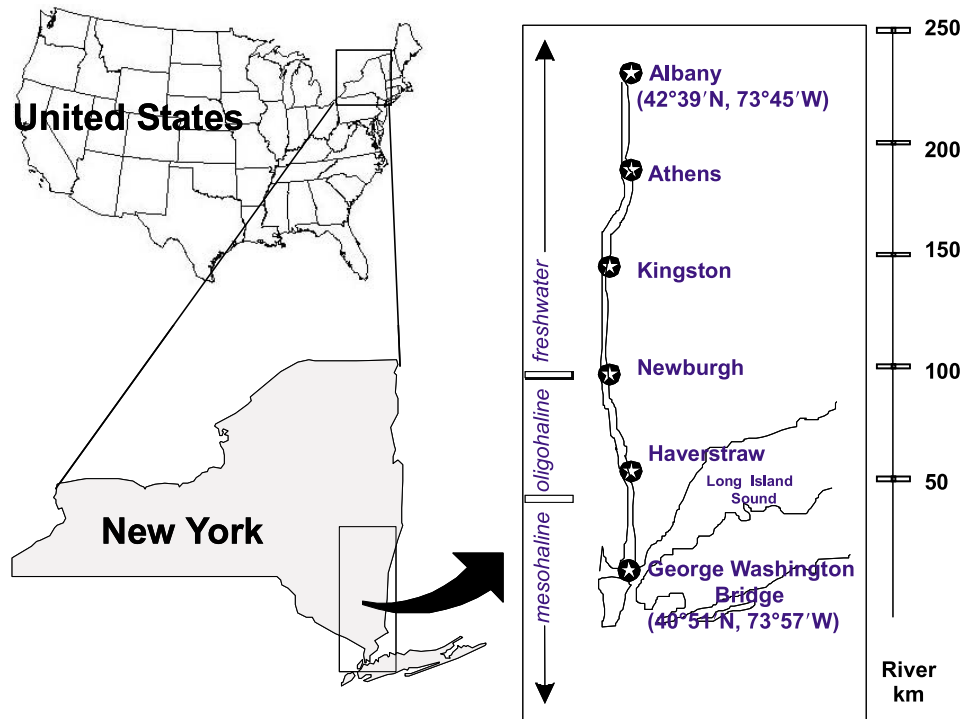
Eels were tagged using liquid nitrogen brands (Sorenson et al. 1983) and insertion of PIT (passive integrated transponder) tags. Branding was used to identify batches of eels according to site and day of capture, whereas PIT tags identified individual eels for growth measurements. Eels were sedated using MS-222 or clove oil, tagged, and then placed temporarily (approximately 15 min) into a recovery tank before being returned to the water near their location of capture. To brand the eels, a copper letter 0.75 cm high was attached to a copper nut (the nut allowed letter brands to be easily changed). This copper nut was attached to a long copper rod inserted into a 4-L thermos containing liquid nitrogen. Sedated eels were placed against the cold copper brand for 3–8 s, depending on humidity (branding took longer on humid days). Laboratory holding trials showed that brands were visible for at least 30 days after they were applied; eels showed no adverse responses as a result of the branding procedure. PIT tags were injected using a hypodermic needle into the dorsal musculature (1998) or visceral cavity (1999) of a subsample of eels. Eels ($n = 12$) held in pots for 6 days showed no adverse effects or loss of PIT tags over the 6-day period. In the field, retention of PIT tags was measured through identification of a scar at the place of insertion. In 1998, 250 eels at two sites, Athens (river km 190) and Haverstraw (river km 60), were tagged with PIT tags. In 1999, 75–150 PIT tags were utilized at all six sites (total = 600 tags). PIT tag recaptures were attempted twice, at both 2 months and 1 year after tagging, to record growth and dispersal. Brands (>18 000 eels branded) were recorded for all eels at all times to document movement between sites.

To measure home range at different temporal scales, we returned to the same site twice, 2 months and 1 year after the original tagging. A single line of pots was placed inside the original potting grid and extended 7–11 km above (north)

Table 1. North American yellow-phase eel home range estimates from the literature, noting collection and tagging methods.

Location	Home range estimate	Methods	Source
Louisiana	Moved <400 ft (121.92 m)	Electrofishing; fin clip and wire tag	Gunning and Shoop 1962
Georgia tidal creek	1 ha	Potting; anchor tags	Bozeman et al. 1985
Rhode Island river	Maximum movement 4.7 km; 87% recaptured where tagged	Electrofishing; branding	Oliveira 1997
Hudson River, N.Y.	Maximum movement 4.2 km; >80% recaptured where tagged	Potting; brands	This study
Massachusetts tidal stream	2 ha	Potting; fin clip	Ford and Mercer 1986
Penobscot Estuary, Maine	6.7±1.6 km or 325±64 ha	Potting; transmitters	Parker 1995
Vermont lake	0.6±4.9 km or 2.4±65 ha	Electrofishing; transmitters	LaBar and Facey 1983

Fig. 1. Map of the Hudson River, New York, U.S.A. Study sites are depicted by stars, the distance upriver is presented on the right, and salinity is presented on the left. Oligohaline, 0.1–5‰; mesohaline, 6–18‰.



and below (south) the tagging area. In 1998, local dispersal was measured for two sites (ATH and HAV). For this year, there was no documentation of tagging location within the grid, and therefore dispersal was estimated as the distance that eels had moved away from the center of the original tagging grid. In 1999, local dispersal was measured at all sites except HAV (because of equipment failure). At this time, location of the eels within the grid during tagging was recorded, permitting more precise estimates of dispersal.

For laboratory analysis, 100 eels were collected during June or July from three sites (HAV, NEW, and ATH) in 1997 and from all six sites in 1998 and 1999. In 2000, only eels with PIT tags were collected for laboratory analysis. Eels were euthanized with MS-222 (1997 and 1998) or clove oil (1999, 2000) and frozen for later analysis. Length was measured on a subset of eels before and after being frozen, and it was determined that freezing caused approximately 3% decrease in total length ($n = 30$). All lengths reported here are based on uncorrected preserved length measurements.

Morphological measurements recorded on each eel varied between years, with weight and head width recorded for 1999 and 2000 only. Gender was identified through gross visual inspection. Histological subsamples (46 females and 8 males) were prepared according to methods described in Dolan and Power (1977). All specimens showed histological characteristics that confirmed gross visual identification. An index of condition was calculated as Fulton's condition factor K (in $\text{g}\cdot\text{mm}^{-3}\cdot 10^5$; Ricker 1975) for eels collected in 1999. Differences between male and female condition were not testable because of the small sample of males collected. For this study, gut fullness was not recorded, which may have introduced small (2–6%) error (based on adjustment from Helfman and Bozeman 1984) to weight measurements. Head width (HW) was measured using calipers to the nearest millimetre at the widest section of the head. Head width to total length ratio (HW:TL) was calculated to determine if different ecotypes of eels are present in the Hudson River as has been reported in European yellow-phase eels (*Anguilla*

anguilla). Eels with HW:TL greater than 0.033 have been designated as “fat-headed” eels and have shown differences in relative weight, growth, and diet (Tesch 1977; Proman and Reynolds 2000). No study has reported head width in American eels. The presence and number of *Anguillicola crassus* nematodes found inside the swim bladder were recorded. Prevalence (number of infected eels divided by total number of eels examined) and mean intensity (average number of nematodes found among the infected eels) are defined as in Bush et al. (1997) and were calculated for each site.

To evaluate age structure, growth rate, and loss rate of estuarine yellow-phase eels, we required a valid ageing method. Annual periodicity of annuli within sagittal otoliths has been verified for American and European eels (Berg 1985; Oliveira 1996). Supernumerary rings or “false annuli” are common in eel otoliths and can introduce substantial bias if not correctly distinguished from true annuli. New techniques and criteria that minimize impacts from false annuli were recently introduced. We utilized a slight modification of Oliveira’s (1996) and Graynoth’s (1999) sectioning and dyeing techniques combined with Graynoth’s (1999) criteria for identifying real annuli. Sagittal otoliths were extracted, soaked briefly (3 min) in 10% hypochlorite solution, rinsed in deionized water, and stored until dry. Right and left otoliths were randomly selected and embedded in epoxy resin. Transverse sections were cut using a wafering saw and then polished using wetted carborundum paper and alumina powder until the primordium was exposed (Secor et al. 1991). Otoliths were cleaned and etched with a solution of 5% toluidine blue and 2% EDTA (ethylenediaminetetraacetic acid). Under this treatment, transmitted light exposed blue opaque zones that correspond to annuli.

Ages represent the entire life span, including the marine leptocephalus stage, rather than the duration of the estuarine phase of life. There are two distinct checks on the otolith during the early life of an eel. The first check represents metamorphosis from the leptocephalus to the glass eel stage (Otake et al. 1997). The second check is described as the “transition” check (Michaud et al. 1988; Cieri and McCleave 2000), but its origin is uncertain. It may be associated with first feeding during the glass eel stage, entrance into fresh water, the end of metamorphosis, or settlement to demersal habitats. Because spawning occurs in March–April and eels enter the estuary (coincident to the deposition of this check) during March and April in the Hudson River (Mattes 1989), we assigned the transition check as age = 1 year.

Annular rings were counted at least four times for each section, with estimated age calculated as the mean of the counts. Two counts were made each along dorsal and ventral regions immediately adjacent to the sulcal groove (Fig. 2). The same counts were repeated at least 2 weeks later, and those with discrepancies >1 year were recounted a fifth time. Error in counts was estimated as the difference between the minimum and maximum counts for each otolith. The effect of site and number of annuli on ageing error was tested.

Seasonal and annual growth measured in the field through mark–recapture experiments and lifetime growth (size-at-age relationships) were measured and analyzed for differences due to capture location and time. For each eel aged, average lifetime growth was calculated by dividing total length by

age. To account for growth before entering the Hudson River, the first year of life was discounted by subtracting 7.66 cm (Mattes 1989) and 1 year from the length and age, respectively. Results from field mark–recapture experiments suggested that female eels >30 cm exhibited linear growth across age classes. Therefore, we assumed that linear growth was a reasonable approximation. Estimates of seasonal and annual growth from recaptured eels were adjusted to reflect growth over 1-year or 2-month periods by dividing actual growth by the number of days at large (334–403 and 41–68 days for 1-year or 2-month growth periods, respectively) and then multiplying by either 365 or 61.

Loss rate was analyzed through catch-curve analysis. Because of the fishing ban, fishing mortality can be assumed to be negligible. For this analysis, all years were combined; age counts from 1997 and 1999 were increased and decreased by 1 year, respectively, to allow pooling by year class. In addition, individual eels were assigned to 3-year age-class bins based on mean measured error for all aged eels. For example, all eels aged 10, 11, or 12 years were combined into one group. We assumed that eels were fully recruited to the gear at and above the age at which the highest frequency occurred. Other important assumptions include constant rates of recruitment, natural mortality, and catchability across sites (Hilborn and Walters 1991).

Ricker (1975) defines total production as “the total growth in weight of fish during the year, including growth in the part of the population that dies before the year is finished”. Because only length measurements were taken in the field, length measurements were converted to weight (W) estimates based on the following relationship $W = 0.001TL^{3.2}$ (1999; $N = 543$, $r^2 = 0.92$).

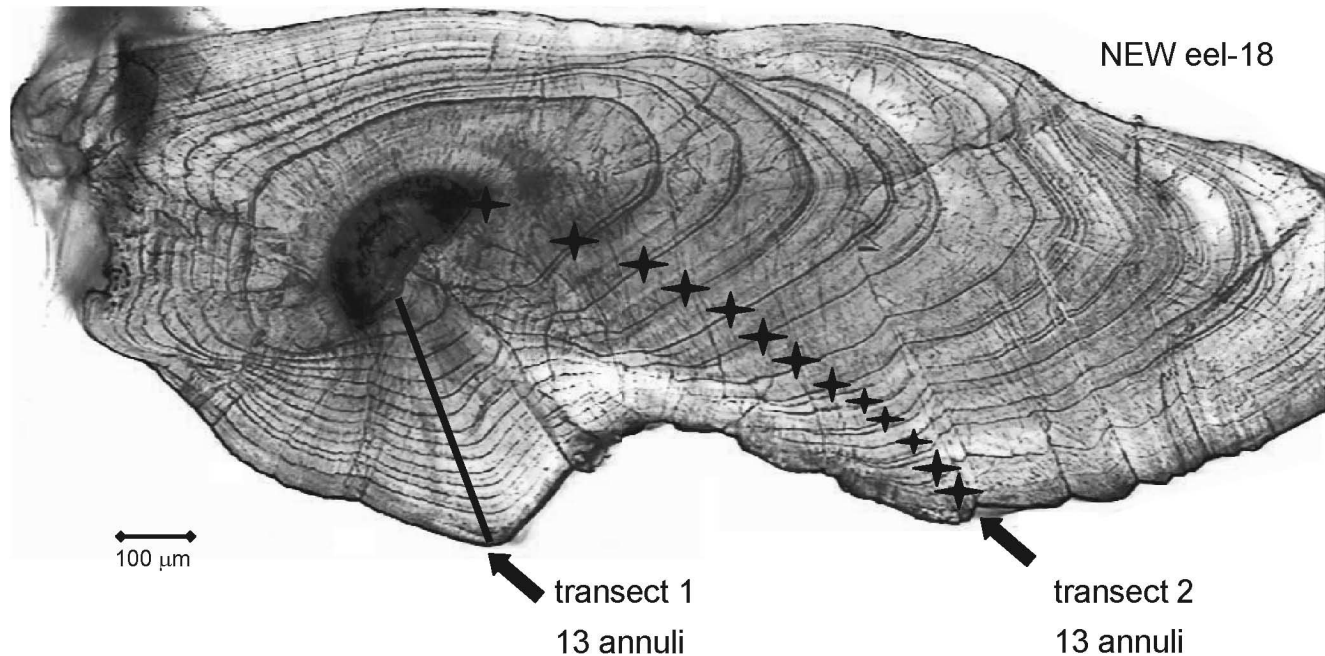
Average biomass throughout the year was estimated as

$$\bar{B} = B_0(e^{G-Z} - 1)/(G - Z)$$

where B_0 is initial biomass (calculated by measuring average biomass of eels at a site and multiplying it by the abundance of eels at that site), G is an average yearly instantaneous growth for each site calculated from mark–recapture growth estimates, and Z is the instantaneous yearly loss rate calculated from the catch curve. Abundance was estimated using a modified Peterson mark–recapture estimate that minimized effects due to trap-shy behavior and immigration from outside areas adjacent to grid sample sites (mean recapture rate model; Morrison and Secor 2004). Production was estimated by multiplying the average biomass (\bar{B}) throughout the year by instantaneous growth (G) (Ricker 1975). This equation does not explicitly account for new recruitment of small eels to the pots during the period of production estimates. Still, because abundance is estimated during week-long trials, the assumption of negligible effects of new recruits may be valid. Sufficient data existed to compare production rates between HAV (brackish-water site) and ATH (freshwater site) in 1998 and 1999.

All site comparisons were made with standard one-way and two-way analyses of variance and covariance. For many analyses, assumptions of normality and homogeneous variances of the residuals were not met. Transformations (natural log and square root) were attempted, and if successful, the results were analyzed and the use of a transformation

Fig. 2. Micrograph of an otolith from a yellow-phase eel (*Anguilla rostrata*) collected in the Hudson River. Transects where annuli were identified are shown. Stars designate annuli.



was noted. Where transformations did not remedy the violations, nonparametric Kruskal–Wallis rank tests were used and noted. All pairwise comparisons were made with Tukey’s multiple comparisons.

Results

Dispersal

Retention of PIT tags was 89%; at two sites in 1999, 72 out of 81 eels retained PIT tags 2 months after tagging. PIT-tagged eels showed expected home range behaviors. For eels tagged in 1998 at ATH, 80% (54/67) and 88% (51/58) of recaptured eels were within the original tagging grid 2 months and 12 months after they were originally tagged, respectively. Ninety percent ($n = 9/10$) of recaptured eels at HAV in 1998 were sampled within the original tagging grid 1 year later. For eels tagged in 1999, dispersal was evaluated at all sites and results were similar across sites, with >70% (mean = 88%) of eels recaptured within 1 km of their original tagging location 2 months and 12 months later (Table 2). Recapture rate within 1 km of release site was variable among sites, with highest recapture rates at upriver locations. The longest individual dispersal was measured at NEW, where one eel moved 4.2 km from its tagging location. For the 2-month interval, the dispersal at GWB was significantly less than at all other sites except ALB.

Only four recaptured branded eels showed evidence of long distance dispersal. In 1998, four eels branded at ATH during June were recaptured 1 month later at KIN, 55 river km downstream. Estimated mean dispersal rate for those four eels was approximately $3.5 \text{ km}\cdot\text{day}^{-1}$. During 1998–2000 field seasons, no other branded eels were recaptured ($N > 18\,000$ branded eels) at sites other than where they were originally branded.

Gender, condition, and head morphometry

Nearly all (97%) examined eels (1999 samples; $n = 543$) were female. Of the 14 male eels identified, 11 were from GWB, two were from HAV, and one was from NEW. The mean length of males was $33.3 \pm 2.2 \text{ cm}$; all were less than 37 cm TL. Because of insufficient sample size, gender differences in condition, growth, dispersal, or nematode mean intensity were not tested.

Condition factor K varied significantly between sites (1999, $N = 542$, $df = 5$, $P < 0.0001$). The condition factor at NEW was significantly higher than at the other five sites, and the condition factor at ATH was significantly lower than that at GWB and NEW (Table 3). According to criteria established for European eels, 98% of eels collected in the Hudson River in 1999 were “wide-headed” ($\text{HW:TL} > 0.033$; Proman and Reynolds 2000). Although no modalities in HW:TL occurred, the metric varied significantly between sites ($N = 530$, $df = 5$, $P < 0.0001$), with significantly greater head widths at NEW, KIN, and ATH than at ALB, GWB, and HAV (Table 3).

Nematode infection

The percent of infected eels increased during the 1997–2000 study (Fig. 3). In 1997, only four sites were analyzed (HAV, NEW, KIN, and ATH) and all sites had prevalences less than 20%. At HAV in 1997, no parasites were noted. By 2000, >60% of eels were infected by *A. crassus* at all freshwater sites. Prevalence of the parasite tended to be less at the two most saline, down-estuary sites in 1999–2000. The number of nematodes per infected eel (mean intensity) also increased with time (Fig. 3). The mean number of nematodes found in infected eels was low in 1997 and 1998, with all sites except ATH showing average mean intensities <4. By 1999, mean intensities were between 3.2 and 23.7 among sites. The maximum number of adult nematodes recorded

Table 2. Short-term dispersal of yellow-phase American eels tagged in the Hudson River, 1999.

Site	Duration	<i>N</i>	Recapture (%)	Maximum distance (m)	Mean distance (m)	Recaptured <1 km from release site (%)
GWB	2 month	8	11	200	138	100
	1 year	7	10	600	243	100
HAV	2 month	7	5	1400	843	71
	1 year					
NEW	2 month	13	12	4200	1008	85
	1 year	14	14	1400	714	93
KIN	2 month	22	20	3600	655	91
	1 year	4	5	1600	750	75
ATH	2 month	18	24	1900	544	89
	1 year	4	7	1800	575	75
ALB	2 month	24	32	1000	383	100
	1 year	17	33	1600	618	88

Note: GWB, George Washington Bridge; HAV, Haverstraw; NEW, Newburgh; KIN, Kingston; ATH, Athens; ALB, Albany. No data were collected in Haverstraw after 1 year because of technical difficulties with the PIT (passive integrated transponder) tag reader.

for an individual eel increased from 17 during 1997–1998 to 82 during 1999–2000. Mean intensities were not influenced by total length but were significantly different among sites (analysis of variance (ANOVA) on 1999 TL data, $N = 542$, $df = 1$, $P = 0.62$; Kruskal–Wallis test on 1999 site data, $df = 5$, $P < 0.0001$). Mean intensities were significantly lower at the brackish-water sites and NEW than at the three most upriver sites ($P < 0.05$). Data at KIN, ATH, and ALB indicate that between 1998 and 1999, there was at least a five-fold increase in mean intensity.

Age and length structure

Mean precision in age estimates was 1.4 ± 0.95 years. Sixty-four percent of the estimates had an error less than 1.5 years, and 95% of age differences were less than 3.5 years. There was a significant relationship between the number of annuli and error ($r^2 = 0.045$, $P < 0.0001$), but the difference was slight: mean error was 1.1, 1.5, 1.6, and 1.6 for ages 3–10, 10–15, 15–20, and 20–39, respectively. Using a two-way ANOVA, there was no significant effect on error due to capture locations after accounting for effects on error due to age ($df = 5$, $P = 0.26$).

Estimated ages differed significantly among sites but not among years ($n = 543$; Kruskal–Wallace rank test on year effect, $df = 2$, $P = 0.25$; site effect, $df = 5$, $P < 0.001$). Overall, ages were much lower for the two brackish-water sites than for the freshwater sites (Fig. 4). For pooled years (1997–1999), mean ages at GWB, HAV, NEW, KIN, ATH, and ALB were 8.2, 8.7, 17.1, 19.5, 16.4, and 16.9 years, respectively. The oldest eels tended to occur at KIN, with mean ages at that site of 19.1 and 19.8 years for 1998 and 1999, respectively. The oldest individual eel aged during the entire study was from GWB and was estimated to be 38 years old with a total length of 39.5 cm. The youngest eel, from HAV, was estimated to be 3 years old at 29 cm TL. Age structure was skewed towards older ages at one freshwater site (ALB) and skewed towards younger ages at both lower river sites (HAV and GWB).

Length frequencies were similar among sites (Fig. 5; Table 3) and were skewed towards smaller sizes at four of the six sites (GWB, NEW, ATH, ALB). When comparing mean total lengths with ANOVA, both site and year were signifi-

cant ($n = 649$; year, $df = 3$, $P = 0.03$; site, $df = 3$, $P = 0.001$), but differences in mean lengths between sites and years were small; mean lengths varied <4 cm among sites and years. Only four site combinations out of 15 were significantly different using Tukey's pairwise comparison: HAV and GWB were significantly different from NEW and ATH. For pooled years (1997–1999), mean lengths at GWB, HAV, NEW, KIN, ATH, and ALB were 44.2, 44.1, 47.3, 46.0, 47.4, and 45.4 cm, respectively.

Growth

Length-at-age plots indicated high individual growth rate variation within sites (Fig. 6). Based on estimated ages, a 50-cm eel could range from 5 to 29 years old. Within sites and years, correlations (r) between age and length were low, ranging from 0.09 to 0.79. Only eight of 15 possible regressions were significant ($P < 0.05$). The highest correlation was for HAV in 1999 ($r = 0.79$). Overall, there was a significant relationship between age and length ($n = 649$, $r = 0.30$, $P < 0.0001$), but the relationship was weak. Annual growth calculated for individual eels based on length-at-age was higher in brackish-water sites (5.48 ± 1.80 cm) than in freshwater sites (2.48 ± 0.64 cm) for all years (Kruskal–Wallis rank test, $n = 649$; site, $df = 5$, $P < 0.0001$; year, $df = 2$, $P = 0.19$; Table 3).

Summer growth (June to August), estimated from mark–recapture, were higher for eels caught at brackish-water locations ($2.5\text{--}2.8$ cm·(2 months) $^{-1}$; Table 3) than those from freshwater sites ($0.2\text{--}2.1$ cm·(2 months) $^{-1}$). Two-way analysis of variance for 2-month growth increments showed that differences in growth among sites were significant, but inter-annual differences in growth between 1998 and 1999 were not detected ($n = 94$; site, $df = 5$, $P < 0.0001$; year, $df = 1$, $P = 0.12$). Similar results were found for annual growth increments ($n = 135$; site, $df = 5$, $P < 0.0001$; year, $df = 1$, $P = 0.10$). Two-month growth increments were not significantly related to length or age ($n = 94$; Kruskal–Wallis test on length, $df = 1$, $P = 0.30$; age, $df = 1$, $P = 0.33$). Annual growth rates estimated from mark–recapture ranged from 2.4 to 10.4 cm·year $^{-1}$ and were in general similar in range to growth estimated through size at age (Table 3). Growth rates were significantly higher at brackish-water sites (8.0 cm·year $^{-1}$) than at fresh-

Table 3. Demographic characteristics of yellow-phase American eels for the Hudson River.

Site	Total length (cm)	Estimated age (years)	Condition index (g·mm ⁻³ ·10 ⁵)	HW:TL	Mark–recapture 2-month growth (cm)	Mark–recapture 12-month growth (cm)	Growth based on age-at-length (cm)
GWB	44±9 (118)	8±5 (118)	0.191±0.002b (86)	0.04±0.05a (97)	2.8±0.5a (7)	8±3a (7)	6.5±1.7 (54)
HAV	44±8 (117)	9±2 (117)	0.192±0.003ab (70)	0.04±0.04b (99)	2.5±1.6a (7)	10±3a (12)	5.2±1.1 (30)
NEW	47±8 (123)	17±4 (123)	0.205±0.003c (76)	0.05±0.07cd (76)	0.5±0.7b (13)	3±2b (37)	2.8±0.5 (31)
KIN	46±6 (89)	19±3 (89)	0.186±0.003ab (99)	0.05±0.06d (71)	2.1±1.1a (21)	4±2b (17)	2.6±0.5 (50)
ATH	47±6 (117)	16±3 (117)	0.181±0.003a (99)	0.05±0.05c (97)	0.7±0.7b (24)	3±2b (42)	3.1±0.9 (30)
ALB	45±6 (85)	17±2 (85)	0.187±0.003ab (96)	0.04±0.06b (96)	0.1±0.7c (22)	2±3b (20)	2.7±0.4 (33)

Note: Total length and age are means for 1997–1999; condition index, age-at-length growth, and the head width to tail length ratio (HW:TL) are for 1999, and mark–recapture growth is for 1999–2000. Values reported are mean ± standard deviation and sample size (N). Different letters represent significant differences using Tukey's multiple comparisons at $\alpha = 0.05$. GWB, George Washington Bridge; HAV, Haverstraw; NEW, Newburgh; KIN, Kingston; ATH, Athens; ALB, Albany.

water sites (3.4 cm·year⁻¹). Year did not influence annual growth increments ($n = 135$; site, $df = 5$, $P < 0.0001$; year, $df = 1$, $P = 0.10$). The annual growth increments, although not related to length, were significantly related to estimated age ($n = 135$; $\log_{10}(\text{age})$, $df = 1$, $P = 0.03$; length, $df = 1$, $P = 0.44$).

At ATH, 53 eels were captured both 2 months and 1 year after tagging, allowing for a comparison between summer and annual growth for individual eels. On average, 40% of their annual growth occurred during the 60-day summer interval (June to August; $n = 53$). Thirty-one eels tagged at ATH in 1998 were recaptured in 1999 and 2000. Analysis of these data indicated no significant difference in mean annual growth increments between 1998–1999 and 1999–2000, using a paired t test ($n = 31$, $t = 1.54$, $P = 0.13$). Individual growth was variable between years, with some eels exhibiting up to three times higher growth in one year versus the other. Despite this variability, there was a positive correlation between individual growth rates between the two years ($n = 31$, $r = 0.55$).

Loss rate and production

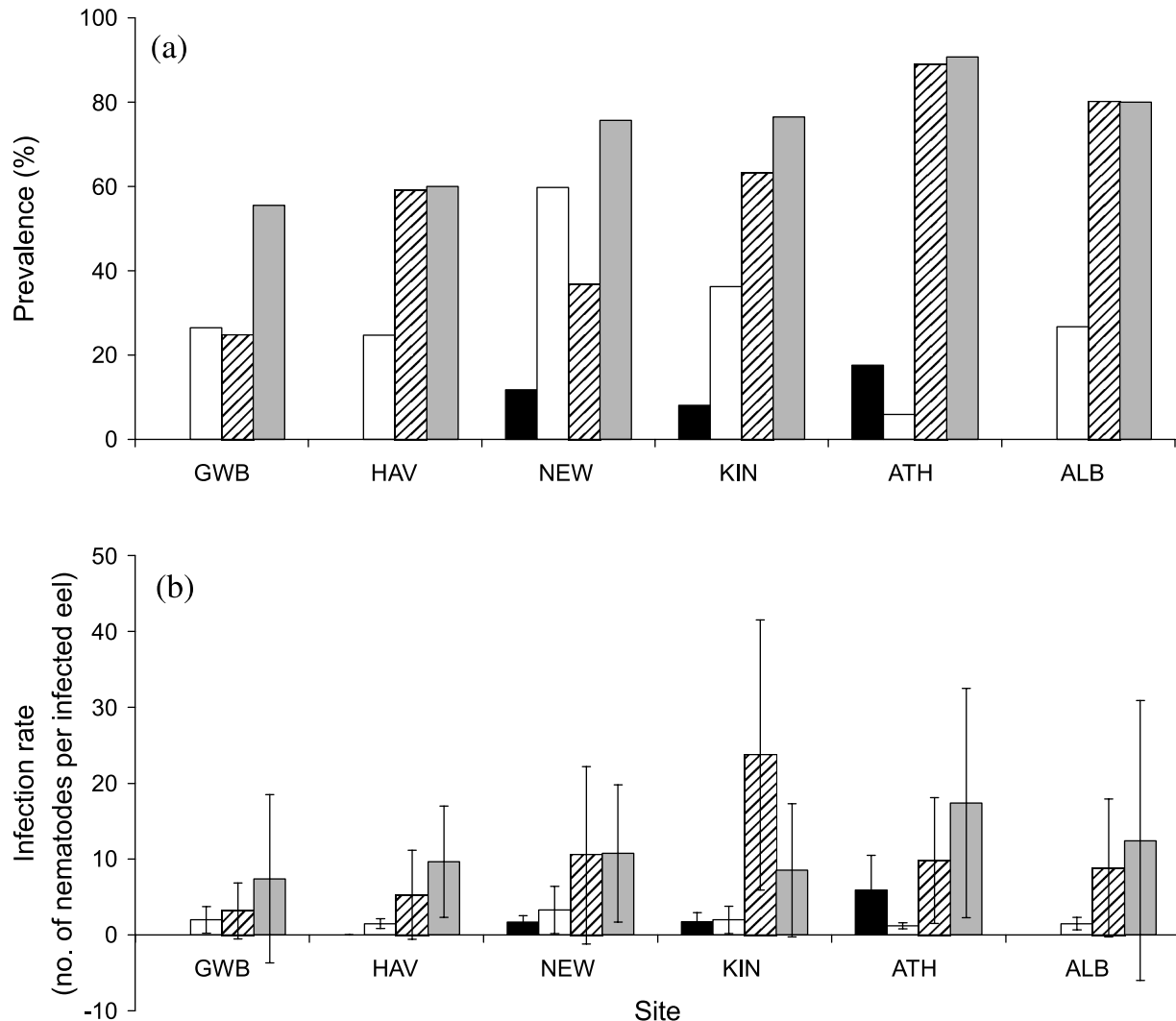
Loss rates estimated from age-class frequencies were similar across sites (Fig. 7). The overall mean loss rate was 0.16 ± 0.06 (15%·year⁻¹), with maximum and minimum rates of 0.27 (24%·year⁻¹) and 0.09 (9%·year⁻¹), estimated at ALB and NEW, respectively. Loss rates were similar between the two brackish-water sites (GWB = 12%·year⁻¹; HAV = 15%·year⁻¹) but were more variable among freshwater locations (Fig. 7). Estimated loss rates were not significantly different between freshwater and brackish-water sites (analysis of covariance, $df = 1$, $P = 0.13$). There was, however, a difference in the most frequent age (age at which the catch curve began). The descending portion of the age–frequency distributions began at age classes 5 and 8 for the two most down-estuary sites and between ages 17 and 20 for the other four up-estuary sites.

Total production of yellow-phase eels was higher at the brackish-water site (HAV) than at the freshwater site (ATH) in both 1998 and 1999, but the magnitude of the difference was variable. Across years, estimated production at HAV was approximately 2–3 times higher than estimated at ATH. HAV showed slightly higher production in 1998 (1.77 kg·ha⁻¹·year⁻¹) compared with 1999 (1.10 kg·ha⁻¹·year⁻¹), but ATH showed higher production in 1999 (0.58 kg·ha⁻¹·year⁻¹) compared with 1998 (0.21 kg·ha⁻¹·year⁻¹).

Discussion

Large differences in growth between brackish-water and freshwater sites affected the age structure and productivity of the eels in the Hudson River. These differences in growth, production, and age structure were supported by mark–recapture experiments that documented very limited exchange of yellow-phase eels among sites during summer. Other attributes that varied among freshwater and brackish-water habitats included condition, head morphometry, and prevalence of infection by the parasitic nematode *A. crassus*. Loss rates did not differ between estuarine regions.

Fig. 3. (a) Percentage of Hudson River yellow-phase eels (*Anguilla rostrata*) infected (prevalence rate) with *Anguillicola crassus*, 1997–2000. (b) Mean intensity (number of nematodes per eel) of yellow-phase American eels in the Hudson River, 1997–2000. Error bars represent standard deviations in mean intensity. GWB, George Washington Bridge; HAV, Haverstraw; NEW, Newburgh; KIN, Kingston; ATH, Athens; ALB, Albany. Solid bars, 1997; open bars, 1998; hatched bars, 1999; shaded bars, 2000.



Dispersal

The limited home range and seasonal attachment to a location measured in this study were similar to results found by other researchers in various habitat types. Despite strong evidence for limited dispersal within a 1-year period, other evidence indicated that some yellow-phase eels did disperse among estuarine regions over longer periods of time. Otolith Sr-to-Ca ratios showed that some eels will spend the first 2–19 years of their life in fresh water before moving to, and residing in, brackish-water habitats (Morrison et al. 2003). The four branded eels observed to have migrated 55 km downriver could have been initiating such a migration. Otolith microchemistry showed no evidence of regular seasonal movements into and out of water of different salinity (Morrison et al. 2003), but the method cannot distinguish movements within freshwater areas, so it is possible that eels have undetected seasonal migrations within freshwater portions of the river. The long-distance migration that we documented for four eels occurred during the first weeks of the

1998 field season, suggesting that it might have been a seasonal migration. Still, because only four recaptures between sites were recorded among >18 000 marked eels during the 4-year study, interannual long-distance migration (>10 km) appears to be rare.

Helfman et al. (1987) hypothesized that eel home ranges are smaller in brackish water compared with fresh water. Dispersal was quite different at the two brackish-water sites in this study, with limited dispersal at GWB and comparatively high dispersal at HAV. The habitat characteristics of these sites may have influenced dispersal. GWB contained only a thin band of shallow habitat next to a deep channel, whereas HAV was located in an extensive shallow-water bay. Both sites had lower recapture rates (5–11% recaptured) compared with freshwater habitats (12–33% recaptured). Low recapture rates in brackish water could suggest a difference in home range and feeding behavior between the freshwater and brackish-water areas but could also be the result of higher growth and higher loss rates for brackish-water

Fig. 4. Age–frequency distributions for Hudson River yellow-phase eels (*Anguilla rostrata*), 1997–1999 combined: (a–d) fresh-water locations; (e and f) brackish-water locations. (a) Albany; (b) Athens; (c) Kingston; (d) Newburgh; (e) Haverstraw; (f) George Washington Bridge.

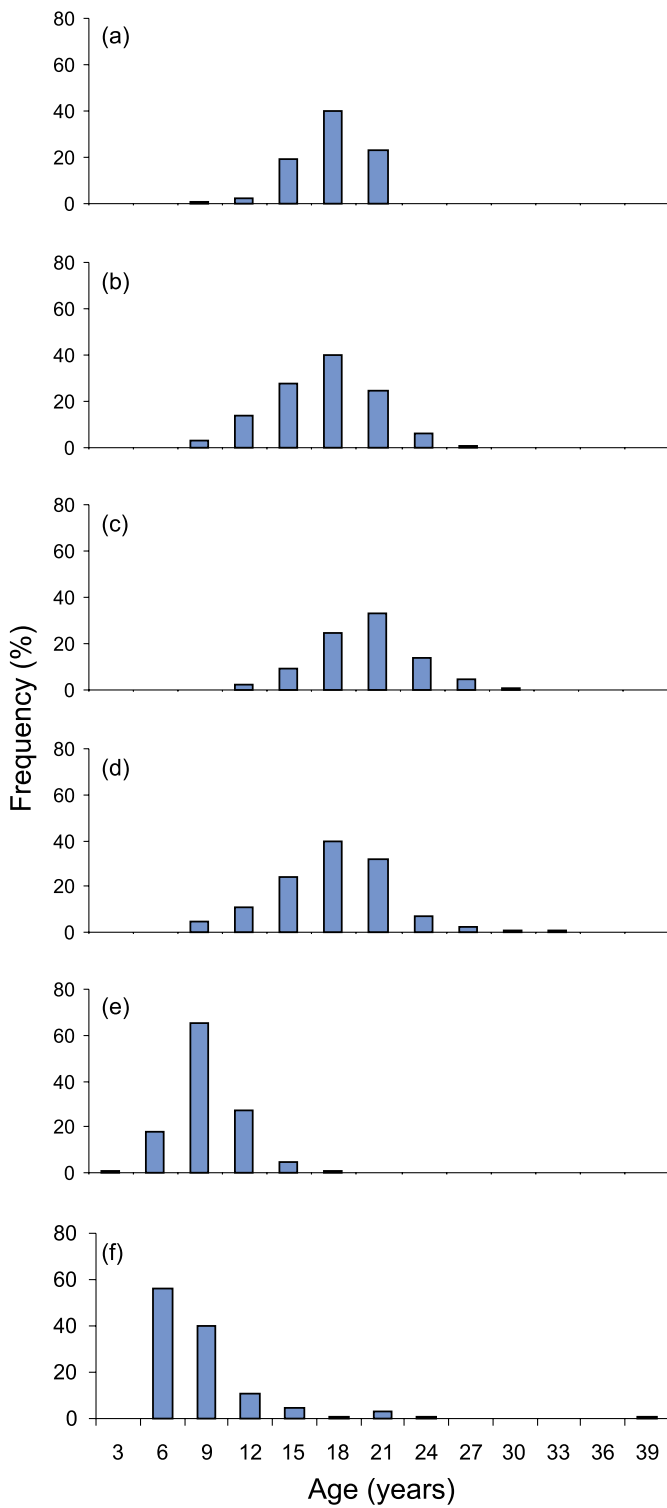


Fig. 5. Length–frequency distributions for Hudson River yellow-phase eels (*Anguilla rostrata*), 1997–1999 combined: (a–d) fresh-water locations; (e and f) brackish-water locations. (a) Albany; (b) Athens; (c) Kingston; (d) Newburgh; (e) Haverstraw; (f) George Washington Bridge.

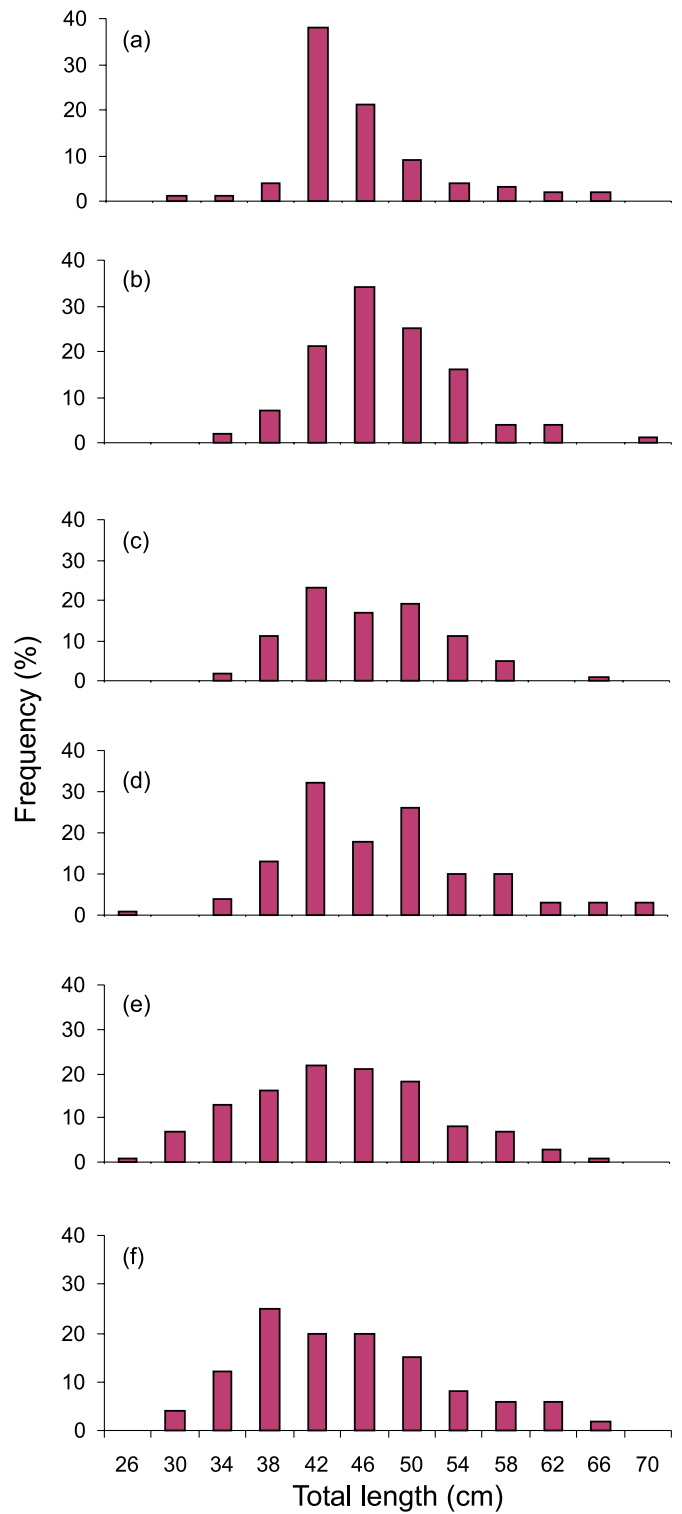
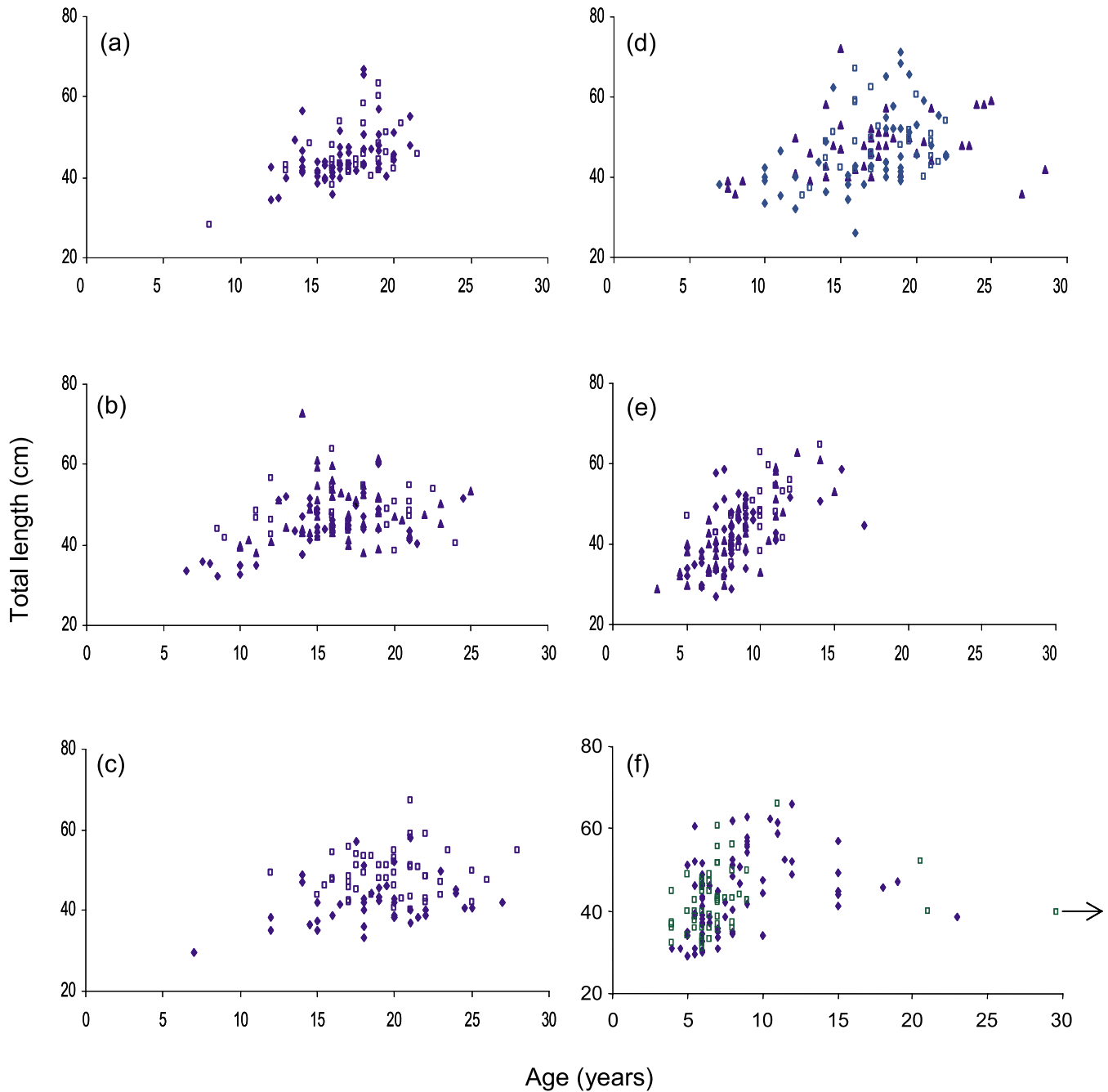


Fig. 6. Length versus age for yellow-phase American eels (*Anguilla rostrata*) collected from the Hudson River, 1997–1999: (a) Albany; (b) Athens; (c) Kingston; (d) Newburgh; (e) Haverstraw; (f) George Washington Bridge. Solid triangles, 1997; solid diamonds, 1998; open squares, 1999.



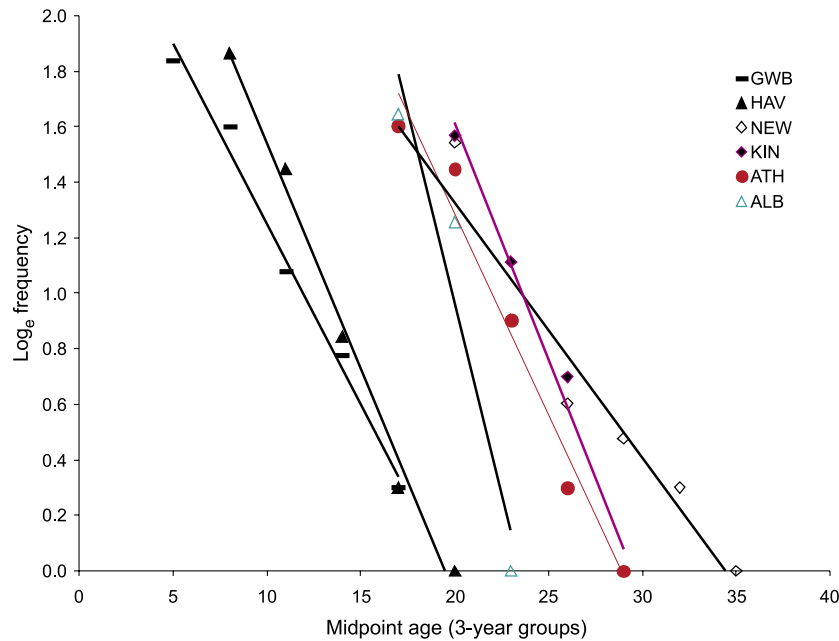
eels. Mean dispersal distance showed no obvious trend between brackish-water and freshwater sites.

Sex, condition, and head morphometry

Captured Hudson River American eels mainly consisted of female “wide headed” eels with mean condition indexes that varied little among sites. Males are smaller than females and rarely exceed 40 cm TL (Oliveira 1999); however, it is unlikely that males would emigrate before being vulnerable to pots, and the low abundance of males is probably an accurate reflection of their relative abundance ≥ 30 cm TL.

Differences in condition index, albeit small (<15%), coincided with growth differences between sites. The three most upriver sites (ALB, ATH, and KIN) had the lowest condition index, whereas the two brackish-water sites showed relatively high condition indexes. The NEW site was an exception to this trend: the highest condition index was observed, despite growth rates that were low relative to other sites. Yellow-phase eels from this site also had the widest heads, suggesting that for whatever reason, the morphometry of eels was different at NEW than at other sites. Interestingly, eels at NEW were significantly more contaminated by

Fig. 7. Catch curves among sites for yellow-phase American eels (*Anguilla rostrata*) from the Hudson River, 1997–1999. Frequencies were binned into 3-year age classes. GWB, George Washington Bridge; HAV, Haverstraw; NEW, Newburgh; KIN, Kingston; ATH, Athens; ALB, Albany.



PCBs than eels at other sites, except ALB (Steinbacher 2001).

Nematode parasitism

Anguillicola crassus, native to Japanese eels (*A. japonicus*), infects the swimbladder of *Anguilla* spp. and has spread across most of Europe and recently into several areas in North America (Barse and Secor 1999; Barse et al. 2001; Moser et al. 2001). The large increase in prevalence and mean infection documented here demonstrated the capacity of the nonindigenous *A. crassus* to quickly invade an entire estuary. Overall, both prevalence and mean intensity were higher in freshwater than brackish-water areas. Results were comparable with those of Moser et al. (2001), who found mean prevalence in North Carolina rivers in 1998 and 1999 to be 52% (range 26–100%), with a mean intensity of 3.9 (range 1–12). Research has shown that the nematode prefers fresh water but that a smaller percentage can survive in brackish water, and even full salt water (Kirk et al. 2000). The ecological consequences of the parasite have been studied for European eel (*A. anguilla*), and studies have documented changes in growth (Thomas and Ollevier 1992), swimming speed (Sprengel and Lüchtenberg 1991), and serum cortisol levels (Sures et al. 2001), as well as changes to the morphology of the swimbladder (Nimeth et al. 2000; Lefebvre et al. 2002). We were unable to analyze the effect of parasite intensity on growth because nematode infection rates were confounded by underlying differences in growth between freshwater and brackish-water regions.

Age and length structure

American eel lengths were relatively similar across sites, whereas eel ages were substantially and significantly younger in brackish-water sites vs. freshwater sites. This difference in age based on salinity is similar to results of Helfman

and Bozeman (1984) in Georgia, where average age was younger in brackish water (4.6 years) than in fresh water (6.2 years). The age composition of freshwater eels measured in this study was similar to that found in Maine rivers (Oliveira and McCleave 2000) but older than most other studies on eels from freshwater habitats (Table 4). Annuli in otolith sections have been validated for *A. rostrata* in other systems (Oliveira 1996), and the similarity between growth rates determined from mark–recapture and those determined by estimated age at capture provides some evidence that our age interpretations were accurate.

The results of this study support the hypothesis that silver eel metamorphosis and emigration are more dependent on length than on age (Helfman et al. 1987; De Leo and Gatto 1996). This conclusion is based on the observed sharp reduction in the number of eels >55 cm across sites and the concurrent lack of a sharp decline at a given age across the same sites. In addition, the decrease in abundance of eels between 50 and 55 cm is similar to sizes of emigrating female silver eels in Rhode Island and Maine (Oliveira 1999; Oliveira and McCleave 2000).

Growth

Growth calculated from mark–recapture was substantially higher (twofold) in brackish-water eels than in freshwater eels, corresponding to the age differences recorded in these areas. Faster growth by eels in brackish water has been documented (Helfman et al. 1987), but Gray and Andrews (1971) found the opposite trend. Average growth was much higher at both ATH and HAV in 1998 than in 1999, suggesting that conditions that affect growth act on an estuary-wide scale.

Growth rates measured in the Hudson River were similar to those estimated for other systems (Table 5). The highest estimate of mean brackish-water growth in our study

Table 4. North American eel age estimates from the literature, noting stage of eels.

Location	Salinity	Phase	Age (years)	Source
Georgia tidal creek	Brackish	Yellow	2–7	Helfman et al. 1984
	Fresh	Yellow	3–13	Helfman and Bozeman 1984
	Brackish	Yellow	3–7	
South Carolina river	Both	Yellow	2–11	Hansen 1978
New Jersey streams	Fresh	Yellow	3–19	Ogden 1970
Rhode Island river	Fresh	Silver	4–20	Oliveira 1999
Hudson River, New York	Both	Yellow	1–12	Mattes 1989
	Brackish	Yellow	3–39	This study
	Fresh	Yellow	7–30	This study
Maine rivers	Fresh	Elver and Yellow	1–33	Oliveira and McCleave 2000
Newfoundland	Both	Silver	12–13	Gray and Andrews 1971

Table 5. North American yellow-phase eel growth estimates from the literature, noting estimation method.

Location	Salinity	Growth rate (cm·year ⁻¹)	Method	Source
Louisiana creek	Fresh	up to 32.5	Based on one fin clipped eel	Gunning and Shoop 1962
Georgia creek and marsh	Brackish	5	Age–length regression	Helfman and Bozeman 1984
	Fresh	5.3		
Georgia creek	Brackish	5.5–6.2	Mark–recapture study	Helfman et al. 1984
		4.4	Age–length regression	
Rhode Island river	Fresh	4.0 (F), 3.1 (M)	Age–length regression	Oliveira 1999
Rhode Island river	Fresh	3	Mark–recapture study	Oliveira 1997
Hudson River	Both	3.9	Age–length regression	Mattes 1989
Hudson River	Brackish	8	Mark–recapture study	This study
Hudson River	Fresh	3.4	Mark–recapture study	This study
Hudson River	Brackish	5.5	Age and length at capture	This study
Hudson River	Fresh	2.8	Age and length at capture	This study

Note: Where known, gender is specified: F, female; M, male.

(10.4 cm·year⁻¹) was based on a small sample size (12 eels; mean TL = 41 cm) captured in HAV during the 1999–2000 season. Because of the random order of sampling sites, these 12 eels were at large for 400 days, approximately 1 month longer than most other recapture eels. Although growth was adjusted for time at large (measured growth/400 × 365), the extra month during the high growth season (see below) could explain the high growth measured that year. Growth rates at GWB in 1999–2000 and HAV in 1998–1999 (7.5 cm·year⁻¹ and 6.1 cm·year⁻¹, respectively) were similar to those estimated in Georgia (Helfman and Bozeman 1984).

Our estimation that summer growth comprises 40% of the annual growth is supported by Helfman et al. (1984), who found the highest growth in summer, with lower growth in spring and fall, and no growth in winter. The correlation between growth in 1999 and 2000 was noteworthy and suggests that either some eels have a genetic predisposition for faster growth and (or) some eels consistently choose or out-compete other eels for better food or habitat resources. Feeding hierarchies have been observed in eels in captivity, which lends credence to the latter explanation (Tesch 1977).

Estimates of growth from size at age of capture were slightly lower than mark–recapture growth rates. Mark–recapture estimates of growth could have been negatively affected by the tagging procedure or positively affected by supplementing diets with bait. However, highly variable growth rates and the presence of both high (5.5 cm) and no (0 cm) growth documented 2 months after tagging suggest

that these influences may be minimal. Length was a poor predictor of age in this study. Despite poor fits of size at age regressions, estimated lifetime growth rates were similar in amplitude to those estimated through mark–recapture. Still, we advise that given the large variance in size at age and errors associated with ageing eels, tagging studies are a much more rigorous method for estimating growth rate assuming minimal effects from capturing and tagging.

Loss rate and production

Loss rate estimates (natural mortality and emigration) for eels >30 cm were similar between brackish-water and freshwater locations but showed differing age-specific patterns. Few young eels were captured at freshwater sites, and we believe that this was due to slow growth, with the younger, smaller eels escaping from the pots. Loss rates included both emigration plus natural mortality. There are only two estimates of natural mortality in American eels: (i) 0.25 year⁻¹ (22%·year⁻¹) for natural mortality and emigration on Prince Edward Island, and (ii) 0.13–0.79 year⁻¹ (12–55%·year⁻¹) for 10-year-old eels in the northwestern Gulf of St. Lawrence (Anonymous 2001). Compared with these estimates, the rates of loss measured in this study (15%·year⁻¹) were low. However, eels less than 30 cm, with potentially much higher predation, were not included in these estimates.

One of the assumptions for using the catch equation is that recruitment is stable through time. By binning eels into 3-year age classes, the effect of interannual recruitment vari-

ability will be reduced. Evidence suggests that eel recruitment varies from year to year but also follows longer-term decadal shifts associated with oceanographic conditions (Castonguay et al. 1994). If recruitment has been declining throughout the American eel's range (including the Hudson River; Anonymous 2001), then our loss rates may be underestimated (less than expected representation of younger age classes).

Production for 1998 and 1999 were both substantially higher for the brackish-water location (HAV) than for the freshwater location (ATH). The high production calculated for HAV in 1998 was influenced by the high eel abundance measured for that year (18 and 8 eels·ha⁻¹ in 1998 and 1999, respectively; Morrison and Secor 2004), whereas the high production in 1999 was influenced by the high growth rate for that year. Even though ATH experienced a slightly higher growth in 1998 than in 1999, the abundance was lower (5 eels·ha⁻¹ and 9 eels·ha⁻¹ in 1998 and 1999, respectively), leading to an overall reduction in production. A simple sensitivity analysis found that the abundance parameter affects production estimates the most and that implementing a length–weight equation or adjusting weights for food in the stomach (according to correction factor from Helfman and Bozeman 1984) reduced the production estimate by only 1%.

Vøllestad and Jonsson (1988) estimated European eel production at 3.51 kg·ha⁻¹·year⁻¹ in the Imsa River, Norway, which is much higher than the estimates for this study (0.43–1.44 kg·ha⁻¹·year⁻¹). The difference could be due to the low mortality rates and abundance estimates measured here compared with those of other systems. The low production in the Hudson River might also be related to the lack of commercial harvests. Fishing may increase the productivity of an area by keeping the population below carrying capacity, decreasing competition between conspecifics and perhaps allowing for increased regional recruitment by elvers (Tyler and Gallucci 1980).

Management implications

The results from this study suggest that brackish-water areas could support a higher fishing mortality level than freshwater areas. The mechanism for higher growth and production in brackish water is not yet understood. Possible causes include an increase in quality or quantity of food, increase in habitat quality (Barker and Cone 2000), lower resting metabolism resulting from living in near-isoosmotic conditions, increased water temperature, which reduces the amount of time that eels are dormant during winter (Walsh et al. 1983), reduced effects from parasites, decreased predation, or decreased intra- or inter-specific competition.

We hypothesize that the higher brackish-water eel production measured here is general to most large North American estuaries. Therefore, allowing harvest in brackish-water areas only, as recently proposed by an international team of scientists (Anonymous 2001), may be a defensible management policy. The lower productivity and the late age of maturity of eels in freshwater habitats suggests that fisheries would have a much larger impact in these areas. Keeping freshwater areas as a “reserve” or protected area would allow a certain percent of the population to mature, emigrate (escape), and reproduce. Freshwater areas in the Hudson

River supported only female eels, and it is the female eels that are most impacted by fishing (because of their large size and older ages) and most in the need of protection. Such a strategy of escapement would depend on the assumption that freshwater eels effectively contribute to the spawning stock, evidence for which exists for congeneric species (Tsukamoto and Arai 2001; Limburg et al. 2003).

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