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Abundance of Yellow-Phase American Eels in the Hudson River Estuary

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Abstract.—Fisheries for American eel *Anguilla rostrata* occur mostly in estuaries, yet eel abundance in large estuaries is poorly understood and the methods for estimating eel density underdeveloped. During 1997–1999, mark–recapture experiments were conducted for six consecutive days at six sites spanning the 250-km tidal portion of the Hudson River estuary, New York. Each experiment comprised 36 baited eel traps arrayed at 200-m intervals over 144-ha sampling sites. Estimates of local density were complicated by eel behavior, including trap-shy responses to marking and immigration into the experimental grid in response to bait attraction. We compared two open-population models, both modified Peterson methods: Jolly–Seber and a model created to account for eel behavior termed the mean recapture model (MRM). The biases in model outputs in response to trap-shy behavior and immigration were analyzed through simulations; the MRM showed less bias (−13%) than the Jolly–Seber model (+36%). Density estimates for the sampled regions ranged from 2 to 18 eels/ha for MRM and from 3 to 24 eels/ha for the Jolly–Seber model. The lowest density (1.6 eels/ha) was estimated for Albany (river km 240), but all other sites were estimated to have similar densities (5–18 eels/ha). The mean local density in the Hudson River estuary, 9.5 eels/ha, was much lower than those estimated for other systems. An overall abundance of 118,000 was calculated for Hudson River estuary eels larger than 30 cm (total length) at depths of 2–10 m.

American eels *Anguilla rostrata* are among the most ubiquitous of North American ichthyofauna and support important fisheries throughout their range. They inhabit diverse habitats, including salinities from freshwater to oceanic water; water bodies such as lagoons, marshes, swamps, lakes, streams, and large rivers; and latitudes from Venezuela to Greenland. Despite the fact that a large proportion of the American eel fishery takes place in large rivers and estuaries (ICES 2001), little information exists about American eel population dynamics for these habitats, particularly how density varies both within and among estuaries. It is important to understand how a species reacts in response to exploitation, but it is equally important to look at the characteristics of a species in the absence of exploitation.

In this study, we evaluate methods for estimating the density of American eels in the Hudson River estuary, a large middle-Atlantic estuary. The system is amenable to the study of eel density because it is a linear basin with well-defined gradients of salinity and depth. Unlike other middle-Atlantic estuaries (e.g., the Delaware and Chesapeake bays), the Hudson River has a deep, fjord-like bathymetry that is the result of glaciation (Paul 2001). Contamination of the sediment and fauna of the Hudson River by polychlorinated biphenyls led to a ban on harvesting of American eels in 1976 that remains in place today. The closure provides a unique opportunity to study eel stock dynamics in the absence of the major exploitation that occurs in large estuaries elsewhere.

The density of yellow-phase (subadult) American eels is highly variable among latitudes, watersheds, and habitat types (Table 1). In estuarine habitats, a principal hypothesis is that the growth, density, and productivity of yellow-phase eels are higher in downstream brackish habitats than in upstream freshwater locations (Helfman et al. 1987; Morrison and Secor 2003). Despite the recognized importance of estuaries as productive habitats and for eel fisheries, few studies have estimated eel density in estuaries (Helfman and Bozeman 1984;

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TABLE 1.—Density estimates from the literature for yellow-phase American eels, along with fishing method and sizes of eels captured.

Study	Location	Fishing method	Density (eels/ha)	Total length (cm)
Bozeman et al. 1985	Georgia tidal creek	Pots	182–232	20–80
Ford and Mercer 1986	Massachusetts tidal creek	Traps	875	15–63
Oliveira and McCleave 2000	Maine freshwater rivers	Electrofishing	800–2,200	>10
Oliveira 1997	Rhode Island freshwater river	Electrofishing	450–3,230	16–74
LaBar and Facey 1983	Vermont lake	Electrofishing	232–636	Not stated
This study	Hudson River estuary	Pots	1–30	28–67

Bozeman et al. 1985). No study that we are aware of has compared eel density among regions within a major estuary.

The lack of synoptic surveys of yellow-phase American eel density in major estuarine systems is due in part to the difficulties associated with sampling in these areas. In particular, no single gear can effectively sample all of the salinity zones, depths, and structured bottom types inherent to large estuaries. Electrofishing is not feasible in brackish water; seines, bottom trawls, fyke nets, weirs, and other trap nets are size selective and cannot be deployed across all depths and bottom types. Here we evaluate potting or trapping as a relatively easy method for catching and monitoring eels in estuaries. However, American eels possess physiological and behavioral characteristics that influence their catchability in pots. Catch rates in pots and traps are influenced by soak time, bait quality, environmental variables (e.g., temperature, salinity, and current velocity), gear saturation and escapement, inter- and intraspecific interactions, and behaviors related to tidal or seasonal cycles (Miller 1990). Some of these effects can be minimized by standardizing the elements related to soak time, bait quality, gear saturation, and lunar or diurnal cycles.

Of principal concern in developing pot indices of density are American eel behaviors related to homing and their keen olfaction (Tesch 1977). Home ranges in yellow-phase eels depend on habitat and vary from 1 ha in a Georgia tidal creek (Bozeman et al. 1985) to 65 ha in a Vermont lake (LaBar and Facey 1983). The yellow-phase eels we studied in the Hudson River also showed limited ranges; 88% of the recaptures ($N = 58$) at a freshwater tidal site occurred within a 144-ha area 1 year after the eels were marked (Morrison and Secor 2003). Displaced eels use selective tidal stream transport to precisely home to the regions from which they were removed (Parker 1995). Although yellow-phase eels have small home ranges, it is not known whether or how far an eel will travel outside its home range to follow a scent. As eels tend to feed only once every 2−3 d (Moriarty 1978), the catchability of an individual could change across days.

Mark–recapture models often require the assumption of homogeneous capture probabilities. There are two situations that can lead to heterogeneous capture probabilities. The first occurs when capture probability is constant over time for each individual but differs among individuals (referred to as ‘‘permanent heterogeneous capture’’). The animals with high capture probabilities are captured first and recaptured more easily than those with lower probabilities, thereby biasing the results. The second type of bias occurs when animals are temporarily influenced by the act of being captured. Here, individual capture probability varies through time depending on recent capture history (referred to as ‘‘temporary trap response’’). Individuals exhibiting such responses have been called ‘‘trap-happy’’ or ‘‘trap-shy’’ depending on whether being caught increases or decreases an individual’s probability of recapture (Pollock et al. 1990).

In this study, we compared two open-population methods of estimating the relative density of potted American eels at six sites in the Hudson River estuary, New York, covering the entire tidal extent of the estuary (250 km; 0–20‰ salinity; Figure 1). The critical assumptions of mark–recapture models were evaluated, particularly those related to heterogeneous capture probabilities among individuals and the ingress of eels into the study site from outside areas. Finally, density estimates were extrapolated for the entire estuary to calculate an overall abundance for eels longer than 30 cm in the Hudson River estuary.

Study Area

The Hudson River estuary (Figure 1) occupies a long, straight, and relatively deep basin that was formed by glaciers during the last ice age. The estuary is well mixed, with tidal influence from

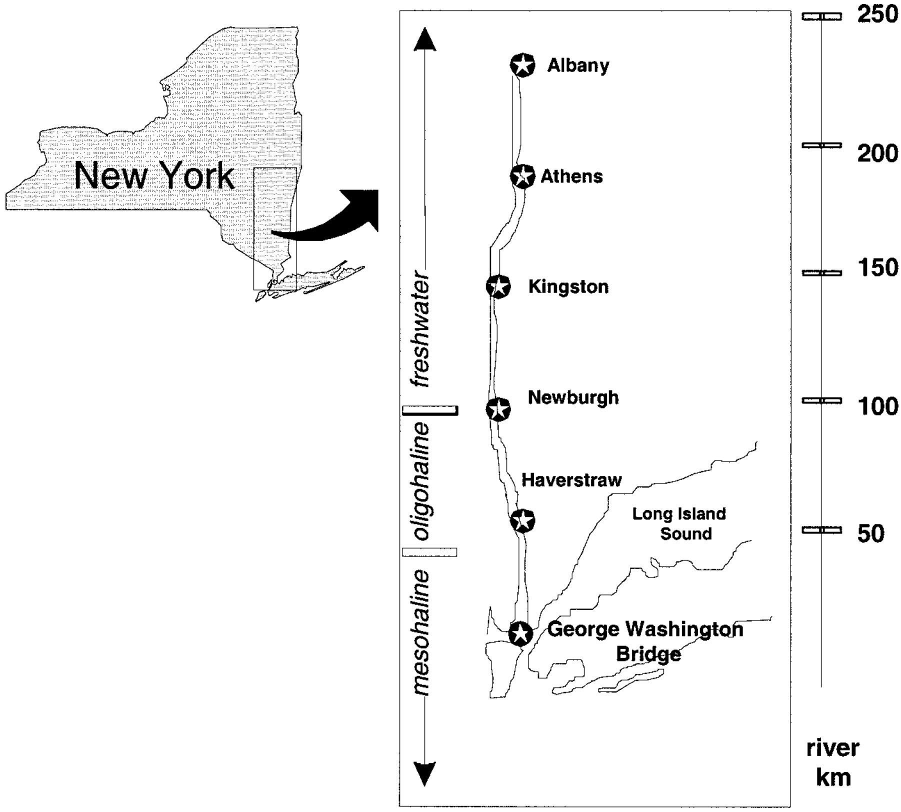

FIGURE 1.—Map of the Hudson River, New York. Study sites are indicated by stars; the distance upriver is shown on the right, salinity zones on the left.

New York City Harbor to its first barrier at Troy Dam (river km 255 [all sites are designated by distance from the mouth]). The salt wedge is usually found near Yonkers (river km 25) in high-flow months (late winter to early spring) and occurs upriver near Newburgh (river km 100) when the water flow decreases during summer months (Dovel et al. 1992).

Methods

Study design and capture methods.—Mark–recapture experiments were conducted during summer 1997–1999 at six sites within the tidal portion of the river. The sites were chosen to represent the entire length of the estuary but also because they had similar depths and bottom characteristics. All sites were located in shoal habitats in 2–10 m of water in areas immediately adjacent to the main channel. Nearshore areas were targeted for this study due to the higher density of American eels found in such areas (ASMFC 2000). Bottom sediments were fine clay and silt at all sites. Yellow-phase eels were captured in 100-cm-long, 25-cm-diameter, double-funnel eel pots (1.3-cm × 1.3-cm mesh) baited with a single large (>25 cm total length [TL]) Atlantic menhaden *Brevoortia tyrannus* and soaked for 24 h. Bait was replaced for each 24-h soak. Bait quality was held constant through time by using the same size and species of bait throughout the experiment.

A grid of 36 pots (50 pots were utilized in 1997) was deployed in either a 12 × 3 (Haverstraw [HAV], Newburgh [NEW], and Kingston [KIN]), 18 × 2 (Athens [ATH] and Albany [ALB]), or 36 × 1 configuration (George Washington Bridge [GWB]) depending on the topography of the river at each site. All deployment and recovery of pots was completed between 0800 hours and 1500 hours, depending on the location of the site and the number of American eels to be marked. Even though eels can respond to lunar cycles (Cairns and Hooley 2003), we did not standardize to the lunar cycle. However, any effects on catch per unit effort (CPUE) would be minimal through implementation of the density models. Because the recapture rate of marked individuals is inversely re-

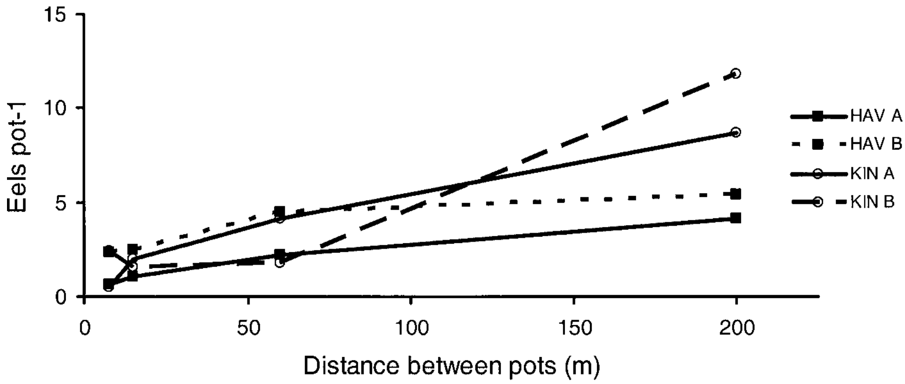

FIGURE 2.—Comparison of yellow-phase American eel catch per pot and the distance between pots during two gear saturation trials in the Hudson River during summer 1997. The sites involved were Kingston (KIN) and Haverstraw (HAV); the trials are designated A and B.

lated to catch, a high recapture rate should balance any increase in catch during the full or new moon. Pots were deployed approximately 200 m apart at all sites, creating grids of 144 ha. The bait plume (attraction radius) from each pot needs to be evaluated to convert pot catches to density estimates (eels/ha). Ideally, the distance between pots should not be too close (causing overlap of the attraction radius and reducing sampling efficiency) or too far (causing gaps in the grid where eels are not attracted to a pot). The 200-m distance between pots was chosen based on preliminary studies with 3 × 17 grids of pots that showed continued increases in catch per pot with increasing distance between pots (Figure 2). For three of the four experiments, the rate of increase in catch per pot declined between 55 and 200 m. We inferred from these trials that at 200 m the attractiveness of the bait plume from individual pots was attenuated. Although some interference between pots would be expected at distances of 200 m, we wished to ensure that the pots were sampling the entire grid. While estimates of absolute density could be biased (see Discussion), the relative density estimates should be robust because the distance between pots was the same among sites and years.

Several factors that might affect catch rates were considered. The influence of American eel presence in the trap on gear efficiency is unknown. We do not believe that escapes from or avoidance of occupied pots occurred but rather found that the presence of eels in traps may increase the catch for that trap. Because eels are gregarious animals (Tesch 1977), it is not surprising that we often found pots with more than 15 eels next to empty pots. We decreased the influence of environmental variables (temperature, salinity, depth, habitat, and season) by scheduling the fieldwork for the same season each year. The mean temperature of the river (measured at 1-m depth concurrent with fieldwork) was similar across summers (24 ± 2°C). However, in August 1999 at HAV, water temperatures were high (mean, 29°C), perhaps because of the shallow depth at this site, and eel catches were extremely low (a mean of 3 eels/pot, compared with 8 eels/pot in June 1999 when the mean temperature was 25°C). Drought conditions in 1999 reduced current velocity and may also have affected catch.

The pots captured eels between 25 and 75 cm long (Figure 3). Smaller American eels probably escaped from the pots, but we do not believe that larger eels (>75 cm TL) were excluded. In earthen ponds, Hornberger (1977) found that 1.3-cm × 1.3-cm-mesh pots captured eels of a similar length distribution (range, 30–70 cm TL) as that of the eels originally released into the ponds. Helfman and Bozeman (1984) poisoned a section of the stream after potting and found that 1.3-cm × 1.3-cm-mesh pots captured eels exceeding 20 cm in proportion to the length distribution of eels within that section. For the purposes of this study, we have assumed that all eels 30 cm and longer were vulnerable to the gear.

Captured American eels were anesthetized in either MS-222 (tricaine methanesulfonate; 1997–1998) or clove oil (1999), marked, and placed temporarily (for approximately 15 min) into a recovery tank before being returned to the water within 1 h of being captured. Eels were returned approximately 100–300 m away from original capture location after the baited trap had been replaced.

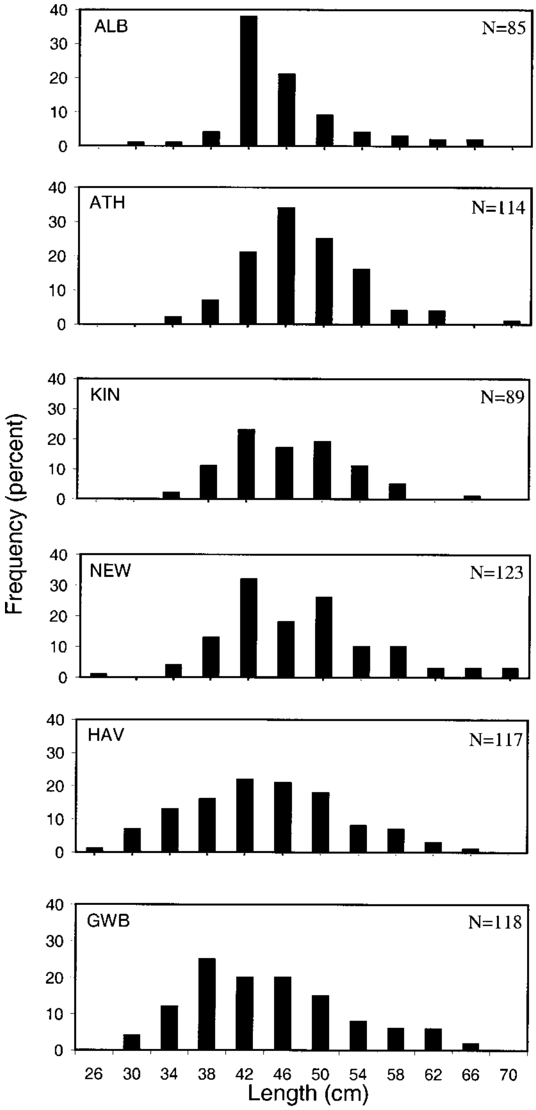

FIGURE 3.—Yellow-phase American eel length frequencies at various sites in the Hudson River in 1998. Site designations are as follows: ALB = Albany, ATH = Athens, KIN = Kingston, NEW = Newburgh, HAV = Haverstraw, and GWB = the George Washington Bridge (see Figure 1).

Liquid nitrogen brands (Sorensen et al. 1983) were used to mark all eels captured with a batch mark identifying the day 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 persisted for at least 1 month (unpublished data); eels showed no adverse responses to the branding procedure.

In 1997, marking studies were run for 8–9 consecutive days (7–8 soaks) at HAV and KIN to initially determine whether mark–recapture studies were feasible using pots. Batch branding was done on consecutive days to evaluate pot efficiency and determine whether a depletion method could be employed to estimate local density. At both sites, the number of unmarked American eels decreased linearly over time, providing initial support for the assumption of a closed local population and the potential for application of the Leslie depletion method. In 1998, the study was extended to all six sites, with trapping and marking for seven consecutive days (six soaks) at each site. After analyzing the second summer's data, we realized that the baited pots were attracting eels into the study area, violating the closed-population assumption. Therefore, in 1999 mark–recapture experiments were directed at measuring the degree of daily ingress into the grid at two sites. For 2 d of soaks and marking, a line of pots (7.2–10.8 km long) was initially deployed that centered on the grid but that also extended up- and downriver. Captured eels were given unique brands depending on whether they were captured inside the grid or north or south of it. The pots were then rearranged into the grid-sampling array used in 1997 and 1998 and soaked for six additional days. Immigration into the sampling grid was measured as the percent of eels marked north and south of the grid that were subsequently caught inside the grid.

Model assumptions.—To test for temporary trap-shy behavior, at each site analysis of variance (ANOVA) was used to test the effect of days at large on recapture rate. To test for trap-shy behavior, we combined the data from all sites within years (to increase sample size) and found that the recapture rates for American eels that had been at large for 1 d were lower than those of eels that had been at large for other time intervals but that there were no significant differences among recapture rates for the 2-, 3-, 4-, and 5 d-at-large groups (see Results). To increase the statistical sensitivity of the tests specific to each site, the recapture rates for eels at large 2–5 d were combined and compared with those of eels at large for 1 d by means of a *t*-test.

If permanent differences in capture probabilities were present, American eels with high probabilities of capture should have been caught during the beginning of the week and those with lower probabilities captured as the week proceeded. An ANOVA was run comparing eel recapture rates depending on the day they were originally captured.

Density models.—Two open-population, multiple mark–recapture methods were employed: a Jolly–Seber model and a mean recapture model (MRM). In multiple mark–recapture experiments, individuals are marked on several occasions with different batch codes, the population is sampled on subsequent occasions, and the number of eels marked with unique batch codes recorded. The MRM population estimates were obtained from the equation

$$\hat{N} = C \bullet A^{-1}, \quad (1)$$

where N = the size of the local population, C = the number of eels captured, and A = the mean percent recaptured for 2–5 d at large. The MRM assumed that eels have the same probability of capture before being marked and two or more days after marking (allowing for short-term trap-shy behavior the day after marking), no mark loss or misreading of marks, and homogeneous capture probability. In applying the MRM method, data from the six consecutive mark–recapture days were used to estimate probability of capture, but this probability was only applied to the catch from the first day of potting at each site to minimize the effects of immigration on density.

The program Popan5 (Arnason et al. 1998) was used to provide estimates of population density for the Jolly–Seber mark–recapture model (Jolly 1965; Seber 1965; Pollock et al. 1990). Because immigration into the grid was present due to the bait plume (see Results) and emigration was assumed to be negligible, we applied the Jolly–Seber ''births-only model'' (Pollock et al. 1990):

$$\hat{N}_i = \frac{n_i \cdot M_i}{m_i}, \quad (2)$$

where N_i = the population size at time i, M_i = the number of marked eels at large in the population at time i, n_i = the number of eels caught at time i, and m_i = the number of marked eels caught at time i. The variance of this estimate is calculated from the equation

$$V(\hat{N}_i) = N_i(N_i - n_i) \cdot \frac{N_i - M_i}{N_i, \cdot m_i}, \quad (3)$$

where N_i, n_i, and m_i are as above except that they are now the expected values over all samples (pooled across i). An additional variable, B_j, provides an estimate of immigration or the number of new animals joining the population in the interval between sample times j and $j + 1$, where j is any time period earlier than i such that $1 \leq j \leq (i - 1)$. Variable $N_{i(j)}$ is the expected number in the population at time i that first joined the population between sample times j and $j + 1$. Births (or immigration) for a given time interval (i or j) are estimated by the following equation:

$$\hat{B}_i = \hat{N}_{i+1} - \hat{N}_i. \quad (4)$$

The variance of this estimate is calculated from the equation

$$V(\hat{B}_i) = N_{i+1}(N_{i+1} - n_{i+1}) \cdot \frac{N_{i+1} - M_{i+1}}{N_{i+1} \cdot m_{i+1}} + N_i(N_i - n_i) \cdot \frac{N_i - M_i}{N_i \cdot m_i}, \quad (5)$$

where parameters are the same as in equation (3). The assumptions for the model included no mark loss or misreading of marks and homogeneous capture probability. In addition, we modified the model under the assumption of no losses on capture, which is supported by the high recapture rates experienced. For example, in June 1998 all but 1 of the 254 eels captured in ATH on the first day of capture were recaptured at least once during the remaining 5 d. Jolly–Seber estimates were based on data collected from the six-consecutive-day mark–recapture experiments (four sites in 1997, six sites in 1998, and three sites in 1999). Only estimates for the third day of potting were used, balancing the expected biases due to the temporary trap-shy behavior the day after marking and increased immigration from regions outside of the grid as the experiment progressed.

Catch per unit effort (mean number of eels per pot) for the first day of potting was compared with mark–recapture density estimates. Overall estuarine abundance was calculated on the basis of a mean local density estimate for combined years and sites. Using ArcMap 8.0 (Booth and Mitchell 2001) and a digitized bathymetric map from river km 21 to river km 210 (http://oceanservice.noaa.gov/mapfinder/welcome.html), we calculated the amount of area between 2 and 10 m deep. This area was multiplied by the mean density to estimate absolute abundance.

Model bias.—The Popan5 program does not explicitly account for heterogeneous capture probabilities but it does permit programming of specified populations, each with a different capture probability, for estimation of bias. Using Popan5, we simulated 5-d mark–recapture experiments based on a programmed population with a specified temporary trap-shy effect (capture probabilities variable through time but constant across individuals). To clarify terminology, the term ''programmed population'' refers to the values directly input into the Popan5 program. The outputs from the program (number of eels captured each day, average recapture rates, etc.) were then input into the Jolly−Seber or MRM models, the output being referred to as a ''simulated population.'' The bias was estimated by comparing the programmed input with the simulated output.

The programmed populations were based on data generated from the ATH site (river km 190) in 1998, namely, an initial local population size of 1,500 American eels and an immigration rate into the grid of 315 eels/d. This value was based on 28% and 35% immigration rates over the 6-d period north and south of the grid, respectively ($[0.28 \times 1{,}500 \times 2]/6 + ([0.35 \times 1{,}500 \times 2]/6$; see Results). This estimate of immigration assumed that similar densities occur inside and outside the grid (1,500 eels/grid) and that the bait plume attracts eels equally from an area the size of 2 grids above and below the marking area. The 2-grid area of outside attraction was chosen as a conservative multiplier due to considerations of the bathymetry of the Hudson River, where contiguous shoal areas (>0.6 km wide) comprised stretches 8–20 km in length, and evidence that eels were attracted to the central grid area from locations 10 km distant. The programmed population with a trap-shy effect was initiated with capture probabilities of 0.35 for unmarked eels, 0.2 for marked eels at 1 d at large, and 0.4 for eels at 2–5 d at large. These capture probabilities were calculated from field data at ATH in 1998. The recapture rate for 1 d at large was 0.16 ± 0.06 (mean $\pm$ SD), which was rounded to 0.20 for simulations. The field estimate for 2–5 d at large was 0.39 ± 0.09, which was rounded to 0.4. The estimate of a 0.35 capture probability for unmarked eels was a compromise value. We speculated that trap-happy behavior was present for days 2–5 at large based on the high recapture rates measured and the observation that a subset of eels returned to the pots daily. This suggested that the original capture probability was greater than 0.20 (the mean for trap-shy days) but somewhat less than 0.40 (the mean for trap-happy days).

To evaluate the magnitude of the bias between the density models, daily recapture data for the programmed population (number of American eels captured, mean catchability, and number of unmarked eels caught) were used as input parameters in the MRM and Jolly–Seber model (Figure 4). The simulated output from the models was compared with the known programmed population size (i.e., 1,500 eels) to calculate the bias due to heterogeneous capture probabilities in the population. Bias was calculated as follows:

$$\text{Bias} = 100 \cdot (\text{simulated } N - \text{programmed } N)/\text{programmed } N. \quad (6)$$

Simulations were run to evaluate the sensitivity of the model to estimates of capture probability, initial population size, and immigration rate. Populations with combinations of the original estimates and the following variations were simulated: capture probability for unmarked eels set to 0.3 and 0.4; initial population size set to 1,000 and 2,000; and immigration set to 160 and 630 eels/d. The influence of the input parameters on bias was assessed by plotting the bias that resulted from varying two of the programmed parameters while keeping the third one constant. A comparison of programmed input with simulated output values was also performed to assess the bias in the birth or immigration parameter calculated with the Jolly–Seber equation.

Results

Tests of Assumptions

On average, 32% of the American eels marked outside of the experimental grids at KIN and ATH in 1999 were recaptured in the sampling grid within a 6-d period (Table 2). Immigration estimates were similar for both sites, suggesting that immigration rates were similar at all sites. Temporary trap-shy behavior was found to be present, though it was only significant for eels that had been at large for 1 d (test for pooled sites; df = 6, $P < 0.0001$; Table 3). Eels at all sites except HAV displayed significant temporary trap-shy behavior the day after marking (1 d at large) when compared with their behavior after 2–5 d at large (Table 4). Recapture rates did not suggest the presence of permanent heterogeneous capture probabilities among eels, as they did not differ significantly according to the day of the experiment on which eels were initially marked (df = 3; $P = 0.90$).

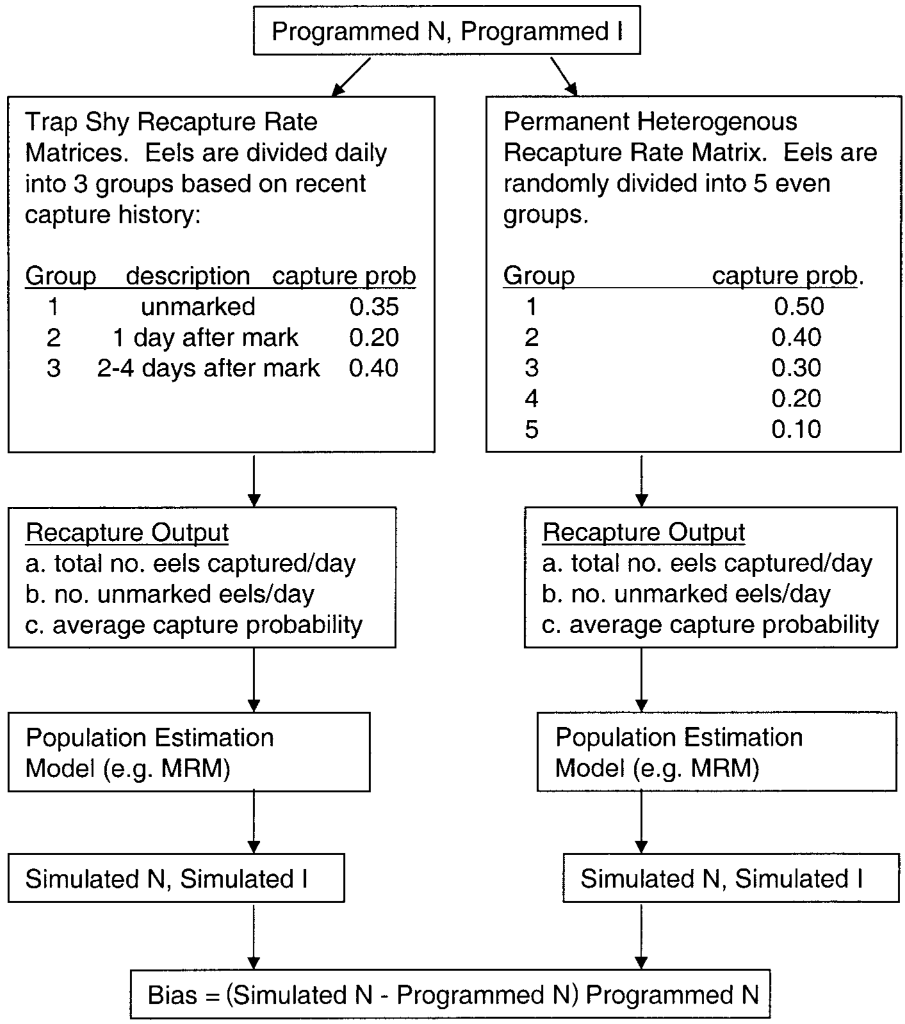

FIGURE 4.—Flow diagram depicting the procedure used to estimate the bias due to heterogeneous capture probabilities, immigration (*I*), and initial population size (*N*). The term ''programmed population'' refers to the values directly input into the Popan5 program. The output from this program (number of eels captured each day, average recapture rates, etc.) was then input into the mean recapture (MRM) and Jolly−Seber models; the output of the latter is referred to as a ''simulated population.'' The bias was estimated by comparing the programmed and simulated populations.

Density Model Results

During the period 1997–1999, a total of 33,491 brands were applied to more than 18,000 American eels. Estimates of recapture rates after 2–5 d at large were variable across sites (the results for 1998 are shown in Figure 5). The lowest mean daily recapture rates after 2–5 d at large were recorded at HAV in 1997 (16%) and GWB in 1998 (17%). The highest mean recapture rates (38%) were observed at ATH in 1998 and KIN in 1999. Density estimates using MRM, which were based on the 2–5-d-at-large recapture rates, ranged from 228 to 2,598 eels/grid or 2–18 eels/ha (Table 5). Overall, the results from the MRM analysis indicated that KIN, HAV, and GWB had the highest densities (>8/ha) (Table 5).

The Jolly–Seber estimates of immigration on potting days 2–3 (equations 4–5) were highly variable, ranging from 0 to 785 immigrants/d. The coefficients of variation (CV = 100 × SD/mean) for immigration estimates ranged from 236% to 10,393%, indicating that the Jolly–Seber model estimated immigration poorly. The highest immigration rates, calculated for ATH in 1998 and

TABLE 2.—Immigration of yellow-phase American eels into two study grids from surrounding areas, Hudson River, 1999. Recaptures occurred within 6 d of marking.

Marking location	Marked eels	Eels recaptured inside grid: Number	%
Athens			
North of grid	281	80	28
Inside grid	434	374	87
South of grid	177	62	35
Kingston			
North of grid	295	82	28
Inside grid	551	431	78
South of grid	88	33	38

TABLE 3.—Analysis of 1998 American eel recapture rates in the Hudson River (all six study sites combined) after 1–5 d at large. Different lowercase letters represent significantly different values according to Tukey's comparison.

Days at large	Recapture rate (mean ± SD)
1	0.14 ± 0.08 z
2	0.32 ± 0.14 y
3	0.28 ± 0.07 y
4	0.29 ± 0.11 y
5	0.29 ± 0.09 y

HAV in 1997, were slightly less than 800 eels/d. Immigration was estimated to be close to zero at KIN in 1997, GWB in 1998, and ATH in 1999. The immigration rate across sites and years was estimated to be 276 ± 307/d.

The Jolly–Seber birth-only model (Table 5) predicted densities that ranged from 466 to 3,512 eels/grid or 3–24 eels/ha; modeled density was highest for KIN in 1997 (24 eels/ha). In 1998, there was a decreasing trend in density with distance upriver; the highest estimates were for GWB and HAV, and the lowest occurred for ATH and ALB. Interestingly, over half of the estimates were lower than the total number of American eels branded at each site (eels/grid = 144 eels/ha), indicating that substantial immigration had occurred (Table 5).

There was more similarity between the MRM and Jolly–Seber estimates within years than there was among the estimates within models across years, the former varying less than twofold (Table 5). Across models, density estimates ranged from 1.6 to 24 eels/ha; density estimates generally were higher at HAV, KIN, and GWB but lower at NEW, ATH, and ALB. Catch per unit effort (Table 5) was not a good predictor of modeled density; the correlation was low between both CPUE and the MRM estimates ($r = 0.58$, $n = 11$, $P = 0.06$) and CPUE and the Jolly–Seber estimates ($r = 0.34$, $n = 11$, $P = 0.30$). However, CPUE was consistently low for the first year of potting at each site (HAV and KIN in 1997 and GWB and ALB in 1998), and the correlation increased if these data were omitted (MRM: $r = 0.87$, $n = 7$, $P = 0.01$; Jolly–Seber: $r = 0.74$, $n = 7$, $P = 0.06$). Conversely, the correlations using just the first year's data were also much stronger, albeit nonsignficant: $r = 0.89$ for MRM ($n = 4$, $P = 0.11$) and $r = 0.77$ for Jolly–Seber ($n = 4$, $P = 0.23$).

The entire Hudson River estuary (from 40°53′N to 42°23′N) covers 25,979 ha, 12,370 ha of that area being between 2 and 10 m in depth. The mean density estimated among all six sites was 9.5 eels/ha, which yields an estuarywide abundance of approximately 118,000 eels exceeding 30 cm TL. It is interesting to note that we sampled approximately 7% of the areal extent of shoal (2–10-m) habitats within the Hudson River estuary (6 grids × 144 ha) and in so doing captured and marked 18,000 individual eels, or 15% of the American eels estimated to occur in these habitats.

Bias

In simulations varying the initial population size, probability of capture, and immigration rate, the magnitude of the bias was much less for MRM

TABLE 4.—Student's *t*-tests of temporary trap-shy behavior the day after marking for American eels at six locations in the Hudson River in 1998; R_2 is the mean recapture rate after 1 d at large, $R_{3–6}$ the mean recapture rate after 2, 3, 4, or 5 d at large. Site designations are as follows: GWB = the George Washington Bridge, HAV = Haverstraw, NEW = Newburgh, KIN = Kingston, ATH = Athens, and ALB = Albany.

Site	R_2	$R_{3–6}$	df	T	P
GWB	0.04 ± 0.02	0.17 ± 0.04	13	−7.35	<0.0001
HAV	0.20 ± 0.07	0.26 ± 0.06	13	−1.58	0.1387
NEW	0.12 ± 0.02	0.30 ± 0.05	13	−8.24	<0.0001
KIN	0.22 ± 0.12	0.37 ± 0.07	13	−3.11	0.0083
ATH	0.16 ± 0.06	0.39 ± 0.09	13	−5.2	0.0002
ALB	0.14 ± 0.05	0.36 ± 0.03	13	−10.24	<0.0001

A. GWB 98

Day recaptured	Day marked 1	2	3	4	5	Mean
day 2	**0.06**					
day 3	0.24	**0.04**				
day 4	0.2	0.15	**0.02**			
day 5	0.16	0.16	0.15	**0.01**		
day 6	0.19	0.11	0.18	0.14	**0.05**	0.17

D. KIN 98

Day recaptured	Day marked 1	2	3	4	5	Mean
day 2	**0.4**					
day 3	0.48	**0.25**				
day 4	0.35	0.48	**0.15**			
day 5	0.27	0.35	0.4	**0.13**		
day 6	0.27	0.39	0.36	0.32	**0.15**	0.36

B. HAV 98

Day recaptured	Day marked 1	2	3	4	5	Mean
day 2	**0.23**					
day 3	0.35	**0.28**				
day 4	0.22	0.36	**0.22**			
day 5	0.17	0.27	0.27	**0.09**		
day 6	0.23	0.25	0.23	0.22	**0.19**	0.26

E. ATH 98

Day recaptured	Day marked 1	2	3	4	5	Mean
day 2	**0.20**					
day 3	0.54	**0.23**				
day 4	0.4	0.39	**0.17**			
day 5	0.48	0.36	0.28	**0.12**		
day 6	0.44	0.33	0.28	0.34	**0.10**	0.38

C. NEW 98

Day recaptured	Day marked 1	2	3	4	5	Mean
day 2	**0.13**					
day 3	0.38	**0.12**				
day 4	0.29	0.35	**0.10**			
day 5	0.27	0.25	0.28	**0.14**		
day 6	0.34	0.29	0.23	0.27	**0.10**	0.30

F. ALB 98

Day recaptured	Day marked 1	2	3	4	5	Mean
day 2	**0.15**					
day 3	0.35	**0.09**				
day 4	0.36	0.32	**0.16**			
day 5	0.38	0.36	0.42	**0.21**		
day 6	0.3	0.37	0.35	0.34	**0.11**	0.35

FIGURE 5.—Recapture rates of marked American eels at **(A–F)** all study sites in the Hudson River in 1998. Numbers in bold are recapture rates after 1 d at large; mean recapture rates for eels at large 2–5 d are shown to the right of each box. See the caption to Figure 3 for site designations.

estimates than for Jolly–Seber estimates (Figure 6). Simulations of programmed populations with trap-shy behavior resulted in a moderate underestimate for MRM estimates (maximum bias, −25%) and a large overestimate for Jolly–Seber estimates (maximum bias, 91%). For these simulations, bias was most sensitive to initial catchability in the MRM model and to daily immigration in the Jolly–Seber model. Conversely, the MRM model was least influenced by daily immigration and the Jolly–Seber model by catchability. For the range of programmed immigration levels evaluated, the Jolly–Seber model consistently underestimated immigration by approximately 23% (Figure 7).

Discussion

Density Model Assumptions

Estimating the density of yellow-phase American eels required explicit consideration of their behavior. The immigration of the eels into the bait-

TABLE 5.—Density of Hudson River American eels as estimated by the mean recapture (MRM) and Jolly–Seber models. Density estimates and CPUE are means ± SEs. Site abbreviations are defined in Table 4.

Site	Year	No. eels marked	MRM (eels/ha)	Jolly–Seber (eels/ha)	CPUE (eels/pot)
GWB	1998	1,168	15 ± 3	12.6 ± 0.9	10 ± 8
HAV	1997	2,111	11 ± 3	6.7 ± 0.6	4 ± 6
	1998	1,875	18 ± 3	14.4 ± 0.5	19 ± 13
	1999	987	8 ± 2	5.4 ± 0.4	8 ± 9
NEW	1998	1,719	7 ± 1	7 ± 1	9 ± 5
KIN	1997	2,828	18 ± 4	24 ± 1	9 ± 5
	1998	2,188	15 ± 2	11.8 ± 0.3	22 ± 13
	1999	1,580	11 ± 2	7.3 ± 0.2	17 ± 11
ATH	1998	2,129	5 ± 1	4.4 ± 0.4	9 ± 5
	1999	1,519	8 ± 3	12.1 ± 0.5	13 ± 7
ALB	1998	526	1.6 ± 0.1	3.2 ± 0.4	2 ± 3

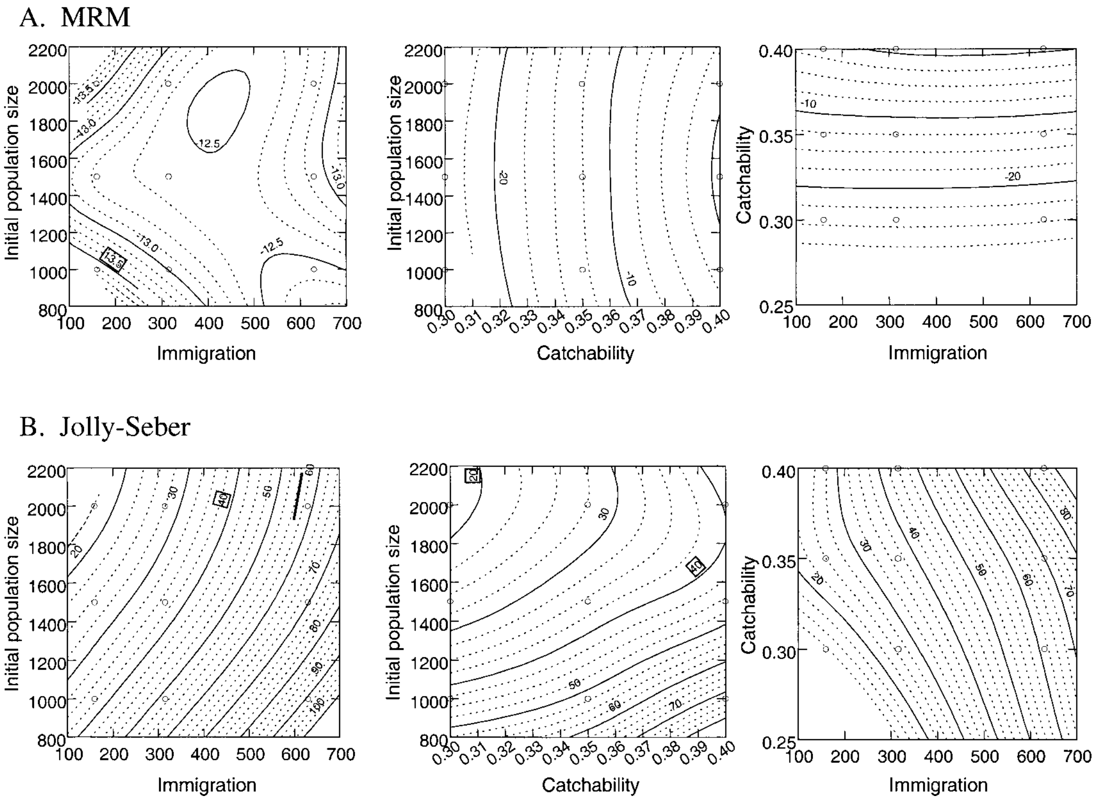

FIGURE 6.—Surface response plots of percent bias in the **(A)** mean recapture (MRM) and **(B)** Jolly–Seber model density estimates as functions of the initial population size, immigration, and catchability of unmarked American eels. The extrapolated surface responses were based on nine simulated scenarios, which are represented as open circles in each plot.

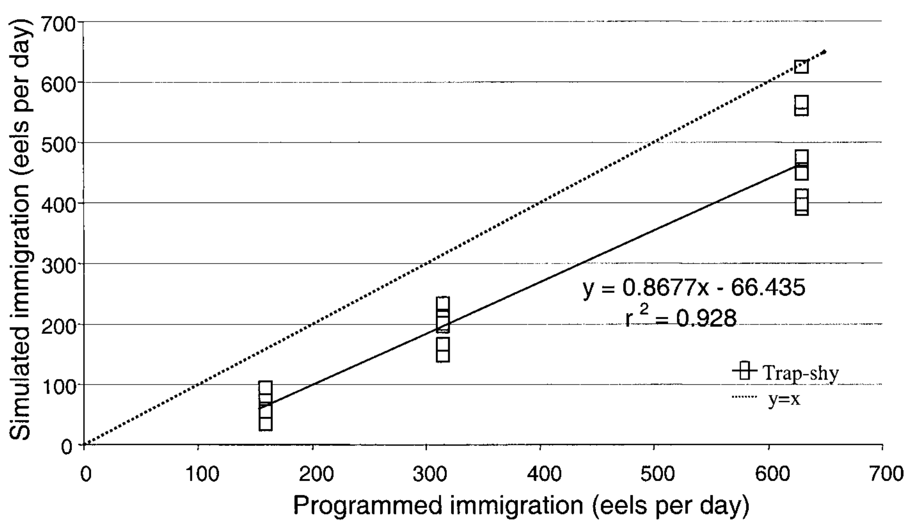

FIGURE 7.—Regression of known immigration (input) on Popan5 estimate of simulated immigration (output) for programmed populations with trap-shy behavior, heterogeneous capture probabilities, variable levels of initial population size, and differing initial capture probabilities. The dotted line represents equality of inputs and outputs.

ed sample grid prohibited accurate estimates using closed-population models, while trap-shy behaviors biased the results for open-population models. Immigration into the grid was substantial, an estimated 315 eels entering the grid per day. Modeled immigration rates (Jolly–Seber) were highly variable among sites, ranging from 0 to nearly 800 eels/d, with coefficients of variation as high as 10,393%.

Mark–recapture experiments failed to detect permanent heterogeneous capture probabilities across eels. The lack of evidence for permanent heterogeneous capture does not confirm its absence because the experimental duration (days at large) may have been insufficient to detect heterogeneous recapture rates. In addition, we did not explicitly test whether marked and unmarked eels behaved similarly. If there were a group of eels that completely avoided the pots, they would be undetected and this would result in the underestimation of density. Still, we believe that if permanent heterogeneous catchabilities exist among eels, the effect is minor in comparison with the trap-shy behavior that we detected.

There are three possible explanations for the trap-shy behavior we documented. First, the eels could be experiencing a short-term effect from the anesthetic; second, the eels may not be hungry the day after being caught (and fed); and third, the eels might have been present in the traps but the marks were not detected. We speculate that the first explanation is the most probable. Although the marks on the eels were often lighter the day after marking, we feel that with our diligence most of the marks were detected. In addition, the majority of the eels regurgitated their stomach contents when placed in anesthetic, suggesting that the short-term effects from the anesthetic were more influential than lack of hunger.

The MRM provided the less biased estimation of local density. Immigration into the grid should have had little influence on the model's estimates because density was modeled for the first marking day, thereby minimizing the influence of immigration on subsequent days. The bias simulations supported this view, in that the MRM was relatively insensitive to large daily changes in immigration rate ($<$13% bias). Trap-shy behavior was excluded in MRM analyses by explicitly ignoring recapture rates the day after marking (the only day with significantly lower recapture rates). If, as suspected (see Methods), trap-happy behavior occurred among eels at large for 2–5 d, then the mean recapture rate would have been artificially increased, resulting in an underestimate of density. Simulations showed that the MRM was most sensitive to estimates of the initial capture probability. Low estimates of initial capture probability resulted in the highest bias, suggesting that if trap-happy behavior did occur density estimates could have been underestimated by up to 25%.

The Jolly–Seber birth-only model either overestimated or underestimated density depending on how the assumptions of the model were violated. This model was intended for open-population estimation, but the results were sensitive to uncertainty in the immigration rate. According to our simulations, the magnitude of the bias varied directly with immigration rate and indirectly with initial population size. Pollock (1975) introduced a maximum likelihood model that allowed for permanent heterogeneous capture probability, but because it did not explicitly account for short-term responses to tagging it was not implemented. In addition, Program MARK (G. White, Colorado State University) was investigated to determine whether a better model existed. It was concluded that the MRM best handled the behavioral problems unique to potting eels.

Simple CPUE data were not strongly correlated with the mark–recapture estimates for pooled sites and years. However, when the data were analyzed for a subset of years or by individual years, much higher correlations occurred. We speculate that catchability (CPUE) was low during the first year of potting because eels had not previously been exposed to pots. Therefore, it may be possible to use CPUE as an estimate of relative eel density among sites with the same potting history. Our results suggest that CPUE can give a coarse index of the relative density among sites if external factors (soak time, bait quality, etc.) are standardized. However, CPUE results will be influenced by environmental effects such as flow, temperature, and natural forage availability.

We conclude that of the two models tested the MRM is more robust. In our simulations, the MRM exhibited lower bias than the Jolly−Seber model. The results also suggest that the temporal extent of the mark–recapture experiment could be shortened without impacting the density estimates. Recapture rates did not change as the week progressed (mark days 3–6), suggesting that a 3-d mark–recapture experiment is of suitable duration to obtain reliable estimates of recapture rates.

Absolute Density Estimates

Absolute density estimates (eels/ha) embody assumptions related to the effective fishing area (q), defined by Miller (1990) as the area from which 100% of the animals are caught. This interpretation of *q* means that the effective fishing area is smaller than the bait plume. In American eel studies, this definition is difficult to apply owing to the behavioral characteristics of eels, including their propensity to feed only once every 2−3 d (Tesch 1977; Moriarty 1978). Eels may be located within the bait plume of a pot but not caught due to insufficient appetite. On the other hand, with their excellent olfaction, eels could be attracted from areas quite peripheral to the pot or grid of pots. Relating CPUE to increasing distance between pots is one approach to evaluating *q*, but it is problematic because the area of influence is often not centered on the trap or circular in shape (Himmelman 1988). Still, based on preliminary trials with pot spacing, we believe that 200 m between pots (4 ha [200 m × 200 m] per pot) provided a reasonable estimate of the effective fishing area. This area was applied to allow comparisons with other studies.

The MRM density estimates for Hudson River American eels (2–18 eels/ha) were one to two orders of magnitude lower than other published estimates. The large discrepancies among estimates are probably related to (1) differences in the size range of eels included in the studies, (2) habitat and latitudinal effects, and (3) estimating errors. Because small (<30-cm) eels were not included in this study, their numbers and relative contribution to overall density among sites in the Hudson River are unknown. Analyzing bottom-trawl surveys of channel areas of the Hudson River, Mattes (1989) recorded that 55% of all sampled eels ranged between 7.5 and 30 cm. Assuming that this size composition is representative of all American eels in the Hudson River, a liberal projection would approximately double our estimate, giving density estimates of 4–36 eels/ha for Hudson River eels exceeding7.5 cm; however, such an estimate would still be much lower than those elsewhere. The density estimates in this study reflect biases resulting from unequal capture probabilities among eels and immigration into the grid of pots. According to our simulations, the maximum error associated with these biases in the MRM was 25%. While this bias is substantial, it is minor compared with the magnitude of the differences in density between this study and the others alluded to above.

Within the Hudson River, the density per hectare was similar at all sites except ALB, for which it was less than one-third as great. The low estimate at ALB could be due to its location in the uppermost section of the river, which would be consistent with the finding of decreased densities at greater distances from coastal waters in other studies (Oliveira 1997; Smogor et al. 1995; but see Oliveira and McCleave 2000). Alternatively, it could be due to the particular habitat at this site. The banks of the river at ALB are channelized by concrete slabs, which could result in a decrease in the amount of detritus or sediment deposited in the river. Because American eels often burrow underground (Tesch 1977) and feed on detritivores and other benthic organisms (Tesch 1977; Moriarty 1978), this could have a detrimental effect on the eel population. Apart from the situation at this site, the trends in density did not support the hypothesis raised in Helfman et al. (1987) that brackish water areas should support a higher density of eels. Density estimates (excluding ALB) did not differ significantly between brackish and freshwater locations. Density estimates were variable among years and showed no clear temporal trends. Studying an unexploited stock of European eels *A. anguilla* in Scotland, Carss et al. (1999) also found high variability in density between years and hypothesized that decreases in yellow-phase eel density were due to variable predation rates and losses due to emigration by mature silver eels.

In summary, local density estimates of American eels for the unexploited Hudson River estuary, while uncertain, were substantially less than those from other studies. This suggests that the Hudson River estuary has a lower carrying capacity for yellow-phase eels than other ecosystems. It is interesting to note that fishery yields in Delaware and Maryland in 2001 were 55 and 189 tons, respectively (NMFS 2003). These yields are equivalent to 270,000 and 905,000 yellow-phase eels (assuming an average weight of 200 g), which represents a much higher catch in 1 year than the 118,000 eels that we estimated for the entire shallow portion of the Hudson River. In response to the uncertainties noted in this paper, we recommend a mark–recapture study that utilizes two separate capture methods for marking and recapturing eels to balance the respective biases of each method. While mark–recapture and other census experiments in large estuarine systems such as the Hudson River require much higher levels of effort in terms of design, implementation, and analysis than those typically done in smaller systems (e.g., streams and marshes), we believe that continued research and monitoring of eel densities in estuaries is particularly warranted because eel fisheries are concentrated in these systems (ICES 2001).

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