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PATTERNS OF FISH SPAWNING IN HUDSON RIVER TRIBUTARIES: RESPONSE TO AN URBAN GRADIENT?[1]

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Introduction

Large rivers, for all their importance to humans, are not well understood with respect to ecological patterns and processes. Although some generalizations have been made, e.g., the "river continuum" concept (Vannote et al. 1980) and the "nutrient trap" created at salt–freshwater interfaces (Mansueti 1961), the geographic scope of large rivers presents considerable sampling difficulties for evaluation of many system-wide phenomena. Furthermore, studies of large rivers often fail to consider interactions between the lotic portion and surrounding watershed, whereas understanding large-scale processes may require such attention.

Two features of many large river watersheds, their large geographic extent and their occupation and use by humans, should render them good candidates for the manifestation of anthropogenic, ecological gradients. Many urban centers are located along major rivers, a fact that can be confirmed by examining any atlas. The impacts of urbanization, as a source of pollutants, upon rivers and streams have been studied by scientists and engineers for decades (cf. Hynes 1960, Nemerow 1985, Thomann and Mueller 1987); most situations involve point sources and their impacts upon individual waterways. Often, more subtle patterns of point and nonpoint source impacts on regional-scale ecological processes are not addressed. One approach is to examine properties of tributary watersheds within the overall drainage basin, as a function of urbanization.

We demonstrate the approach with a study conducted to evaluate the contribution of nontidal tributaries to anadromous fish spawning within a large, riverine estuary. We will present data that suggest large-scale, human mediation of this part of the fish production process, as evidence of a quantifiable response to an anthropogenic gradient.

As suggested in the discussion by McDonnell and Pickett (this issue), the following questions can be posed:

How do ecological parameters of interest respond to level of urbanization? Are responses linear, or are thresholds involved?

What system parameters will exhibit greatest sensitivity? Will species' responses be more sensitive than indices of ecosystem function, as suggested by Schindler (1987)?

The Hudson River Basin and Its Urban–Rural Gradient

We conducted our study in the watershed of the tidal Hudson River, located in eastern New York State (Fig. 1). The estuary is bounded on the north by the Federal Locks and Dam at Troy and by New York Harbor to the south. The Hudson flows unimpeded along this 243-km course, draining into New York Harbor and the New York Bight. There are 198 streams tributary to the estuary, ranging from first to ninth order (NYSDEC 1988). Although the Hudson Valley is composed of a mosaic of land-use types, tributaries closest to the New York City urban core (and Albany to a lesser extent) are in general more urbanized, whereas upriver landscapes are more rural.

We selected 16 tributaries for this study (Fig. 1), based in part on their size, geographic location, and known occurrences of anadromous fish spawning runs. For analysis, tributaries were grouped into four geographic areas ("reaches"), each containing four tributaries with a range of stream sizes (Fig. 1). The total area drained by the selected watersheds is ≈ 5700 km^2, or 42% of the lower Hudson drainage. Geographic locations of tributary mouths were measured in river miles (RM) with RM = 0 located by convention at the southern tip of Manhattan Island, and ranged from RM 25 to 136 (1 mile $\simeq$ 1.609 km). United States Geological Survey (USGS) land-use maps were overlaid on corresponding topographic sheets with demarcated wa-

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[1] For reprints of this Special Feature, see footnote 1, page 1231.

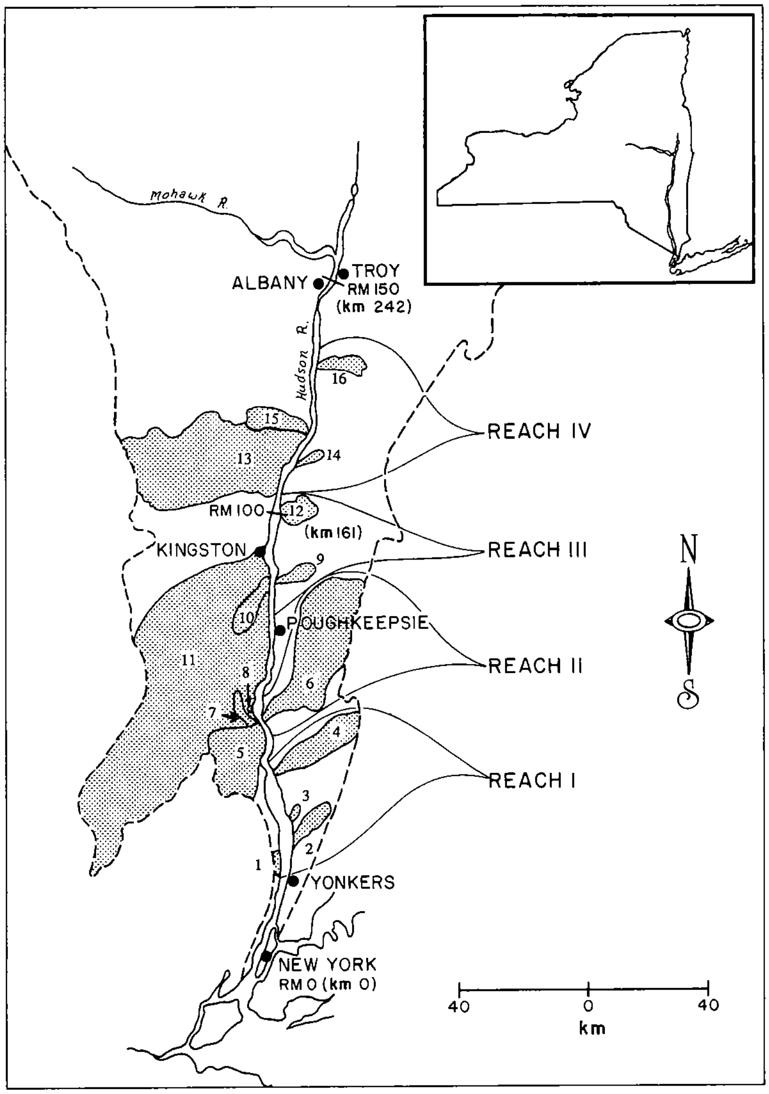

FIG. 1. Distribution and relative sizes of watersheds sampled in the Hudson River estuary. Watersheds were grouped into "reaches" used for many data analyses. Numbers identify individual tributaries: 1 = Sparkill Creek, 2 = Pocantico Brook, 3 = unnamed, in city of Ossining, 4 = Peekskill Hollow Brook, 5 = Moodna Creek, 6 = Fishkill Creek, 7 = Quassaick Creek, 8 = unnamed, in city of Newburgh, 9 = Crum Elbow Creek, 10 = Black Creek, 11 = Rondout Creek, 12 = Saw Kill, 13 = Catskill Creek, 14 = Mill Creek, 15 = Hannacroix Creek, 16 = Vlockie Kill.

tershed boundaries, and the area of each land-use type was measured with a digitizer. Land-use classes were aggregated from 30 categories provided by the USGS into seven land-use types (barren, industrial + roads, urban/suburban residential, agriculture + pasture, woodland, range + scrub, and open water) for the purposes of this study. The "urbanized" portion of watersheds was defined as those lands in residential, industrial, and transportation uses.

As expected, more of the down-estuary watersheds are urbanized (Fig. 2), under the spreading influence of the New York metropolitan area. Much of this pattern is the result of population growth over the last two decades (NARIG 1989). Urbanized land drops off dramatically ≈120 km north of Manhattan, in spite of the presence of two fairly large cities (Poughkeepsie and Kingston) on the Hudson's shoreline (Fig. 3a). Our sample of tributaries did not extend close enough to the Albany metropolitan area to reflect much of its influence on surrounding watersheds.

If urbanization is loosely regarded as a process of human dominance over the landscape, then the extent

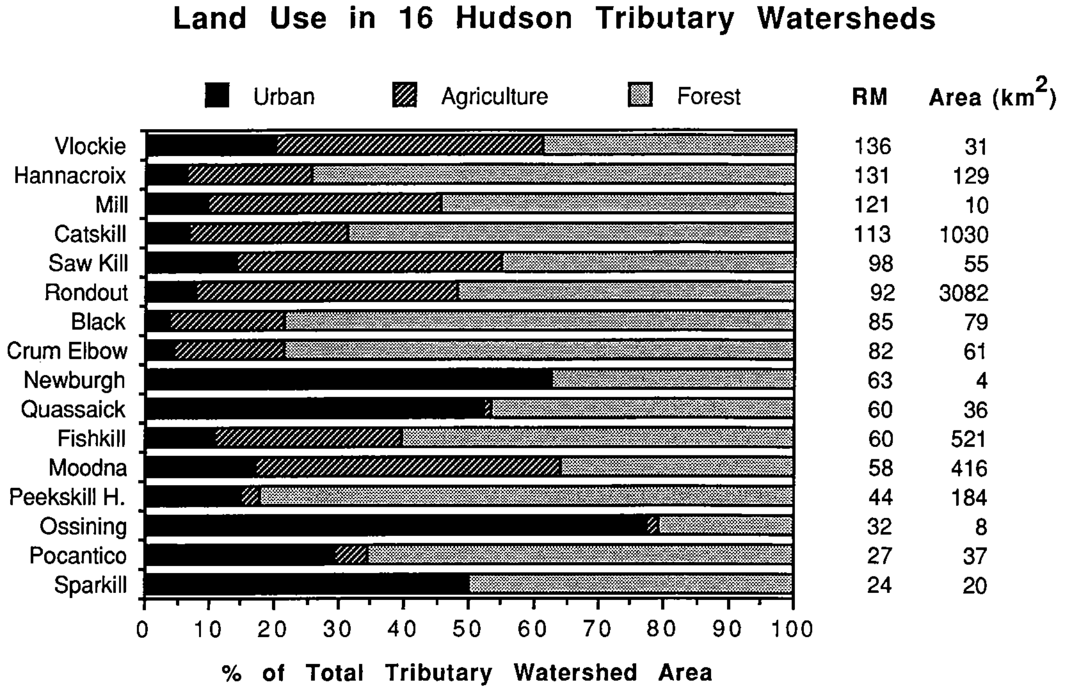

FIG. 2. Land use of the watersheds studied within the Hudson basin. Watersheds are arranged from north (top) to south (bottom). Land use has been aggregated for simplicity: "urban" includes residential, industrial, barren, and paved areas; "agricultural" includes cropland, pasture, and rangeland; "forest" includes woodland, wetlands, and open water. "RM" = point of confluence with mainstem Hudson in River Miles measured from the southern tip of Manhattan Island, New York City.

of urban influence within a given watershed should be a function not only of the position of that watershed in relation to population centers such as New York, but also of watershed size relative to the population center (a scaling factor). If urban land area is plotted against total watershed size (Fig. 3b), those watersheds most closely converging on the 1:1 slope are relatively small (<40 km^2). This suggests that smaller watersheds are more readily "captured" by a relatively large-scale process, as exemplified here with urban spread.

CHANGES IN ECOSYSTEM CHARACTERISTICS ALONG THE GRADIENT

In order to learn what factors might influence tributary contributions to anadromous fish spawning, we gathered a variety of data, including water quality, physiography, stream characteristics, land use, and geographic position in the overall watershed (Schmidt and Limburg 1989). All streams were sampled weekly from mid-March through June 1988, the period bracketing anadromous fish spawning in the mainstem, for a total of 15 wk. All tributaries were sampled during the same 24-h period. For details of sampling, see Schmidt and Limburg (1989).

Correlation, regression, concordance, and graphical analyses were used to explore relationships among the variables. Multiple regression analyses were used to examine the relationship of total, anadromous, and resident species' spawning and survival (measured as densities of eggs and larvae) in relationship to water quality parameters (temperature, pH, and dissolved oxygen), physiography (watershed area, geographic position along the Hudson, and river reach), and land use (Schmidt and Limburg 1989). In one case, fish vs. the urbanized portion of watersheds, the relationship was reciprocal, and the inverse of the independent variable was used to transform the relationship into a linear one (Devore 1987). Stepwise regressions, Mallow's $C(p)$ statistic, and correlation analyses were carried out to select appropriate models and identify multicollinearities (Neter et al. 1985; for further discussion see Schmidt and Limburg 1989).

Dissolved oxygen as an indicator of system state

Dissolved oxygen data collected in this study showed a response to urbanization at a regional scale. Dissolved oxygen levels were monitored, not only because fish eggs and larvae generally require well-oxygenated water (Hunter 1984), but also because dissolved oxygen, when converted to percent saturation values, can provide insight into both the metabolic and pollution

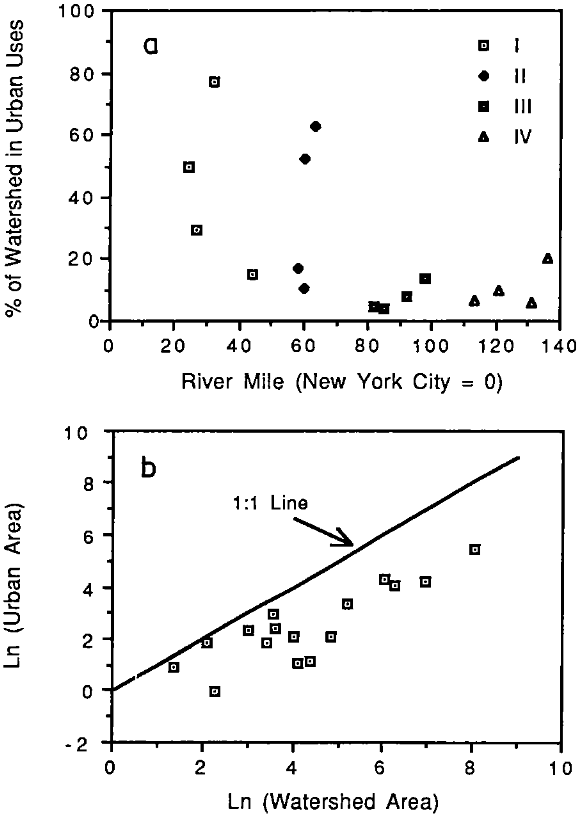

FIG. 3. The urban gradient along the Hudson estuary as measured by percent of watersheds in urban land uses. (a) Urbanization as a function of distance from the river mouth, in River Miles (1 mile ≃ 1.609 km; 0 = mouth = New York City). (b) Relationship of urbanization and size of watersheds (note log-log scale).

status of streams (Thomann and Mueller 1987). Supersaturated values are typical of both well-aerated streams and eutrophic rivers, while undersaturation indicates an oxygen deficit possibly created by an organic load (Nemerow 1985). Reach I (with highest percentage of urban lands) had very supersaturated streams in March when our study began, but by mid-April percent saturation had declined to ≈70–80% and remained there through the study period (Schmidt and Limburg 1989). By contrast, levels remained very close to saturation in Reach III, where urban lands averaged only 7.5% of watershed areas.

Low dissolved oxygen levels near urban centers certainly come as no surprise, given the likelihood of organic matter dispersion there. However, plots of the temporal variability of this parameter vs. river mile (Fig. 4a) and percentage of urban land within a reach (Fig. 4b) reveal an even more striking pattern. Oxygen saturation values were correlated with neither watershed area nor mean depth at the sampling site, but were both spatially and temporally more variable with increasing land under urbanized use. All of our samples were collected as close to sunset as possible, thus avoiding diurnal differences and eliminating this source of sample bias. The causes underlying the spatial trends in variance are unclear, but may be related to the fact that urbanized watersheds are subject to increasing frequencies and varieties of disturbances that affect dissolved oxygen saturation levels (e.g., erosion from housing developments, runoff from paved areas, and direct alteration of stream beds). This suggests the hypothesis that disturbance frequency or intensity (natural as well as anthropogenic) within a watershed may be expressed by variability in some parameters reflecting the state of the system, such as dissolved oxygen in this case.

Fish production in relation to the urban gradient

One of our initial hypotheses was that a "spawning front," proceeding northward up the estuary as spring progressed and temperatures rose, would be observed. In contrast to our expectation, spawning activity was

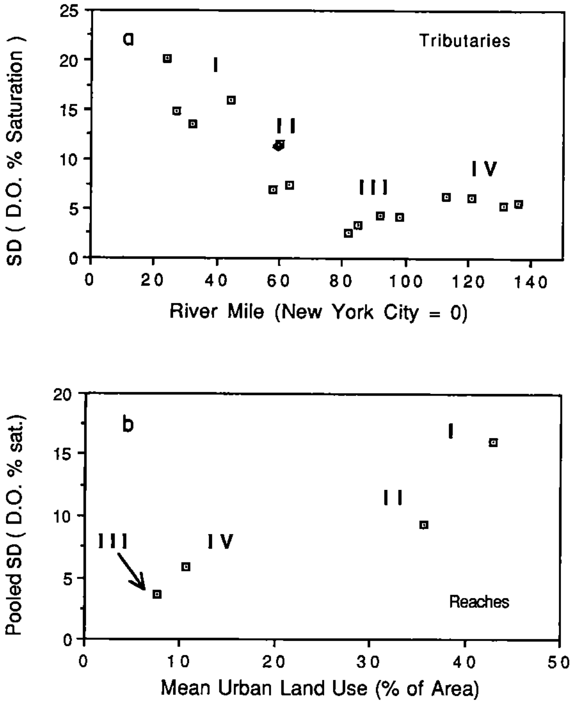

FIG. 4. Variability (over time) in dissolved oxygen (D.O.) percent saturation values. (a) Standard deviations (SD) of D.O. percent saturation values measured weekly for 15 wk in 16 Hudson River tributaries relative to distance upstream from New York City (note that two points overlap in Reach II). (b) Pooled standard deviations (SD) vs. mean percentages of urbanized land for each reach (see Fig. 1 for location of reaches).

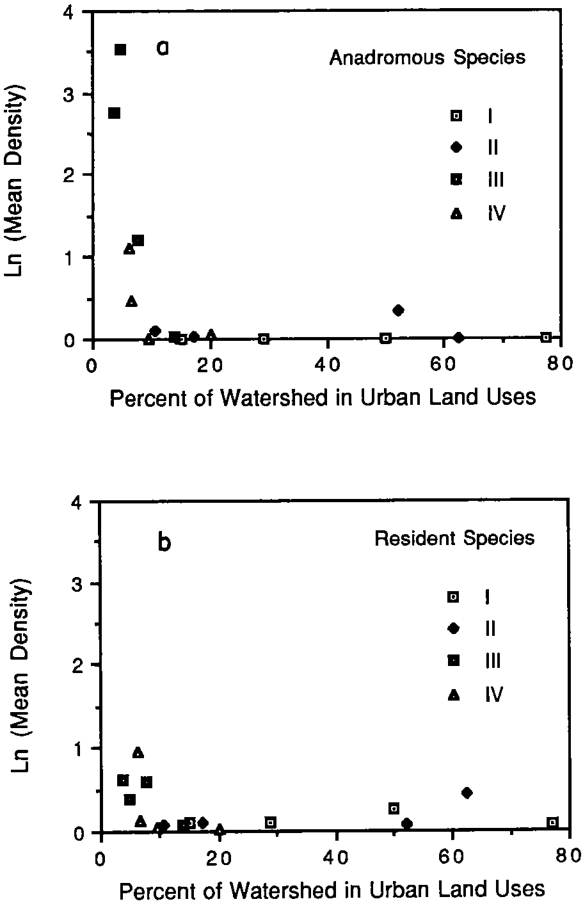

FIG. 5. (a) Natural log of average densities (no./m^3) of eggs and larvae of anadromous fish (mostly alewife) in 16 Hudson River tributaries relative to watershed urbanization. A threshold of ≈10% urbanization is apparent. (b) Average densities of eggs and larvae of all other species (not anadromous) of fishes in 16 Hudson River tributaries relative to watershed urbanization.

highly regionalized. Of the ≈70 000 eggs and larvae collected over the 15-wk period, the vast majority were collected in three streams in Reach III, with two streams in Reach IV also producing large numbers of fish (Schmidt and Limburg 1989). A total of 23 species was collected, but alewife (*Alosa pseudoharengus*), an anadromous herring, composed 93% of the catch, suggesting the importance of tributaries as spawning sites for these fish.

In all of the data analyses on fish, the strongest and most consistent relationship was between densities of eggs and larvae and our index of urbanization [ln(anadromous densities) = $-5.22 + 12.2(1/\text{urban land})$, $r^2 = 0.732$, $P = .0001$]. There is a very strong spatial pattern for anadromous fishes (Fig. 5a; mostly alewife); the mean weekly densities of fish are shown here, but other time-independent measures of density show the same pattern. The data demonstrate a strong threshold effect of urbanization on anadromous spawning success, as measured by densities of eggs and larvae collected at the confluence of stream and estuary. There is the suggestion of such an effect for resident fishes as a group (Fig. 5b), and also holds for the second most abundant species, white perch (*Morone americana*), one of the major resident species in the mainstem Hudson.

The fact that a land-use parameter explained a significant amount of the variability in fish egg and larval densities, and that other variables did not, is somewhat surprising. It is possible that other characteristics not measured here could have confounded interpretation of the urbanization gradient. The salinity gradient of the estuary, for example, should roughly correspond with both river mile and urbanization (excluding the Albany–Troy region). If alewife spawning was directly influenced by the location of the salt front in the estuary (defined as the 0.1 g/kg salinity zone, which migrates on average between RM 24 and 68 during March–June (Wells and Young 1990, *in press*)), the estuarine salinity gradient could hypothetically result in spawning patterns similar to those reported here. Such salinity influence on migratory behavior during the spawning run has not been reported in the alewife literature; moreover, alewives and their congenerics, blueback herring (*Alosa aestivalis*), have been known to run in some Hudson freshwater tributaries located well below the salt front (Boyle 1988), including Pocantico Brook (Fig. 1). Nevertheless, we tested whether tributary spawning was correlated with the estuarine salt front by computing its location from freshwater inflows, following the method of Abood (1974, 1977 as cited in Wells and Young, *in press*), Abood et al. (1990, *in press*), and Wells and Young (1990, *in press*).

Salt front location in the Hudson mainstem, which never advanced past RM 63 during the period of maximum spawning (April–May; Fig. 6a), was not significantly correlated with spawning. However, a comparison of larval and egg densities and the urban land-use index as a function of distance from the salt front reveals the potentially confounding nature of the salt front (Fig. 6b). Whereas the patterns of fish spawning and the inverse land use are remarkably similar for the nine northernmost tributaries ($r = 0.87$), this relationship breaks down in the vicinity of the salt front. Different factors may be controlling spawning above and below the front, and caution must be taken in interpretation, given the spatial correlation. However, we cannot discount the hypothesis that the proximal causes of spawning variability (which we have not identified in this study) result, at least in part, from some aspects of urbanization.

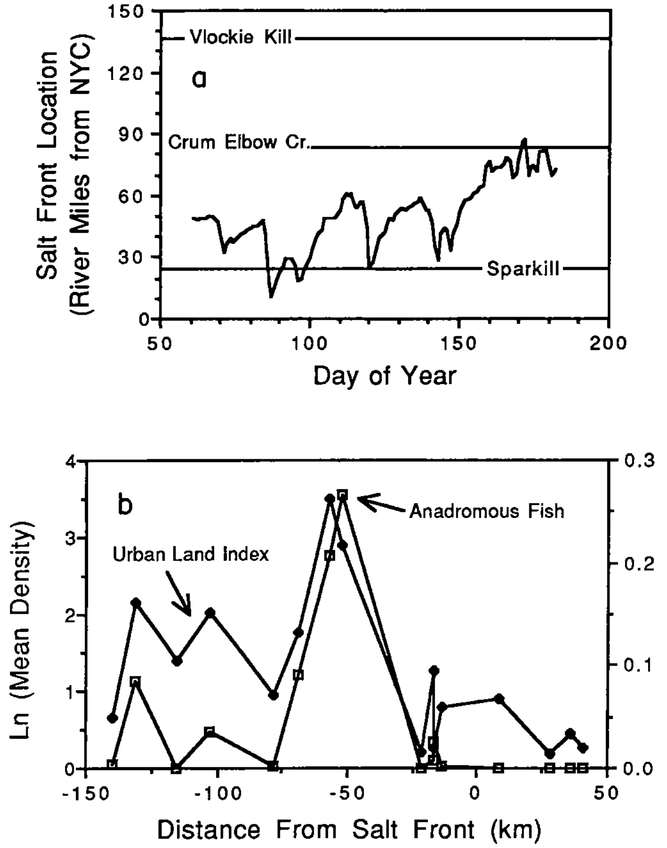

FIG. 6. Location (in River Miles from NYC) of the salt front (defined as the zone of 0.1 g/kg salinity) in relation to tributary spawning of anadromous fish (mostly alewife), for the period 1 March (day 61) through 30 June (day 182) 1988. Lines show points of confluence of the northernmost and southernmost tributaries in the study, along with that of the tributary with highest recorded densities of eggs and larvae. (b) Mean (log-transformed) densities of anadromous fish eggs and larvae for 16 Hudson River tributaries, and the reciprocals of corresponding urban land percentages, plotted at the tributary mouths relative to the mean location of the salt front over the study period. Abscissa increases in direction of higher salinity.

Implications and new questions

It is clear from the above discussion that urbanization gradients in large river basins can be complex ones. Direct responses to urbanization are superimposed upon responses to natural environmental and edaphic factors, so that the "signal" generated by a natural force (e.g., temperature, bedrock type) may be subject either to amplification or interference from urban disruptions. Nevertheless, studies of ecological processes along urban gradients hold implications both for improved management of human-dominated landscapes and for improved understanding of ecological phenomena.

Estimates of export of alewife eggs and larvae from tributaries, together with estimates of juvenile alewife densities in the mainstem, have led us to hypothesize that suitable spawning tributaries may constitute a limiting factor in Hudson River alewife production (Schmidt and Limburg 1989, 1990). If this is true, then this study suggests that the alewife population in the river may be sensitive to processes within the tributary watersheds, including tributary watershed urbanization. The cause of the threshold effect of watershed urbanization on egg and larval densities is as yet unknown. Possible mechanisms that may result directly or indirectly from urban development include alteration of habitat through siltation, impoundment, removal of substrate, or other physical alteration; toxic or organic pollution; or increased acidification of runoff. The latter is not likely to be a factor in most of the Hudson drainage, with its well-buffered soils, except in Reach I where crystalline bedrock predominates. On the other hand, demographic pressure on suburban "bedroom communities" has increased; consequently new construction has increased significantly in counties surrounding the city (Table 1). The material load trans-