SPATIAL ABUNDANCE QUANTILES AS A TOOL FOR ASSESSING HABITAT COMPRESSION IN MOTILE ESTUARINE ORGANISMS

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ABSTRACT: *Estuarine zooplankton, hyperbenthos and nekton often move upstream in response to reduced freshwater inflows. In estuaries with drowned-river-mouth morphologies, this upstream movement repositions organisms within estuarine reaches that have reduced volumes. The movement into more volumetrically confined habitats and into areas near water-control structures raises concerns about habitat compression and associated reductions in estuarine carrying capacity, particularly if this trend is associated with excessive freshwater withdrawal. We present a simple method for identifying habitat compression along the longitudinal estuarine axis and apply it to faunal transect surveys of several west-central Florida tidal rivers. Regression was used to compare the length (km) of the interdecile range (10th–90th cumulative abundance percentiles) under variable freshwater inflow conditions. The use of quantiles frees the analysis from assumptions about the shape of longitudinal abundance distributions. We demonstrate how his approach can also be used to identify sampling artifacts and to quantify the extent of impingement on estuarine dams. In estuaries that have strong seasonal variation in inflow, useful results can be obtained with <2 yrs of monthly transect data. This method offers promise as a tool for inflow management in estuaries where long-term abundance data are not available.*

Key Words: Minimum flows and levels, habitat loss, habitat size, carrying capacity, organism distribution, dam impingement, quantile regression

MANY estuarine organisms move upstream in response to decreasing freshwater inflows (Peebles and Flannery, 1992; Jassby et al., 1995; Flannery et al., 2002; Dege and Brown, 2004; Greenwood et al., 2007). These upstream movements often place estuarine organisms in habitats that have reduced volumes, areas, or shoreline lengths. Habitat dimensions may decrease simply because the organisms move into lower-order estuarine tributaries, or they may undergo rapid reduction within the estuarine main-stem itself due to the drowned-river-mouth geomorphology of many estuaries. In drowned-river-mouth estuaries, physical dimensions characteristically decrease in a strongly nonlinear fashion with distance upstream. Estuarine habitats, as commonly defined (Able, 2005), cannot occur above sea level and therefore become increasingly compressed as freshwater inflows decrease.

Reductions in freshwater inflows and associated upstream organism movement can occur in a matter of days within small, flashy rivers (Flannery et al., 2002); however, most concerns regarding habitat compression involve seasonal or longer time scales. Seasonal dry periods, multiyear droughts, decadal climate cycles, and long-term climate trends may lead to widespread estuarine habitat compression, particularly when coupled with increasing human demands for surface water. Quantifying estuarine habitat compression not only requires documentation of central tendencies in the organisms' upstream movement but also requires assessment of the organisms' inflow-related dispersion responses. Changes in dispersion state (i.e., whether an organism's distribution along an estuary is compressed or scattered) determine the extent of physical habitat loss. For example, the local population of an organism could become more dispersed as it moves upstream, offsetting the potential reduction in its physical habitat dimensions. Such interactions have received very little attention in the scientific literature, and are the subject of this paper.

Kimmerer (2002) presented a graphical representation of habitat dispersion in the form of distribution quantiles for longfin smelt in the San Francisco estuary, but otherwise did not present an exploration of the behavior of these parameters. Distribution quantiles (e.g., 10th, 25th, 50th, 75th, and 90th percentiles) have a clear conceptual interpretation that is independent of the constraining assumptions associated with parametric statistics. In particular, the behavior of the interdecile range (IDR, the range between the 10th and 90th percentiles) is appealing because it represents a large proportion of the distribution (80%) and often does so without being overly susceptible to sample-size effects. Quantiles are of general interest to ecologists and ecosystem managers because they can reveal responses that are not apparent in relationships with the mean—moreover, examining alternative slopes at different quantiles provides a more complete conceptual picture of the response (Scharf et al., 1998; Wang et al., 2001; Kimmerer, 2002; Eastwood et al., 2003). For example, a quantile describing the upstream limit of an organism's estuarine distribution may reveal impingement on an estuarine dam even though the mean of the same distribution appears to remain a safe distance downstream.

Quantiles can be applied to the estuarine habitat compression problem, but only if certain hazards can be avoided. In this paper, we examine the behavior of lower and upper abundance-distribution deciles (10th and 90th percentiles) for several estuarine fishes and invertebrates in west-central Florida, identifying interactions with 1) changing freshwater inflows, 2) sampling artifacts, and 3) habitat impingement on estuarine dams. We also demonstrate a simple method for quantifying estuarine habitat compression.

METHODS—*Survey areas and sampling methods*—The aquatic fauna in the lower, estuarine portions of 12 rivers and streams in west-central Florida have been surveyed in recent years (FIG. 1), primarily to support the development of minimum-flow guidelines or to monitor the impacts of consumptive water use (Flannery et al., 2002; McConnell et al., 2005). These faunal surveys have varied in length from 1.5 to >8 yrs, with sampling generally having a monthly frequency.

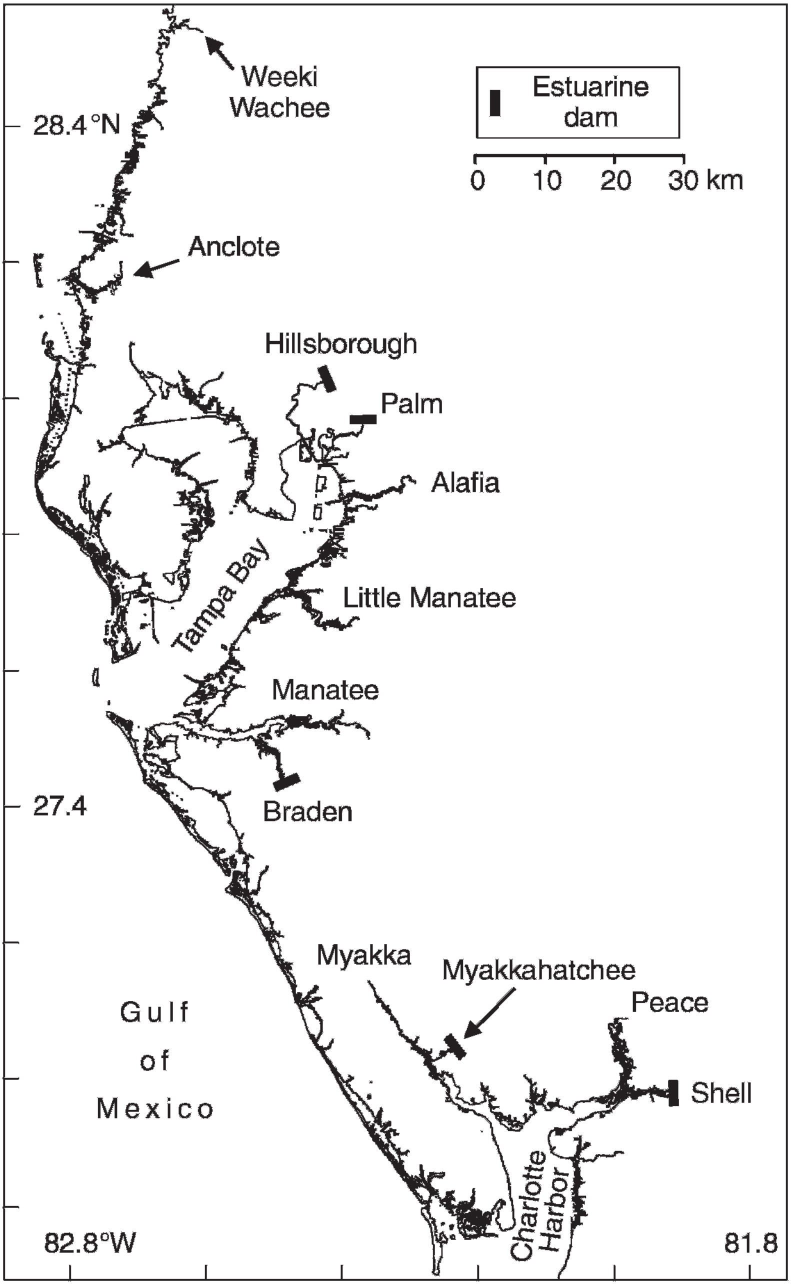

FIG. 1. Tidal rivers in southwest Florida surveyed to assess organism responses to changes in freshwater inflow.

During these surveys, planktonic and very small organisms were sampled during nighttime flood tides using a 0.5-m-mouth plankton net (505-µm mesh) towed obliquely through the water column for 5 min. Small fishes along shallow ($\leq$ 1.8 m) shorelines were sampled during daytime with 21.3-m-long center-bag seines (3.2-mm mesh). Within each estuary, sampling typically occurred along the main channel between the mouth of the tidal river and an upstream limit determined either by the presence of an estuarine dam or the point at which fresh water is usually present throughout the year. For plankton-net sampling, 4-14 fixed stations were established along each estuarine transect. For seine surveys, each estuary's transect was divided into several zones of approximately equal length (typically 2–3 km), and organisms were sampled monthly at two randomly chosen locations per zone. Additional details for these surveys are provided by Greenwood and co-workers (2007) and Peebles and co-workers (2007).

Development of a dispersion measure—The center of abundance of a population in a tidal river is provided by the weighted mean

$$\mathrm{km_U} = \frac{\sum(\mathrm{km}\cdot\mathrm{density})}{\sum \mathrm{density}}$$

where km is the location of capture (river km, which increases in the upstream direction), and density is the number of individuals per standardized area or volume sampled (Flannery et al., 2002; Peebles, et al., 2007). Density may be transformed ($\ln[x+1]$) if there are occasional, very high catches, as was the case for some species in the seine collections.

Center of abundance ($\mathrm{km_U}$) was calculated using data collected along the entire length of each estuarine transect, which were typically obtained on a single day during each month of the survey. The $\mathrm{km_U}$ formula identifies a central tendency in abundance and does not account for dispersion; it is best suited for populations with unimodal distributions, which were often not observed in the seine collections. Variance-based dispersion metrics (Ludwig and Reynolds, 1988) tended to be positively correlated with overall abundance, and this was viewed as an unwanted interaction. In order to avoid this interaction and to accommodate variably skewed or non-unimodal spatial distributions, we adopted the interpolated interdecile range method (IDR) as a robust alternative to conventional quantile regression for describing population dispersion along estuarine transects. Transect data provide estimates of organism abundance at discontinuous locations (i.e., data gaps exist between sampled locations) and are not as readily amenable to conventional quantile regression as are scatterplots of continuous data. We therefore interpolated the locations of the lower and upper abundance deciles on the cumulative catch curve and used these as metrics for describing local population dispersion. Note that our use of this interpolation approach is entirely empirical; an evaluation of conventional quantile regression as a tool for delimiting spatial distributions according to ecological theory is provided by Austin (2007).

Interdecile range (IDR) was calculated as the distance (km) between the 10th and 90th percentiles (i.e., the lower and upper deciles) of the cumulative, effort-corrected catch for a given monthly survey. Lower and upper deciles were interpolated between stations immediately downstream and upstream of each decile (FIG. 2). Interpolation was required because it is very rare for either decile to fall exactly on a sampled location. Months in which the lower and upper deciles could not be calculated were excluded from analysis. This occurred when the first sample exceeded 10% of the cumulative catch, indicating that the sampled transect did not adequately bracket the population of interest, or when there were fewer than three samples with non-zero catches for the population of interest, in which case interpolation of the 10th and 90th percentiles was not mathematically possible.

Regression analyses—Data for selected common taxa inhabiting the estuarine portions of the tidal rivers were included in regression analyses. For each taxon, we regressed IDR, $\mathrm{km_U}$, and the locations of the lower and upper deciles against three-day mean stream flows estimated from U. S. Geological Survey or Southwest Florida Water Management District streamflow data. We also

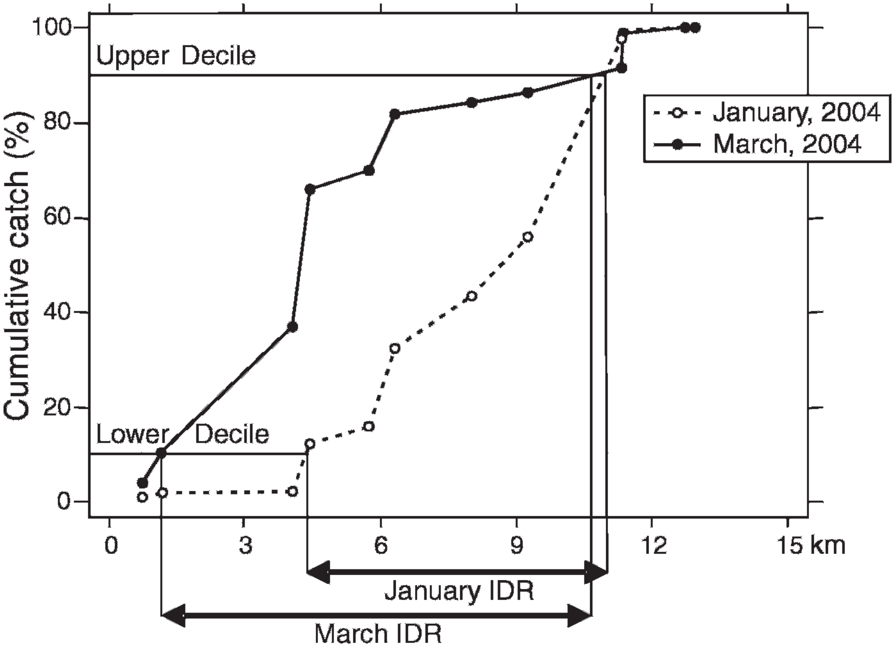

FIG. 2. Two examples illustrating the calculation of the interdecile range (IDR) for bay anchovy, *Anchoa mitchilli* (Valenciennes, 1848), juveniles from plankton-net sampling in the Hillsborough River. The x-axis is distance upstream from the river mouth.

regressed IDR against km_U, and examined various plots of the above variables to assess the effects of estuarine dams on organism distribution.

RESULTS AND DISCUSSION—*Quantifying estuarine habitat compression*—Although we conducted a large number of regressions on a variety of species, we limit this presentation to exemplary cases that illustrate how the method provides new insights. The results discussed here are also limited to species that demonstrated a significant negative km_U-flow relationship (upstream movement with decreasing inflow) and to species for which there was no relationship between IDR and overall mean abundance (i.e., no sample-size effect).

The responses of different population distributions to variation in freshwater inflow are presented together in FIG. 3, where it is clear that the populations moved upstream during periods of reduced freshwater inflow. This response is evident in three of the distribution metrics: km_U, upper decile, and lower decile. However, the distance between the upper and lower deciles (IDR) did not have a consistent response to inflow (slope *p*-values for these regressions are presented in FIG. 3). A common pattern was for IDR to remain unaltered with decreasing inflow and organism movement upstream—in such cases, there was no statistically significant dispersion compensation for the reduced habitat size the animals would have encountered as they moved upstream (FIG. 3a-c). On the other hand, increased dispersion with movement

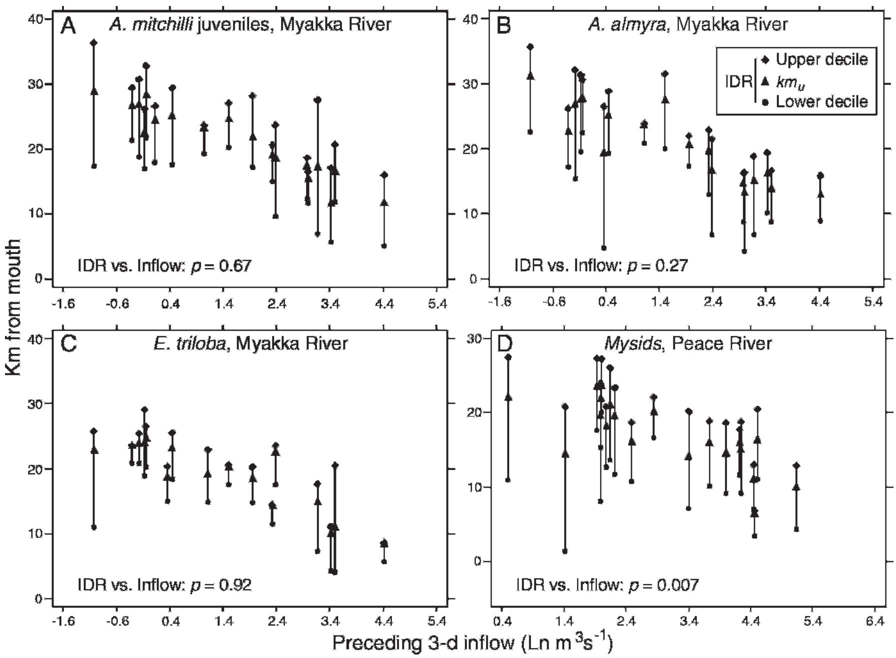

FIG. 3. Responses of four population distribution metrics (see legend) to variation in three-day mean freshwater inflow for A) *Anchoa mitchilli* (bay anchovy) juveniles, B) *Americamysis almyra* (mysid), C) *Edotia triloba* (isopod), and D) aggregated mysids (not identified to species during the Peace River surveys but dominated by *A. almyra* and *Bowmaniella dissimilis*). All data are from nighttime plankton-net samples. The upper decile, km_U, and lower decile demonstrated consistently significant responses to inflow variations (regression slope $p < 0.05$), whereas the distance between upper and lower deciles (IDR) did not always have a significant response to inflow (IDR regression slope p is indicated within each panel).

upstream was sometimes evident in organisms such as the Peace River mysids (FIG. 3d). The mysid *Americamysis almyra* (Bowman, 1964) was also observed to have this pattern in the Alafia River. Using the Alafia mysids as an example, the results of their km_U-flow and IDR-km_U regressions were combined with estimates of water volume to determine if the increased dispersion would offset the apparent km_U trend toward habitat compression (FIG. 4). In this example, the increase in dispersion did little to offset the apparent habitat loss (as volume). Even when dispersion does not appear to respond to inflows, mean IDR values are needed for calculating habitat compression. Rigor in these calculations can be increased by modeling the relationship between km_U and the two deciles. This allows IDR to be positioned asymmetrically about km_U—note that km_U tended to be closer to the upper decile (FIG. 3).

Sampling artifacts—Quantile analysis can provide important information on the limitations of survey coverage and any associated sampling artifacts. In the example of the isopod *Edotia triloba* (Say, 1818) in the Braden River

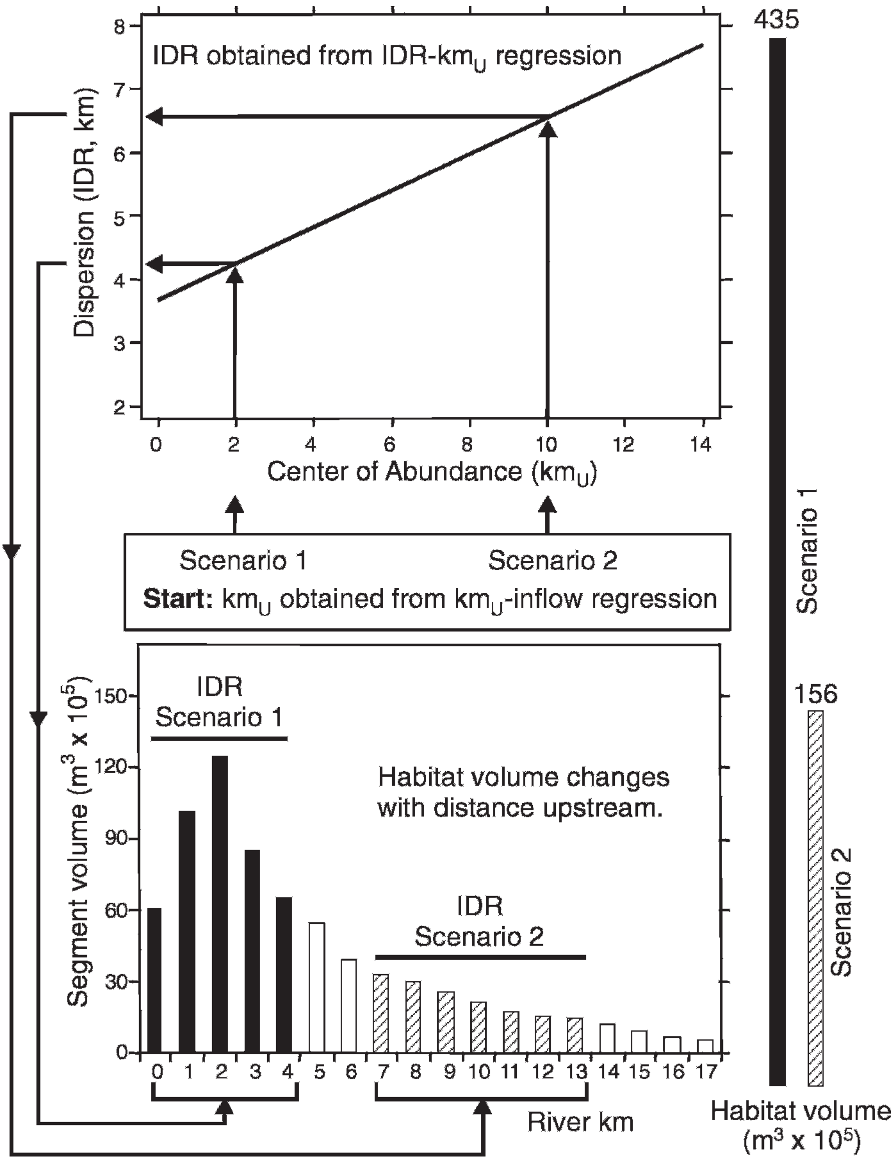

FIG. 4. Increased dispersion (IDR) with movement upstream may not offset geomorphic habitat loss: example using data for the mysid *Americamysis almyra* in the Alafia River (plankton-net data). Volume of water in each 1-km segment of the river is indicated in the lower panel, with cumulative habitat volume change indicated by the two right-hand bars.

estuary (FIG. 5), the lower decile was largely static over the first 3 km of increasing km$_U$, but then began to increase. This suggests that a substantial portion of the population was seaward of the transect, confounding efforts to accurately estimate habitat size. A similar pattern is evident for silversides

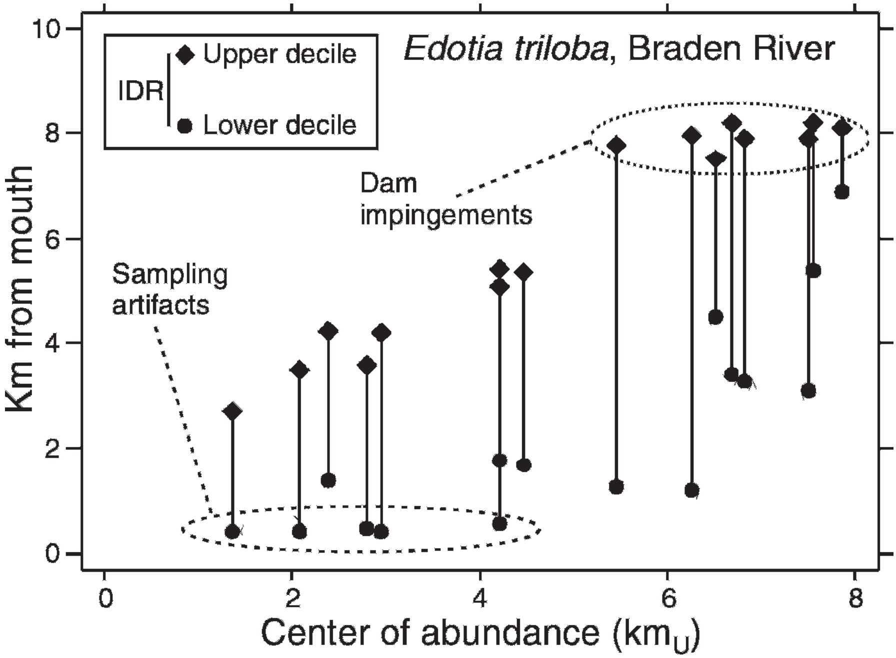

FIG. 5. Changes in dispersion (IDR) of the isopod *Edotia triloba* in the Braden River, illustrating sampling artifacts and habitat impingement on an estuarine dam.

(*Menidia* spp.) in the Myakka River (FIG. 6). The lower decile did not move with changing inflow, whereas the upper decile and center of abundance (km$_U$) moved significantly upstream with decreasing inflow (slope $p<0.05$). As with *Edotia* in the Braden River, the transect apparently did not bracket the majority of the abundance distribution—many individuals must have been located seaward of the transect's downstream limit in Charlotte Harbor. Calculations of changes in habitat size with changing flow that are based solely on km$_U$-inflow relationships would not be able to account for this large, unsampled portion of the population. Habitat compression analyses should be limited to taxa whose distributions appear to have been largely bracketed within the surveyed transect.

Habitat impingement on estuarine dams—Edotia triloba in the Braden River also provided a good example of the utility of quantile examination in assessing habitat impingement on estuarine dams. The Braden River dam is located at river km 9.3. The upper decile for *E. triloba* moved upstream as km$_U$ moved upstream (FIG. 5). At km$_U$>5, the upper decile remained near km 8 and no longer increased with increases in km$_U$. This can be explained by the upper portion of the population being unable to move farther upstream because of dam obstruction. A similar, but less obvious, pattern was found in the seine

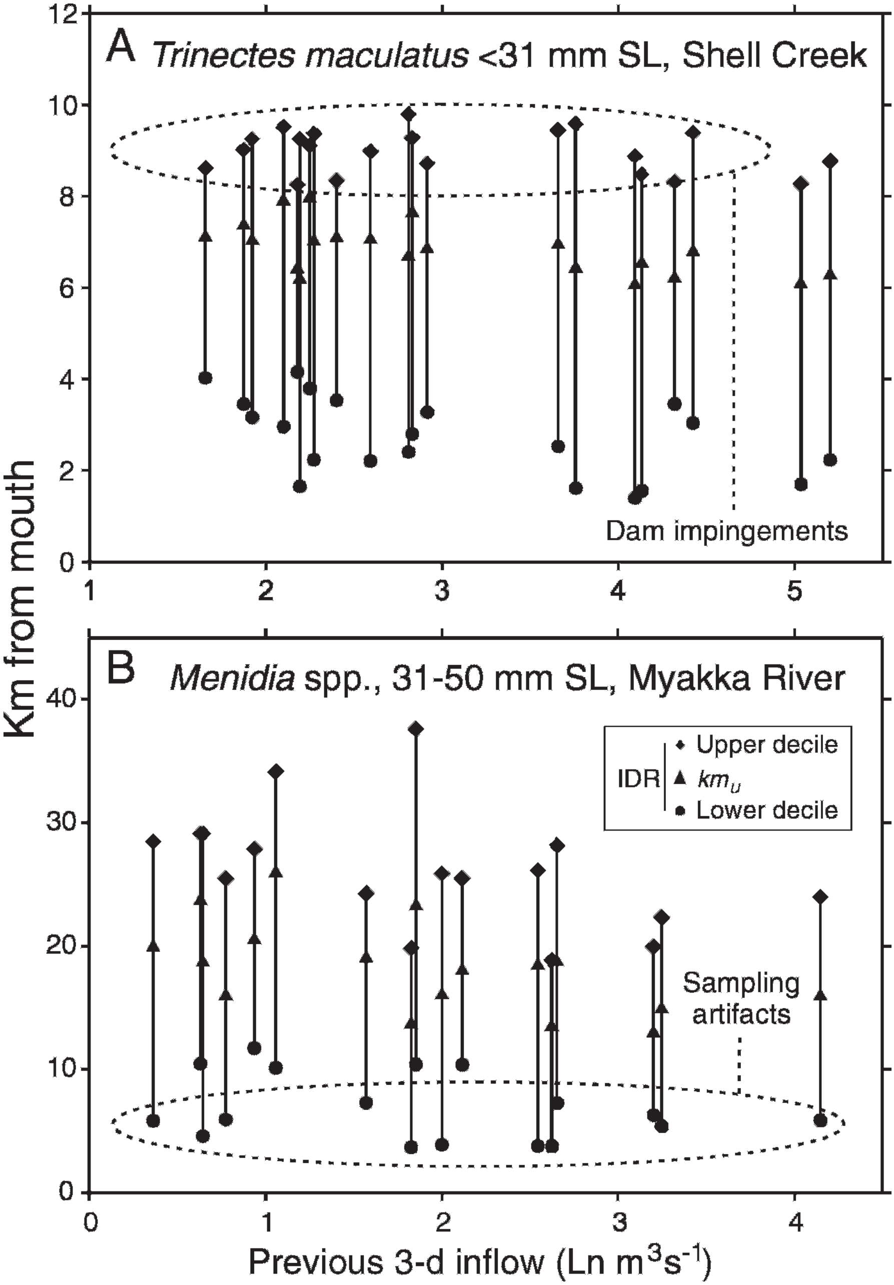

FIG. 6. Changes in center of abundance (km_U) and dispersion (IDR) with changing 3-day mean inflow, illustrating A) habitat impingement by hogchoker (*Trinectes maculatus*) on Shell Creek's estuarine dam and B) sampling artifacts evident in silversides (*Menidia* spp.) data from the Myakka River. Seine data are used in both panels.

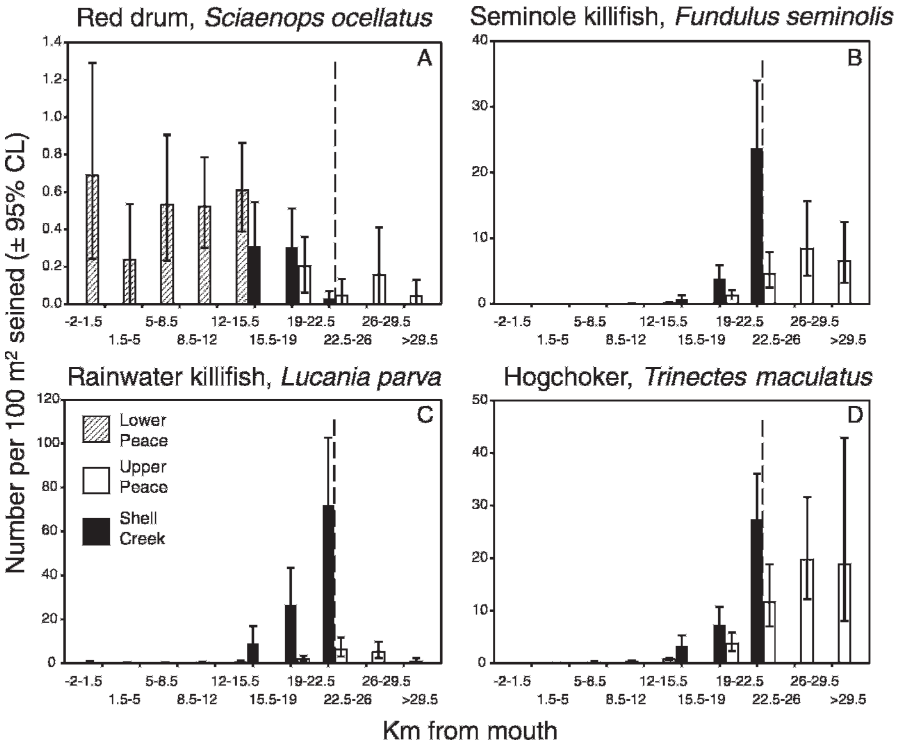

FIG. 7. Seine catch along estuarine transects in the Peace River and Shell Creek indicating that Seminole killifish (*Fundulus seminolis* Girard, 1859), rainwater killifish (Lucania parva, Baird & Girard, 1855), and hogchoker showed evidence of crowding below the dam on Shell Creek (broken line), whereas red drum (*Sciaenops ocellatus*, Linnaeus, 1766)—a species that occupied the lower Peace River—did not show evidence of crowding in Shell Creek (seine data).

data for hogchoker *Trinectes maculatus* (Bloch & Schneider 1801) <31 mm standard length in Shell Creek (FIG. 6); the upper decile did not significantly change position with decreasing inflow, whereas the lower decile and km_U both had statistically significant increases (slope $p<0.05$). Interestingly, the IDR-inflow regression was not significant in this case, suggesting that the quantile method should not be limited to assessing the significance of IDR-inflow regressions but should also consider regressions of IDR with km_U, regressions of deciles with inflow, and graphical inspection of deciles in relation to inflow and km_U. The apparent concentration of animals below the dam on Shell Creek suggested by the quantile trends (e.g., our hogchoker example in FIG. 6) is also supported by the high densities of various species in Shell Creek relative to the equivalent reaches of the Peace River, which has no dam (see FIG. 1, then compare Shell Creek and Upper Peace in FIG. 8).

Validation and refinements—This method of assessing interquantile ranges and the well-established technique of examining changes in center of abundance with inflow both share the objective of predicting changes in habitat size that may result from alterations in freshwater inflows. Quantitative information is useful to managers who must establish ecologically based limits for water withdrawals. Ideally, we would use long-term data to validate the effects that changes in inflow and habitat size have on population parameters such as recruitment success, growth, and survival. Ongoing monitoring programs have the potential to generate some of the necessary data in the future.

We have considered changes in habitat quantity here, recognizing that both the quality and quantity of available habitat are of importance (Peterson et al., 2000). Displacement of organisms away from optimal stationary habitat (e.g., vegetated shorelines providing refuge from predation) could result in decreased population productivity (Browder and Moore, 1981). Our method, and others before it, could be refined by weighting habitat quantity by habitat quality.

Conclusions—Dispersion information should be coupled with shifts in the central habitat tendency in order to accurately quantify habitat-size change. Quantile comparisons have strong utility for identifying and describing estuarine habitat compression, habitat impingement on dams, and potentially misleading sampling artifacts. While dispersion may sometimes increase with reduced inflow and movement upstream, the increase may not be sufficient to offset stronger geomorphic reductions in habitat volume or area at upstream locations.

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