

Measuring individuality in habitat use across complex landscapes: approaches, constraints, and implications for assessing resource specialization

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Abstract Many mobile marine species are presumed to utilize a broad spectrum of habitats, but this seemingly generalist life history may arise from conspecifics specializing on distinct habitat alternatives to exploit foraging, resting/refuge, or reproductive opportunities. We acoustically tagged 34 red drum, and mapped sand, seagrass, marsh, or oyster (across discrete landscape contexts) use by each uniquely coded individual. Using 144,000 acoustic detections, we recorded differences in habitat use among red drum: proportional use of seagrass habitat

ranged from 0 to 100 %, and use of oyster-bottom types also varied among fish. WIC/TNW and IS metrics (previously applied vis-à-vis diet specialization) consistently indicated that a typical red drum overlapped >70 % with population-level niche exploitation. Monte Carlo permutations showed these values were lower than expected had fish drawn from a common habitat-use distribution, but longitudinal comparisons did not provide evidence of temporally consistent individuality, suggesting that differences among individuals were plastic and not reflective of true specialization. Given the range of acoustic detections we captured (from tens to 1,000s per individual), which are substantially larger sample sizes than in many diet studies, we extended our findings by serially reducing or expanding our data in simulations to evaluate sample-size effects. We found that the results of null hypothesis testing for specialization were highly dependent on sample size, with thresholds in the relationship between sample size and associated *P*-values. These results highlight opportunities and potential caveats in exploring individuality in habitat use. More broadly, exploring individual specialization in fine-scale habitat use suggests that, for mobile marine species, movement behaviors over shorter (\leq weeks), but not longer (\geq months), timescales may serve as an underlying mechanism for other forms of resource specialization.

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Introduction

A major goal of ecology is to catalogue diverse biological or behavioral attributes to reveal robust generalizations

across ecosystems. As such, many scientists, resource managers, and naturalists recognize value in frameworks that define “species” as a set of interbreeding organisms exploiting a single niche in environmental space (Elton 1927). While treating conspecifics as functionally equivalent can, at times, satisfy our need to simplify nature in experimental models or for management objectives, it may also belie the importance of inter-individual variation within a population or species in diets (Araújo et al. 2009), movement behaviors (Hammerschlag-Peyer and Layman 2010), habitat selection (Paterson et al. 2012), reproductive strategies (Tabashnik et al. 1981), and even functional morphology (Ralston and Wainwright 1997). Furthermore, the degree to which individuals within a population access overlapping or distinct subsets of the available resource niche space impacts patterns of density dependence (intraspecific competition) and food web dynamics over ecological timescales (Araújo et al. 2011), as well as guides our understanding of evolutionary mechanisms and feedbacks (Bolnick et al. 2007; Post and Palkovacs 2009).

Many populations formerly considered to be made up of generalists based on the breadth of dietary items at the population level actually comprise many specialist individuals (Bolnick et al. 2002, 2003). While this may reflect differences in sex (Bearhop et al. 2006), size (Starck and Schroeder 1971; Sherwood et al. 2002) or ontogenetic shifts in distribution (Svanbäck and Eklöv 2002), individuals within the same sex, age/stage class or site may also be defined by variation in resource use, and this level of inter-individual variation has been termed “individual specialization”. Research on individual specialization has focused primarily on variation in diets (but includes reproductive behaviors, physiological tolerances, and movement patterns), with development of several quantitative metrics for comparing intra- versus inter-individual niche variation (Beaudoin et al. 1999; Bolnick et al. 2002).

Large, demersal, mobile fishes and crustaceans in temperate estuarine ecosystems are routinely collected from a number of habitat alternatives such as sand, seagrass, marsh, and oyster bottoms, and as a result most species are typically portrayed and managed as habitat generalists (Able and Fahay 2010). Recent individual-based tagging work has provided new insights into the movement ecology of fishes, and we now understand that many individuals of a given species show fidelity to distinct locations for days-to-months, while other conspecifics are much more migratory (Szedlmayer and Able 1993; Thomson et al. 2012). To complement these studies highlighting diversity in broad-scale movement behaviors, data are needed to evaluate whether analogous intra-specific diversity exists at the habitat scale.

Within estuaries, heterogeneous, interacting habitats repeated over 10- to 1,000-m scales can be defined

as landscape mosaics (Forman and Godron 1981). To the degree that alternative habitats within a landscape support distinct resources, understanding movement at this scale is intimately tied to understanding the root drivers of individual specialization (Kerr et al. 2009; Kobler et al. 2009; Paterson et al. 2012). For instance, is diet specialization purely the result of differences in prey selectivity among foraging individuals, or are individuals utilizing different microhabitats within an area and therefore foraging among distinct prey assemblages? Moreover, individual habitats (e.g., seagrass, oyster) may vary in structural complexity, shape (e.g., area-to-perimeter) and inter-habitat connectivity based on landscape context (Micheli and Peterson 1999; Grabowski et al. 2005), allowing potential for intraspecific trade-offs in movement or foraging strategies. In many estuaries, large-scale restoration of biogenic habitat (i.e., oyster reefs) provides a unique experimental opportunity to test whether the landscape context (i.e., proximity of oyster reefs to sand, marsh or seagrass habitat) could generate specialization in intra-habitat use among individual mobile fish. In the context of overall resource use, these restoration projects are particularly valuable as we already know they support distinct prey communities for mobile foraging fishes (Grabowski et al. 2005).

For niche axes such as habitat use, the ability to explore the relative magnitudes of intra- versus inter-individual variation may be aided by collecting data longitudinally over repeated sampling periods. Specialization implies some degree of consistency across entire life history stages, yet the application of longitudinal analyses in gut-contents and habitat-use studies to assess the timescale dependence of apparent specialization has been rare. There are also several potential difficulties in testing for individual specialization in habitat use. First, the functional resolution of distinct habitat types sets an upper bound on the ability to examine specialization, which is directly analogous to the constraints of taxonomic resolution in tests for diet individuality (Araújo et al. 2009). Second, whereas each item in a diet analysis is often considered an independent feeding choice (Bolnick et al. 2003), information on habitat use will routinely fail this critical assumption. Sampling habitat use by any individual requires serial measures through time (while diets typically represent a single, integrated measure of resource use), and observations will often be temporally auto-correlated (Sackett et al. 2007). Thus, the manner in which (potentially very large) habitat-use data are synthesized and analyzed will impact quantitative analyses of specialization due simply to the controls of statistical power (*sensu* Araújo et al. 2007). Determining the sensitivity of specialization metrics to the above factors will help elucidate the metrics’ utility in quantifying habitat-use variation, and provide insight for other common applications of individuality metrics (e.g., those based on diet data).

We examined the landscape-scale habitat use of an estuarine fish, red drum (*Sciaenops ocellatus*), to delineate patterns of intra- and inter-individual variation. Traditionally, red drum have been considered habitat generalists based on the widespread distribution of red drum prey, the mobility of juveniles and adults, and the ephemeral nature of estuarine habitats due to tidal and seasonal forces (Scharf and Schlicht 2000). Recent tagging studies involving red drum, however, have revealed considerable individual variability in the estuarine-scale movements of this species (Dresser and Kneib 2007; Bacheler et al. 2009). We asked three related questions regarding habitat use of red drum:

1. Is specialization apparent by this large, mobile fish in its use of sand, seagrass, marsh, and oyster bottoms?
2. Do landscape-scale differences in the location of oyster reefs lead to intra-habitat specialization among fish?
3. Is evidence of specialization collected across short timescales (e.g., days–weeks) conserved over longer timescales (e.g., months)?

To explore potential individuality in habitat use, which may lead to diet specialization (not tested here), we applied metrics previously used to test for diet specialization (Bolnick et al. 2002) on a 135-day, high-spatial-resolution, acoustic tracking data base. Given the wide range of observations (per individual) possible with these acoustic tracking data, as well as multiple data formats available to work with, we conducted additional simulations to examine the relationship between sample size and quantitative metrics of specialization in habitat use.

Materials and methods

Study area and habitat delineation

We tracked the habitat use of red drum within Middle Marsh, North Carolina, throughout the latter half of 2011 (N34°41.1', W76°37.2'; Fig. 1). Middle Marsh is a 1.5-km² complex of salt marshes, sand flats, seagrass meadows and oyster reefs within the Rachel Carson National Estuarine Research Reserve. Large predatory fishes like red drum typically enter the system during flood tides and then exit as water levels fall and expose broad stretches of intertidal habitat. We established an acoustic tracking array in one of the larger (100,000 m²), semi-enclosed embayments within Middle Marsh because we knew from previous survey work that red drum frequently access the study area, which contains a diverse mix of natural habitat types (Grabowski et al. 2005). Additionally, several experimental oyster reefs have been created inside this embayment among

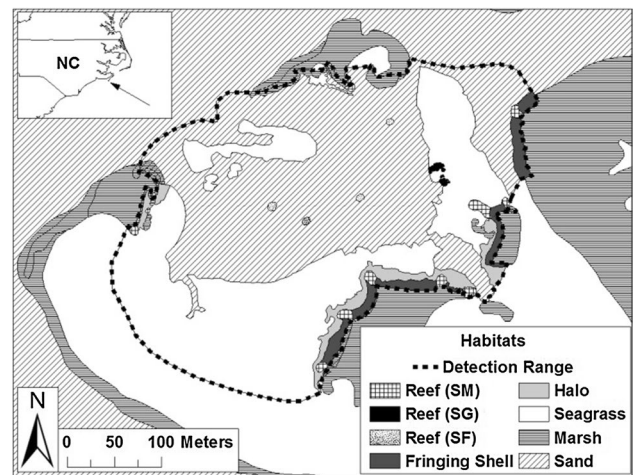


Fig. 1 Distribution of habitat types within the acoustic detection arena at our study site in Middle Marsh, North Carolina. In addition to sand, halo, seagrass and marsh habitats, the study area contained oyster reef habitat across multiple landscape contexts. This example map depicts habitat cover during the early period of the study (15 July–31 August) before the seasonal loss of above-ground seagrass biomass. *SM* salt marsh, *SG* seagrass, *SF* sand flat

distinct landscape contexts: on isolated sand flats, immediately adjacent to salt marsh, and immediately adjacent to seagrass habitat (Grabowski et al. 2005). Thus, we could exploit a large-scale field manipulation of habitat availability and landscape setting in this system to more thoroughly explore individuality in habitat use.

Using high-resolution (<1 m) aerial imagery, we delineated the following habitat types:

1. Sand—areas of bare, smooth substrate generally in the central portion of the study area.
2. Halo—bands of bare substrate 3–5 m in width that separated marsh and seagrass habitats. Halo bottoms were qualitatively muddier and had greater Lebensspuren densities than sand bottoms.
3. Seagrass—mixed *Zostera marina* and *Halodule wrightii* distributed as contiguous and patchy meadows across the study area.
4. Marsh—flooded *Spartina alterniflora* along the perimeter of the study area.
5. Fringing shell—loose, naturally occurring aggregates of both living and dead shell bordering marsh habitat (<25 oysters m⁻²).
6. Reef (salt marsh; SM); natural and restored oyster reefs immediately adjacent to marsh habitat (>100 oysters m⁻²). Unlike fringing shell, reefs were consolidated, raised features within the embayment.
7. Reef (seagrass; SG)—restored oyster reefs immediately adjacent to seagrass habitat.

8. Reef (sand flat; SF)—restored oyster reefs surrounded by a sand matrix and isolated from other structured habitats.

These habitat types were mapped as distinct polygon features in ArcMap 10.0. Aerial imagery was captured three times during our tracking study to account for seasonality in seagrass cover (i.e., *Zostera* senescence due to heat stress). Satellite images were obtained through National Oceanic and Atmospheric Administration data bases (GeoEye and World View; early and middle periods) and eMap International (IKONOS; <http://www.digitalglobe.com/resources/satellite-information>; late period). Subsequently we divided our tracking data set into three equal periods matching when the separate habitat mosaic maps were generated (early, 15 July up to and including 30 August; middle, 1 September up to and including 14 October; and late, 15 October up to and including 30 November).

Fish tagging and tracking

We collected 34 red drum (550 ± 15 mm total length, mean ± 1 SE) via hook-and-line fishing from waters in and around Middle Marsh (Online Resource Appendix 1). Coded acoustic tags (LOTEK Wireless MM-MR-11-28) were surgically implanted following Dresser and Kneib (2007). Following tag implantation, fish were held for 24 h for observation before being released at the center of our Middle Marsh study site. The LOTEK tags emitted a pulsed chirp, unique to each fish, every 5 s that was used to chart each individual's position while in the study area. Once released, each red drum was free to enter or exit the study area without further manipulation (data collection began 12 h after release to allow for acclimation). Broad-scale tracking work in a companion study has shown that, from week-to-week, red drum forage over a $>1\text{-km}^2$ area, which is much larger than our entire detection arena (Kenworthy et al., in preparation). Moreover, at the scale of our LOTEK detection array, auditory cues should transmit far enough to ensure that all habitats were within the ambit of individual red drum (Luczkovich et al. 2008). Therefore, we are confident that all individuals sampled a common resource (habitat) pool in this study.

We deployed a LOTEK MAP 600 Acoustic Telemetry System to detect acoustic signals emitted from tagged red drum and track their fine-scale habitat use. This system consists of eight georeferenced hydrophones, cabled to a central processing unit, that were positioned to allow "line-of-sight" (acoustic) for at least three of the listening stations throughout the embayment. Any signals emitted by a LOTEK transmitter and detected by at least three hydrophones allowed for signal triangulation and determination of a fish's position with sub-meter accuracy (resolution based on serial detections of georeferenced beacon tags). These x - y positions were

mapped across the habitat mosaics created in ArcMap 10.0 to determine the habitat use of individual red drum throughout our study (see Online Resource Appendix 2 for fish-by-fish maps of detection locations demonstrating that most fish sampled large portions of the detection arena).

Individualization in habitat use

To test whether red drum habitat use at the individual level represented the breadth of habitat-use patterns at the population level across an estuarine landscape, we used approaches previously applied on diet information to test for resource/foraging specialization (Bolnick et al. 2002). We did not anticipate that each unique position datum during our tracking study could be considered independent (habitat use at any one time was temporally autocorrelated with preceding and subsequent positions). Therefore, prior to calculating specialization indices, we organized our data in two separate forms of longitudinal information describing habitat use. First, we considered each fish's separate forays into our study area as distinct samples of habitat use. Separate forays were defined by a 10-min gap in detections from any individual, likely representing an exit from and reentry into the embayment. In order to include a foray in our analyses, an individual had to remain within the detection arena for at least five consecutive detections (typically long enough for an individual to sample from at least two distinct habitats, demonstrating that some type of selection was possible). Proportional habitat use was calculated as the number of habitat-specific positions divided by the total number of positions that were recorded during each independent foray. For each fish, we summed those proportions (totaling one for each distinct foray) across all forays that occurred during either the early, middle and late thirds of the study (these separate calculations were conducted because of the seasonal shift in habitat availability). Second, we counted every time a fish made a new visit (i.e., crossed a habitat boundary) to each of the eight habitat types during either the early, middle or late portions of our study (combining all data from distinct forays into our study area). Hereafter, we distinguish these two data types as either proportions or visits, respectively.

To quantify individual specialization using both proportion and visit data, we first used Roughgarden's (1972) index which compares within-individual components of niche width (WIC) to the total niche width exhibited by a population (TNW). Calculations of WIC and TNW followed Bolnick et al. (2002), and we used the average among individuals' proportional habitat use to calculate the population's mean habitat use (i.e., all individuals were weighted evenly, although we also conducted our analyses without equal weighting and found qualitatively interchangeable results). WIC/TNW was used to scale

Table 1 Summary of population-level specialization metrics based on red drum habitat utilization

| | 15 July–31 August | | 1 September–14 October | | 15 October–30 November | | Entire study | |
|---------------------|--------------------------|------------------------------|--------------------------|------------------------------|--------------------------|------------------------------|--------------------------|------------------------------|
| | Proportional habitat use | Visits habitat ⁻¹ | Proportional habitat use | Visits habitat ⁻¹ | Proportional habitat use | Visits habitat ⁻¹ | Proportional habitat use | Visits habitat ⁻¹ |
| All habitats | | | | | | | | |
| WIC/TNW | 0.87 | 0.94 (<0.001) | 0.91 | 0.92 (<0.001) | 0.86 | 0.93 (<0.001) | 0.89 | 0.95 (<0.001) |
| IS | 0.65 | 0.74 (0.001) | 0.74 | 0.71 (<0.001) | 0.72 | 0.75 (<0.001) | 0.74 | 0.78 (<0.001) |
| \bar{W} | 0.68 | 0.77 | 0.78 | 0.72 | 0.78 | 0.79 | 0.77 | 0.80 |
| Oyster bottoms only | | | | | | | | |
| WIC/TNW | 0.84 | 0.82 (<0.001) | 0.82 | 0.85 (<0.001) | 0.86 | 0.96 (<0.001) | 0.85 | 0.85 (<0.001) |
| IS | 0.76 | 0.63 (<0.001) | 0.74 | 0.73 (<0.001) | 0.74 | 0.82 (0.201) | 0.75 | 0.74 (<0.001) |
| \bar{W} | 0.81 | 0.66 | 0.77 | 0.74 | 0.80 | 0.87 | 0.80 | 0.76 |

Values *in parentheses* are the *P*-values associated with Monte Carlo tests indicating the probability of drawing observed results if a null hypothesis of no specialization across the population is true

WIC Within-individual components of niche width, TNW total niche width exhibited by a population, IS mean specialization among individuals, \bar{W} population-level individuality

individual specialization for each red drum to the overall population (approaching 1 = more generalist, meaning that the eight habitats were used by the average red drum in a manner that mirrored the population ‘average’; approaching 0 = more specialized, meaning that each individual only used a distinct subset of the population-level habitat niche). For each individual, we also calculated the proportional similarity index (PS) following Schoener (1968) based on habitat-by-habitat deviations in an individual’s habitat use relative to population-level, average habitat use (as above, approaching 1 = more generalist; approaching 0 = more specialized). Mean PS_i among individuals was used to determine the average amount of specialization in habitat use across all red drum in our study (IS). We also calculated Petraitis’ (1979) index of individualization for each red drum (W_i) and the entire population (\bar{W}), but like other studies, we found a strong correlation between PS_i and W_i (correlation coefficients >0.9; Table 1; sensu Bolnick et al. 2002). Therefore, we focused on PS and IS metrics in subsequent analyses.

These specialization indices were generated based on considering all habitat types, as well as using just the four oyster bottoms (fringing shell, reef SM, reef SG and reef SF). We considered just oyster bottom in separate analyses for multiple reasons. First, we specifically wanted to test if landscape context of oyster bottoms (i.e., proximity to sand, marsh or seagrass habitats) could generate specialization in habitat use. Second, we suspected oyster bottoms were essential foraging areas, and wanted to conduct focused analyses on differences in these habitats that could underlie resource specialization. Third, we were concerned that inclusion of habitats regularly used by most individuals (i.e., sand, seagrass and halo) could obscure specialization

(based on WIC/TNW and IS metrics) occurring within a subset of habitats (i.e., oyster bottoms).

We ran Monte Carlo permutations to test whether observed WIC/TNW and IS (and PS_i) values differed significantly from a random distribution of values subsampled from the population. Using the IndSpec 1.0 platform (Bolnick et al. 2002), we randomly reassigned habitat use [visit data only since Monte Carlo simulation are only recommended for integer data (Araújo et al. 2007)] for each red drum in equal proportion to our observed data and then calculated individual- and population-level metrics for the random population. We generated random habitat-use data for 10,000 populations, thereby creating a null distribution of WIC/TNW and IS values. We concluded that individuals were not sampling from a shared distribution of habitat use if our observed WIC/TNW and/or IS (and PS_i) values were <95 % of all randomly generated values (sensu Araújo et al. 2007).

To explore temporal consistency in habitat use, proportion and visit data from the early, middle or late sampling periods were also analyzed using cluster analyses and displayed graphically using multi-dimensional scaling (MDS) based on Bray–Curtis similarities (visit data were standardized across individuals, Primer-E version 6). For these analyses, we used our longitudinal data and considered individual fish that appeared during multiple time periods as separate entries in our data set to evaluate whether intra-individual changes through time were equal in magnitude to inter-individual differences. Additionally, we used visit data from each unique foray into our acoustic array to test the null hypothesis that intra-individual changes in habitat use through time were equal in magnitude to inter-individual differences. We compared average pairwise Bray–Curtis similarities between

forays within each individual ($n = 26$ individuals with more than one foray recorded; Online Resource Appendix 1) and the average similarity in habitat use between forays for every pair of individuals. We used a two-sample t -test to compare the average similarities within individuals to the average similarities between individuals.

Sampling effects on metrics of individual specialization in habitat utilization

During exploratory data analyses, we observed that results of our hypotheses testing (e.g., calculation of P -values following Monte Carlo permutations) appeared sensitive to sample size. To further explore the effects of sample size on metrics of individual specialization and associated P -values based on Monte Carlo resampling procedures, we executed two simulations manipulating the number of observations per individual. We focused on IS and PS metrics, but found similar results for WIC/TNW. For these exercises, we used our visit data set for all red drum across all three time periods ($n = 27$ fish). Visit data were reduced to “presence/absence” within each foray to simplify these analyses ($n = 3,618$ total habitat visits). We then multiplied our original data set by factors incrementing from 0.1 to 2 (increasing by 0.1 in successive simulations). Because these data manipulations often resulted in numbers of visits that were non-integers, and Monte Carlo resampling is only recommended for integer data, we rounded all the non-integer values up to the nearest whole number. For each simulated population, we ran 10,000 replicates of the resampling procedure, and estimated the IS value and used Monte Carlo resampling to generate a null model distribution of IS values for the population and estimate the associated P -value using the PSiCalc tool in the RInSp package (Zaccarelli et al. 2013) in the software package R (R Core Team 2013).

Next, we manipulated the number of observations to explore effects on associated P -values across a range of PS scores. Again, we used our data set for the number of unique habitat visits for all red drum across all three time periods as our starting point (reducing the visit data to presence/absence during each foray). We focused this exercise on eight individuals with a moderate number of observations (16–56 habitat visits per fish; range for the entire population was from two to 615 habitat visits per fish). Starting values of PS_i ranged from 0.66 to 0.94. We multiplied the original data set for each individual by increasing integers (e.g., 2×, 3×, etc.) until 300 observations were reached. We used Monte Carlo resampling as described above to generate P -values associated with each fish’s PS score at each sample-size level. We plotted observations per fish versus the associated P -values to explore the effects of samples size and PS values.

Results

Individual specialization

We tracked habitat use of 27 red drum (out of 34 tagged) throughout the summer and fall of 2011 (Online Resource Appendix 1). Overall, 144,320 observations were recorded regarding fine-scale habitat use ($7,716 \pm 1,485$ detections fish⁻¹). Across the 27 fish, there were a total of 1,689 forays into the detection area (94 ± 18 forays fish⁻¹). Multiple fish were detected during the early ($n = 8$), middle ($n = 20$) and late ($n = 12$) study periods, and several individuals were tracked across multiple time periods ($n = 13$). Overall, seagrass, sand, and halo habitats were the most frequently used or visited habitats, although all eight habitat alternatives were used by red drum (Fig. 2). Among oyster bottoms, consolidated reefs immediately adjacent to salt marsh habitat (reef SM) and fringing shell aggregations were the most frequently used or visited (Fig. 3). Few individuals utilized oyster reefs closely associated with seagrass (reef SG) or sand flat (reef SF) bottoms.

There was variability in habitat use among individual red drum. For instance, the proportion of time spent by fish in seagrass habitat ranged from 0 to 100 %, as did the relative number of habitat visits by individual red drum to seagrass habitat (Fig. 2). Similar patterns emerged for sand flat (0–60 %) and halo (0–40 %, visit data only) habitats. Among oyster bottoms, fish could be characterized along a continuum from those using only reef SM habitat to those using only fringing shell habitat based on both proportion and visit data (Fig. 3).

Most population-level measures of individual specialization (WIC/TNW and IS) suggested that, on average, individual red drum used a large fraction of the total population niche space (Table 1). For the entire 4.5-month study, specialization ranged from 0.74 to 0.89 and 0.78 to 0.95 across metrics for proportion and visit data, respectively, when considering all eight habitat types. Similar patterns emerged when we considered whether landscape context of oyster bottoms could lead to apparent specialization: all metrics were >0.74 . In analyzing early, middle and late time periods separately, WIC/TNW and IS metrics remained above 0.71 in 22 out of 24 instances. During the early time period, the IS metric indicated that proportional habitat use of the eight habitats in Middle Marsh by the average red drum overlapped 65 % with the population-level niche space. During this same time period, visit data among the four oyster bottoms indicated that the average fish had 63 % overlap with the population-level niche space.

Despite these relatively high WIC/TNW and IS scores, Monte Carlo analyses of individual-versus-population niche variation routinely suggested statistically significant specialization among red drum ($P < 0.001$ in 15 out of 16

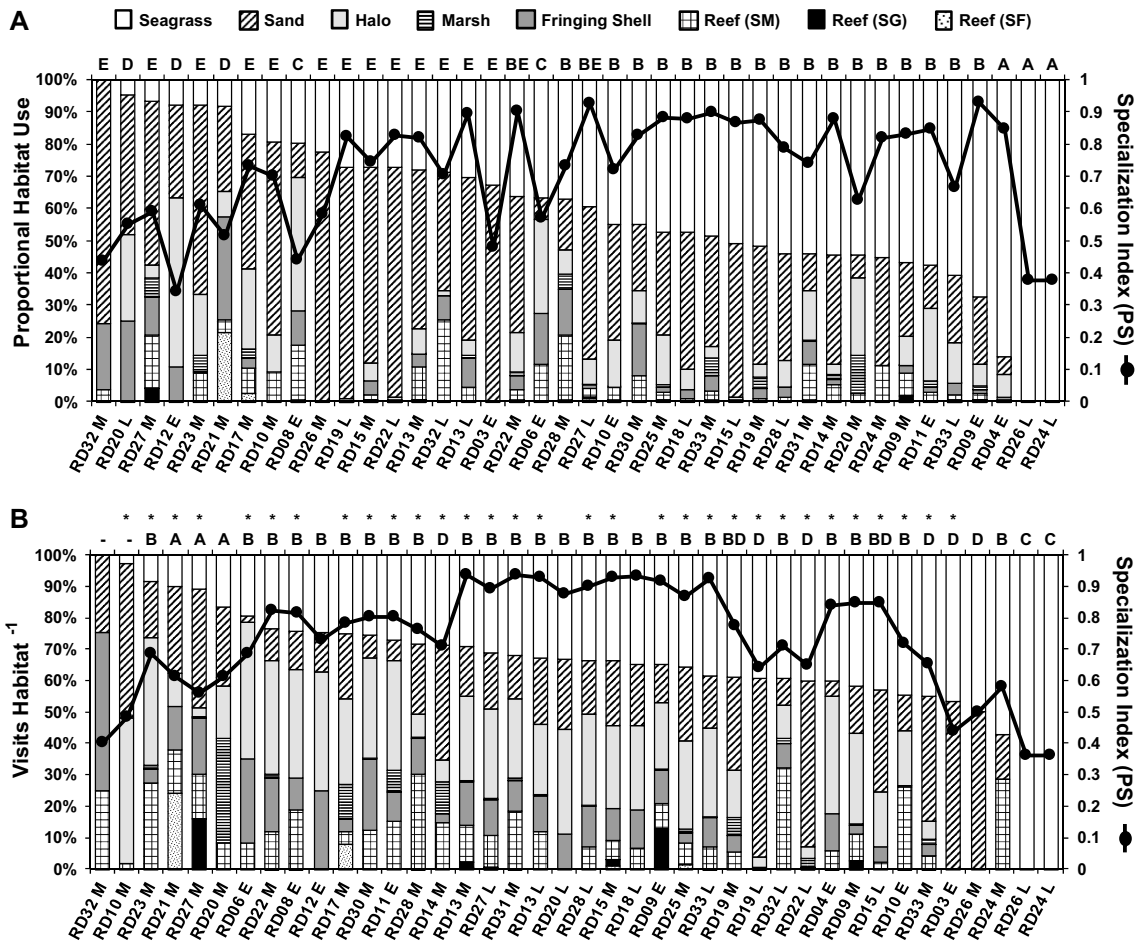


Fig. 2 Habitat use of individual red drum (*RD*) detected during the early (*E*), middle (*M*) and late (*L*) periods of our acoustic tagging study based on: **a** proportion of detections from eight alternative habitats; and **b** number of unique visits to each of eight alternative habitats. Also shown are the proportional similarity (PS) indices for each fish. Statistical significance ($P < 0.05$) of PS values are noted by an

asterisk at the top of the graph for each individual (visit data only), as well as a letter (*A–E*) denoting groupings (>60 % similarity) based on multivariate clustering analyses of habitat-use data [corresponding to clusters represented in multi-dimensional scaling (MDS) space in Fig. 4]

cases; Table 1). Although the average fish typically overlapped >70 % with the population’s mean habitat use, the large sample sizes possible with acoustic detection data gave us significant power in demonstrating that those values were lower than would be expected by random chance without specialization. Alternatively, some fish that visited only one habitat in the course of our study were not deemed statistically specialized due to a low number of detections from those individuals (Figs. 2b, 3b; see below for additional results from simulations testing the effects of sample size). Among individuals, PS values ranged from 0.38 to 0.96 when examining habitat use broadly, and from 0.35 to 0.98 when considering habitat use only among oyster bottoms (Figs. 2, 3).

For proportion data considered across either all habitats or just the oyster bottoms, cluster analyses (at 60 % similarity) indicated two main patterns of habitat use (Fig. 4).

Across all habitat types, two clusters (B and E) distinguished fish that used seagrass habitat routinely or sparingly, respectively (Figs. 2, 4). Among oyster bottoms, two clusters (A and B) also distinguished fish that relied to a greater extent on fringing shell or reef SM habitats, respectively (Figs. 3, 4). Using visit data, major groupings did not emerge at the level of overall habitat use (Fig. 4), but again two clusters (B and D) distinguished fish that relied on fringing shell or reef SM habitats to a greater extent, respectively (Figs. 3, 4). Time period had no obvious effect on the clustering of habitat-use patterns (Fig. 4).

Notably, any indication of individuality observed during one of our 6-week study periods did not appear to be consistently documented over longer time periods. For instance, of the 13 fish that entered our study area during multiple periods, 62–77 % shifted across distinct MDS clusters of habitat use based on proportional and

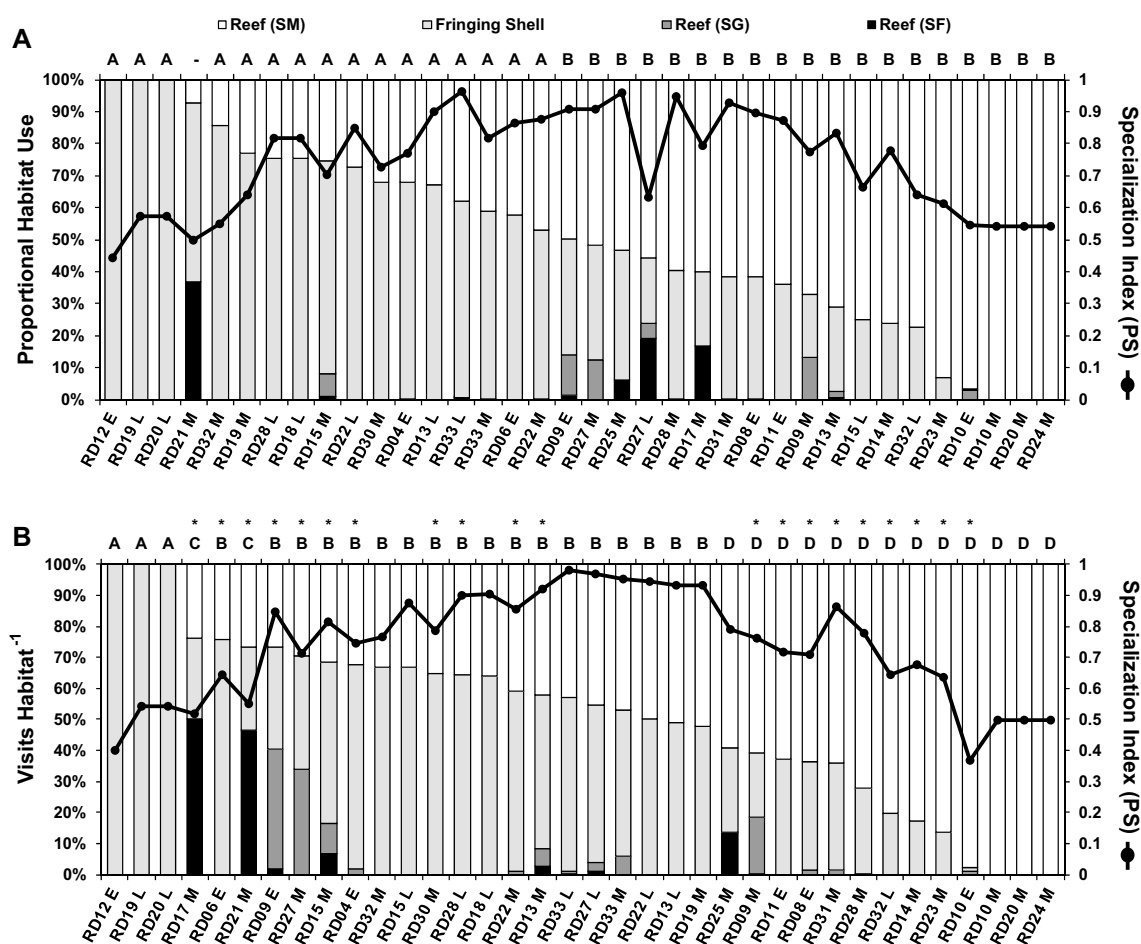


Fig. 3 Habitat use of oyster bottom by individual RD detected during the E, M and L periods of our acoustic tagging study based on: **a** proportion of detections from distinct oyster bottom types; and **b** number of unique visits to each of those four alternative habitats (i.e., excluding sand, halo, seagrass and marsh detections). Also shown are the PS indices for each fish. Statistical significance ($P < 0.05$) of PS values

are noted by an *asterisk* at the top of the graph for each individual (visit data only), as well as a letter (A–E) denoting groupings (>60 % similarity) based on multivariate clustering analyses of habitat-use data (corresponding to clusters represented in MDS space in Fig. 4). For abbreviations, see Fig. 2

visit data, respectively, even though many of these individuals were deemed specialists while focusing just on the early, middle or late time periods separately (Figs. 2, 4). Similarly, 45 % of red drum that visited oyster bottom over multiple study periods jumped between distinct oyster-habitat-use clusters based on either proportional or visit data (Figs. 3, 4). Furthermore, across all forays, individual variability in habitat use did not appear to be less than between-individual variability (Fig. 5). A *t*-test comparing the Bray–Curtis similarities of an individual's separate forays versus the similarities between forays made by two separate fish, indicated that intra-individual variability (average similarity = 53.2 %) in habitat use was not significantly less than of inter-individual variability (average similarity = 49.9 %) ($df = 372$; critical $t = 1.97$; observed $t = 1.58$; $P = 0.114$).

Sampling effects on metrics of individual specialization

We found effects of sample size on the results of null hypothesis testing for both IS and PS values. As should be expected, the calculated IS value for the population did not change with the increasing number of observations, as it is based on relative frequency data (Fig. 6). Slightly lower IS values for populations with the lowest number of observations were likely due to rounding effects associated with scaling (reducing) overall sample sizes for our simulations. The IS values forming the null model distribution from the Monte Carlo resampling increased steadily with sample size, resulting in lower observed *P*-values for similar values of IS. The relationship between sample size and the *P*-value for the IS value was non-linear. For our data, a population with similar proportional habitat use

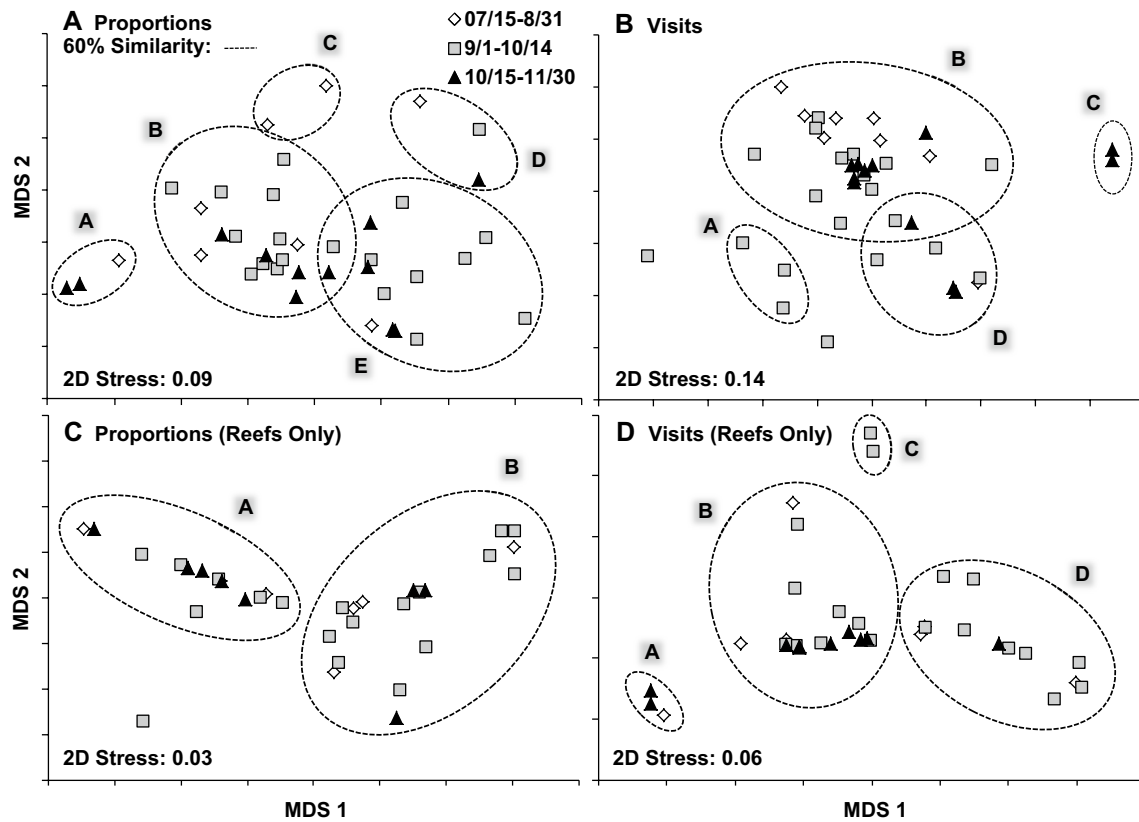


Fig. 4 MDS plots of habitat use by red drum based on proportional (a, c) and visit (b, d) data taking into account all potential habitats (a–b) or just distinct oyster bottom types (c–d). Each datum repre-

sents habitat use by a single fish during either the early, middle of late study periods (denoted by *unique symbols*). Clusters (A–E) in a–d correspond to letters noted for each fish in Figs. 2, 3

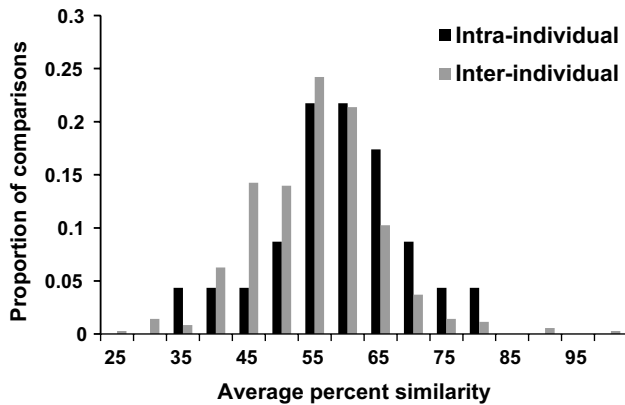


Fig. 5 Frequency histogram of average similarity between forays for comparisons within individuals and across individuals. Intra-individual comparisons involved 26 fish and inter-individual comparisons involved 351 pairwise comparisons between individuals

would be deemed significantly specialized at $\alpha = 0.05$ with ~140 observations per individual fish. Similar results were found for the effects of sample size on PS and associated *P*-values. The PS value did not change as the total number

of observations per individual increased, but the associated *P*-value decreases non-linearly with sample size (Fig. 7). The *P*-value was related to the PS value, as more specialized individuals reached lower *P*-values at smaller sample sizes. For the subset of individuals examined in our data set, all individuals (except the most generalized one) were considered significantly more specialized than would be expected by chance (at $\alpha = 0.05$) upon reaching ≥ 150 observations fish⁻¹.

Discussion

Conditionally, there is some evidence that red drum do partition habitat use of estuarine landscapes at the individual level over ecologically relevant timescales (i.e., several weeks), but the strength of this result is dependent on how data are analyzed. For instance, fish clustered into distinct habitat-use groups based on standard multivariate approaches. Most notably, some fish relied heavily on seagrass habitat, while other red drum did not. Also, fish could be described along a continuum from those that only utilized fringing shell bottom

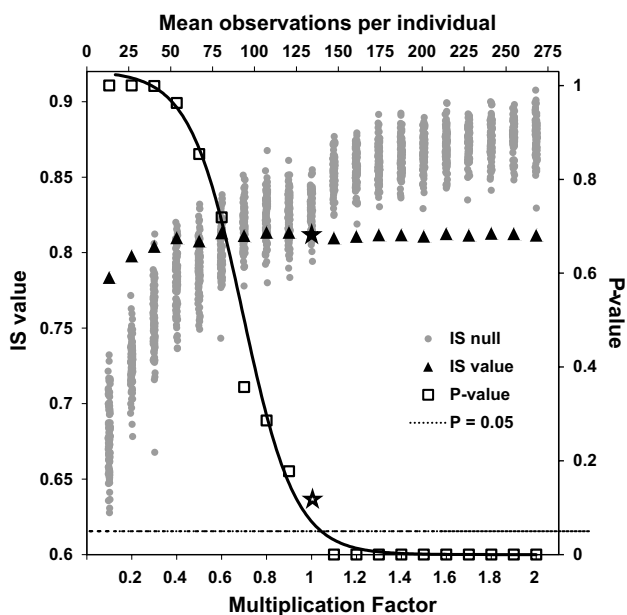


Fig. 6 Effect of sample size (number of visits logged per individual) on Monte Carlo-derived statistical inferences regarding specialization. Simulations of a reduced or expanded data set based on our actual data show the sensitivity of null IS (only the first 100 null values shown) and *P*-values (with an apparent threshold) to the law of large numbers in modeling null (relative to observed) habitat use

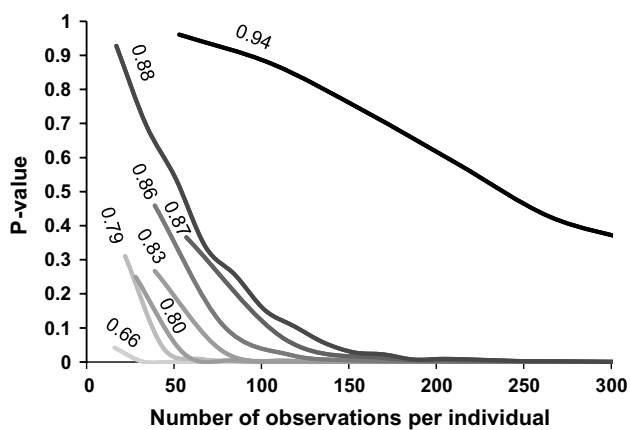


Fig. 7 Interactive effects of PS scores and sample sizes on statistical significance of individual specialization. Each line represents a single red drum, with all lines representing a range of PS scores (value noted for each fish). For each individual, total observations were expanded by serially multiplying the original data set by increasing multiplication factors. Individuals with lower PS values require notably fewer observations for detection of statistically significant individual specialization. For abbreviations, see Fig. 2

to those that primarily used consolidated reefs concentrated on marsh headlands (reef SM). Conclusions drawn from WIC/TNW, PS and IS metrics were more equivocal. Most values gauging specialization were relatively high (i.e., fish appeared to be more generalist) regardless of time period,

data format (proportions versus visits), or the number of habitats included in the analyses (WIC/TNW, PS and IS >0.7 in nearly all cases). These values are on par or higher than the approximate mean values of 0.66 (WIC/TNW; $n = 78$) and 0.47 (IS; $n = 142$) in a review of individual specialization studies across a wide diversity of taxa (Araújo et al. 2011). Still, even in cases when population-level specialization metrics scaled as high as 0.96 in our study, statistical approaches suggested that individuals were not sampling from a common resource pool. Yet, across several months, longitudinal comparisons examining temporal variation in habitat use within individuals (compared to among individuals) revealed that any evidence of specialization did not seem to be consistent over time. Given these somewhat contradictory results, we first consider some potential constraints in examining individual specialization in habitat use, and then discuss implications of potential specialization for a large, mobile estuarine fish.

Specialization analyses for habitat-use data

Increasing the number of observations in our data set increased the likelihood at which we rejected our null hypothesis and deemed a population or individual to be significantly specialized. This phenomenon is not new in statistics and is related to the law of large numbers. For example, in Monte Carlo resampling procedures used to generate a null model of population habitat use based on random chance alone, the more draws an individual had, the less variable its habitat use was and the more closely its use would converge on overall population frequencies. This led to null model populations that appeared increasingly more generalized in habitat use as the total number of observations increased. A similar example of this effect was described in Araújo et al. (2007), although in that case, the authors intentionally varied the number of draws (i.e., number of observations) per individual from the multinomial population probability distribution to manipulate the level of diet variation within individuals.

This sample-size effect may be particularly significant for habitat-use data due to the large number of observations possible for a single individual (i.e., many 1,000s in our study), and in part explain why we documented specialization even when PS values reached as high as 0.96. Furthermore, due to temporal autocorrelation in habitat-use data [especially successive detections in acoustic tracking (Sackett et al. 2007; Hammerschlag-Peyer and Layman 2010)], decisions on collapsing data must be made that may inadvertently beget statistical conclusions. In our study, we explored multiple ways to define independent observations per individual, including the raw number of detections, the number of unique visits to a given habitat, or the proportion of time spent in each habitat summed across seasons, lunar

cycles, days, etc. (not all results shown). Most of these approaches were justifiable both statistically and ecologically, but yielded very different numbers of observations per individual fish, which could affect the interpretation of results. In our analyses, pooling data over longer timescales (from unique forays to days to time periods to the whole study) tended to increase the likelihood of rejecting the null hypothesis that no specialization occurred, even as evidence of temporal consistency in individualized behavior was lacking. Therefore, it was advantageous to bin data over multiple temporal hierarchies (visits, days, seasonal periods, etc.). This approach allowed us to consider the consequences of serially larger data sets, as well as consider our data longitudinally across multiple temporal scales, to investigate the stability of intra- versus inter-individual differences in habitat use.

Across statistical approaches, it is not surprising that increased replication would enhance the power of an analysis (Quinn and Keough 2002). Also, it was intuitive, and confirmed by our simulations, that individuals with lower PS scores (independent of observation sizes) required fewer observations to be qualified as significantly specialized. Still, our simulations serve as cautionary tales in that population-level P -values shifted from >0.85 with 75 or fewer observations of habitat use by red drum (per fish), to <0.05 with 125 or more observations even though mean habitat-use frequencies did not change. Notably, the precise shape and location of this threshold was a function of our data structure, and therefore we cannot prescribe general guidelines regarding sample sizes that are necessarily applicable to other habitat-use studies.

To account for these hurdles, it was beneficial to simultaneously employ cluster analyses and MDS to explore variation in habitat use among individuals. Those analyses, which are less sensitive to sample size, identified clear groupings among red drum in the patterns of habitat use that also suggest niche partitioning within a population (in support of the observed PS values that could be as low as 0.35). However, longitudinal comparisons across time periods in our MDS analyses (and even across separate forays) indicated that individuals did not seem to remain “faithful” to distinct habitat-use groupings across monthly timescales, which cast doubt on the presence of true specialization within red drum. These findings highlight the utility in longitudinal sampling, which is a common attribute of most habitat-use data, in providing more detail on the degree of specialization across ecologically and evolutionary contexts. Extending our observations to diet data (the most commonly explored form of resource specialization), “snap-shot” methods, such as gut-content analyses, may lead to over-estimates of specialization because they represent diet over very short time intervals. These data are subject to pulsed events or short-term resource divisions that

do not necessarily last across the life span of an individual. Alternatively, stable isotope signatures are more integrative measures of resource acquisition over longer timescales, and are likely more robust measures of hard-wired individualization that could lead to evolutionary divergence (Bolnick et al. 2003; Araújo et al. 2007).

Specialization by red drum

At very large scales, it has been demonstrated that individuals within a species may display a variety of movement behaviors that balance tradeoffs in fitness (growth, survivorship, and reproduction), including partial migrations in which a subset of a population remains resident (Kerr et al. 2009). For exploited species such as cod (*Gadus morhua*), these alternative life history strategies can have important, but overlooked, implications for stock productivity and response to stressors (Sherwood and Grabowski 2010). At smaller scales, high individual variation in movement patterns or habitat-use behaviors may be expected in systems with high competition for resources across a heterogeneous landscape (Kobler et al. 2009). Unfortunately, we were not able to recover tagged fish to investigate diet information in conjunction with our exploration of sand, seagrass, marsh and oyster-bottom habitat use to determine whether variation in food resources correlated with apparent differences in habitat use for red drum. However, red drum are likely entering the embayment to forage, and as with broad-scale movement patterns observed for other species, differences in micro-habitat use among individual red drum, as evidenced over short periods (days–weeks), may reflect differences in foraging profiles among fish. Indeed, recent experimental work on the foraging ecology of red drum has demonstrated that these fish rove throughout landscapes, and may have greatest foraging success when they pulse through a system and surprise potential prey items (sensu Kenworthy 2011). In this scenario, red drum could benefit by dispersing throughout multiple habitats, and even more by partitioning habitat use among individuals to reduce local densities while also maximizing foraging efficiency [i.e., development of search images, maximizing successful prey ambushes (Futuyma and Moreno 1988)].

Despite these differences in micro-habitat use, for most individuals, apparent specialization was not particularly strong. One reason why measured individual specialization was not more evident may be related to the relatively low diversity of red drum diets. Red drum are known to primarily feed on penaeid shrimp, crabs [mostly blue crab (*Callinectes sapidus*)], and forage fishes [primarily menhaden (*Brevortia* spp.)] that routinely co-occur in individual stomachs as well as throughout all of the habitats we included in this study (Scharf and Schlicht 2000). Therefore, red drum occupy a fairly narrow trophic niche at the

population level based on broadly distributed prey, and there would be limited scope for further specialization at the individual level (sensu Bolnick et al. 2007). We speculate that the variation in habitat use we observed would not be related to gradients in prey taxa abundances across landscape scales, although this would need to be verified. The relatively ephemeral nature of the micro-habitats examined in this study (i.e., red drum are precluded from accessing these habitat at lower tides twice each day) may also reduce the potential for individual specialization over longer timescales, as reflected in our longitudinal analyses. We note, however, that our study does not exclude the potential for diverse life history portfolios within red drum, in which separate sub-populations exhibit distinct foraging locations (e.g., open coast) or strategies not represented by the individuals we tracked around Middle Marsh.

The hypothesis that individual red drum were consistently targeting unique subsets of habitat distinct from the population in general was not supported by our across-study-period or foray-by-foray longitudinal analyses. Comparisons of habitat use among successive forays for the same individual were not more similar than comparisons of forays between individuals. While overall, individual red drum clearly demonstrated diverse and distinct affinities for a range of habitat types, their habitat use did not seem consistent, at least at the longer temporal scales we examined. These data suggest that red drum may exhibit short-term “tendencies,” perhaps in response to each individual’s unique recent environmental history or food web interactions. However, these tendencies (i.e., habitat affinities) appear to draw from a common population-level behavioral repertoire in response to continuously evolving conditions over a range of spatio-temporal scales, leading to short-term, but not long-term, specialization. Clearly, specialization observed over short timescales should not be extrapolated across entire lifetimes, and information on individualization over different timescales could have varying relevance for ecological versus evolutionary dynamics. Differences in habitat use we observed over days–weeks may be ecologically informative relative to resource acquisition, but would be more evolutionary meaningful had they persisted over timescales long enough for other processes, like selective pressure, to operate (Bolnick et al. 2003). Indeed, if differences in fine-scale habitat use were driven by an underlying genetic or morphological predisposition, we would expect them to have been consistent across our entire study (and longer). For example, variation in the frequency of benthic and pelagic habitat use in brook charr (*Salvelinus fontinalis*) measured over months was found to be correlated with differences in coloration and morphology, suggesting that adaptation to localized feeding conditions was driving specialization in habitat use (Bourke et al. 1997). We also recognize other processes that may have led

to the lack of temporal consistency in red drum habitat use, such as the presence of short-term, stochastic processes obscuring specialization at the population level, or perhaps a spatio-temporal mismatch in the scale of sampling and manifestations of overall population niche width.

Collectively, these data suggest that red drum, a large mobile estuarine predator, may partition habitat use over ecologically relevant timescales (days, perhaps weeks), potentially to reduce competition among foraging areas for a shared resource pool (i.e., shrimp, crabs and forage fish), or simply in response to each individual’s unique, recent foraging experiences. For this mobile fish, however, apparent specialization at the individual and population levels over longer timescales (months) was not particularly evident and we expect that observed movement behaviors may not be “hard wired” or reflect true specialization. We speculate that this short-term specialist, long-term generalist pattern may be common among highly mobile organisms, although we lack the taxa-by-taxa data sets on landscape-level movement patterns to rigorously evaluate this hypothesis. These conclusions represent our consensus model drawn from a range of analyses (WIC/TNW, PS and IS, multivariate clustering analyses, data simulations) that demonstrate the importance of sample sizes and statistical approaches in evaluating specialization in habitat use or related niche dimensions.

Author contribution statement FJF, LAY, JHG, CAL, GDS, MDK conceived and designed the experiments. FJF and MDK performed the experiments. FJF, LAY, MDK analyzed the data. FJF and LAY wrote the manuscript; other authors provided editorial advice.

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