Habitat utilization patterns determine the physiological condition of *Cynoscion regalis* during estuarine residency

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ABSTRACT: For many species, quantifying nursery function of estuarine habitats, including tidal salt marshes, for early life stages is complicated by multiple habitat shifts over their period of estuarine residency. Our study relates the physiological condition of young of the year (YOY) of a marine transient species (weakfish *Cynoscion regalis*) to the quality of habitats frequented during their period of estuarine residency by examining their physiological condition (energetic reserves in the form of triacylglycerol, normalized to the expected changes with length) as a function of habitat use patterns and corresponding stable isotope signatures. In addition, for *C. regalis* preparing to emigrate offshore to wintering grounds, we evaluated the benefit of energetic reserves towards mitigating over-winter starvation in the context of individual metabolic rate. We found significant spatial distribution in the physiological condition of YOY *C. regalis* over their period of estuarine residency, with those utilizing polyhaline salt marshes consistently having comparable or higher condition across all years of the study. For *C. regalis* preparing to emigrate to offshore, we found inter-annual variability both in the relative utilization of marsh versus open bay regions and in their associated energetic reserves. However, variability in reserves was not reflected in the potential benefit of reserves in mitigating over-winter starvation, suggesting plasticity in energy allocation for YOY *C. regalis*. These results demonstrate that both the habitats utilized over the period of estuarine residency and larger-scale inter-annual variability can affect the condition and preparedness of YOY marine transients for the rigors of migration and over-wintering.

KEY WORDS: Nursery function · Tidal salt marsh · Triacylglycerol · Inter-annual variability

INTRODUCTION

While it is generally accepted that shallow estuarine and coastal habitats, including tidal salt marshes, function as 'nursery' habitats for the early life stages of fish and shellfish, details of the links between salt marshes and secondary production have been debated for more than 50 yr (Teal 1962, Odum 1968, Deegan et al. 2000, Beck et al. 2001, Minello et al. 2012). Moreover, the evidence linking habitat use and quality to the drivers and measures of produc-

tion, such as mortality, growth rates, condition, and tissue energy reserves (bioenergetic net benefit, Craig & Crowder 2000) has been restricted to just a few taxa (Weinstein & Walters 1981, Weisberg & Lotrich 1982, Weinstein et al. 2009, 2010, Dibble & Meyerson 2012). For marine transients (Day et al. 1989, Deegan et al. 2000), species that use estuaries for only part of their life, the role of salt marshes in their production has been even less clear. Adults of these taxa generally spawn seaward of coastal embayments, and post-larval stages move into estuaries

where they reside for extended periods before emigrating as juveniles to offshore over-wintering areas (Day et al. 1989). With few exceptions, these species act as 'ontogenetic shifters' (Adams et al. 2006), exhibiting multiple habitat, diet, and behavioral shifts during their period of estuarine residency (Deegan et al. 2000). These ontogenetic shifts in habitat use make it difficult to gauge the role of specific estuarine habitats in supporting transient species (Nagelkerken et al. in press), but tidal salt marshes and other shallow areas are thought to be important contributors (Beck et al. 2001, Weinstein et al. 2012).

For young-of-year (age-0, YOY) marine transients, patterns of residency among estuarine habitats are expected to mediate the bioenergetic constraints that influence rates of growth, condition, mortality, and ultimately the proportion of individuals that recruit to adult populations (Walters & Juanes 1993, Beck et. al. 2001, Kneib 2003, Minello et al. 2003, Nagelkerken et al. in press). Early in their first year of life, the allocation of energy in YOY fishes occurs primarily in somatic growth, to mediate size-selective predation (Werner & Gilliam 1984, Wilbur 1988, Rice et al. 1997, Craig et al. 2006), while later in the year, energy requirements for mitigating mortality due to over-wintering energy deficits and starvation appear to favor allocation of energy toward long-term energy stores (Sogard 1997, Post & Parkinson 2001, Biro et al. 2004, Sogard & Spencer 2004, Litvin et al. 2011). These 2 sources of mortality, viz. predation and over-winter starvation, appear to generate competing energetic demands with strong size-driven allometries that have important consequences for survival (Post et al. 1997, Hurst & Conover 2003, Biro et al. 2003, 2005, Hurst 2007, Mogensen & Post 2012).

Like many other marine transient species, post-larval weakfish *Cynoscion regalis* settle across multiple estuarine habitats in the early summer, often remaining within their settlement habitat over their early period of estuarine residency (Litvin & Weinstein 2004). However, YOY *C. regalis* begin to move out of tidal salt marshes and open waters of the upper estuary in the mid- to late summer or early fall, often exhibiting saltatory behavior, i.e. moving partially down-estuary, before continuing their journey towards the sea (Chao & Musick 1977, Weinstein & Brooks 1983, Szedlmayer et al. 1990, Litvin & Weinstein 2004). Ultimately, young weakfish arrive at the estuary mouth, though not in unison, before migrating off shore in the late fall (Litvin & Weinstein 2004). As they leave the estuary, their condition reflects the physiological suitability and ecological processes within the mosaic of habitats they have frequented since settlement (Deegan et al. 2000, Kneib 2003, Nagelkerken et al. in press). Thus, the evaluation of the nursery function of specific habitats for YOY *C. regalis* and other ontogenetic shifters must be considered in the context of the spatially explicit seascape encompassed by the habitats that are functionally connected through their movements over the period of estuarine residency (Beck et al. 2003, Sheaves et al. 2006, Sheaves 2009, Weinstein et al. 2014, Nagelkerken et al. in press).

In this study we relate the physiological condition of YOY weakfish from Delaware Bay, USA, to the quality of habitats frequented during their period of estuarine residency by examining energetic reserves (Weinstein et al. 2009, 2010, Litvin et al. 2011) as a function of habitat use patterns and corresponding stable isotope signatures (Litvin & Weinstein 2003, 2004). Previous analyses of lipid dynamics in juvenile *C. regalis* (Litvin et al. 2011) indicate that their long-term energy reserves are principally comprised of triacylglycerol (TAG); therefore, TAG was selected as a specific indicator of physiological condition for this study (see also Lochmann et al. 1995, 1996, Lochmann & Ludwig 2003, Heintz et al. 2004, Weinstein et al. 2009, 2010). In addition, as both body size and the magnitude of energy reserves are thought to mediate over-wintering survival (Sogard 1997, Biro et al. 2004), for juvenile *C. regalis* preparing to emigrate to offshore wintering grounds we evaluated a morphometric index of relative mass (Fulton's K) and the benefit of TAG reserves towards mitigating over-winter starvation in the context of individual metabolic rate (Post & Evans 1989, Shuter & Post 1990).

MATERIALS AND METHODS

Study area and fish collections

The size of the Delaware Bay estuary relative to our sampling design necessitated the definition of 'habitats' in broad regional terms (Fig. 1): open waters of the upper (OUB), middle (OMB), and lower bay (OLB), upper bay meso-oligohaline marshes dominated by *Phragmites australis* (UBM), mid-bay mesohaline marshes characterized by a transition from *P. australis* to *Spartina* spp. dominance (MBM), and polyhaline marshes of the lower bay (LBM) dominated by *Spartina* spp. (Weinstein & Balletto 1999).

Details of the field collection and stable isotope analysis methods were reported earlier (Weinstein et al. 2000, 2009, Litvin & Weinstein 2003, 2004, Litvin et al. 2011) but are summarized here. Juvenile weakfish
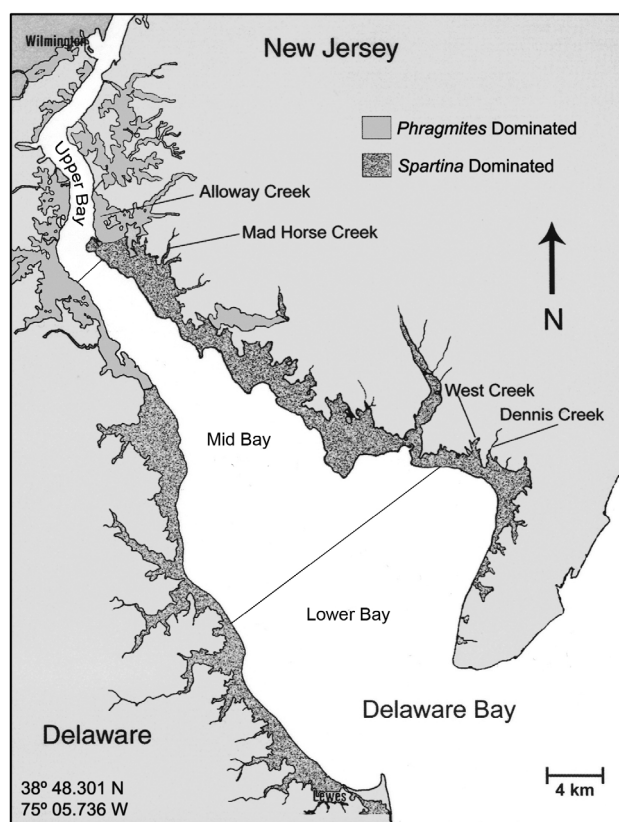
Fig. 1. Six regions in Delaware Bay, USA, that formed part of this study: open waters of the upper (OUB), middle (OMB), and lower bay (OLB), representative polyhaline marshes of the lower bay dominated by *Spartina* spp. (West and Dennis Creeks, LBM), mesohaline marsh of the mid-bay characterized by a transition from *Spartina* to *Phragmites australis* dominance (Mad Horse Creek, MBM), and meso-oligo-haline marsh of the upper bay dominated by *P. australis* (Alloway Creek, UBM)

were sampled with a 4.9 m otter trawl throughout each of the 6 regions. Lower, mid-, and upper bay open waters were sampled as part of a bay-wide monitoring program, while tidal creeks in adjacent salt marshes were concurrently sampled as part of this study (Fig. 1). Tidal creeks, chosen to represent characteristic marsh habitats in each region (see above), included West and Dennis Creeks (LBM), Mad Horse Creek (MBM), and Alloway Creek (UBM, Fig. 1). At each collection site and date, individuals were separated into 3 size classes: <60 mm standard length (SL; 'small'), 60–100 mm SL ('medium'), and >100 mm SL ('large') that reflected size-related changes in diet and acquisition of energy stores (Nemerson 2001, Litvin & Weinstein 2004, Litvin et al. 2011).

Samples comprising this study were: (1) 263 individuals captured in tidal salt marshes in August through October of 1999, 2000, and 2001; (2) 128 individuals collected in open waters throughout the Delaware Bay in September of 2001; and (3) 311 individuals captured at the mouth of Delaware Bay (seaward of the 6 designated regions) in late October or early November of 1999, 2001, and 2002 prior to their migration offshore, and likely more southern, waters to over-winter (Wilk 1979). In all, a total of 702 juvenile weakfish were collected in 1999 through 2002 for use in the stable isotope and physiological condition analyses. Specimens were preserved on dry ice in the field and transported to the laboratory for storage at −80°C (Ohman 1996).

Sample processing

Partially thawed fish were measured to the nearest mm SL, weighed, gut contents removed (Lochmann et al. 1995, 1996), and then freeze-dried to a constant dry weight before grinding to fine powder (Spex CertaPrep® 5100 grinding mill). Fish <120 mm SL were ground whole, while those ≥120 mm SL were first coarsely ground in a Waring® blender, and a randomly selected aliquot was then ground to fine powder (Litvin & Weinstein 2004, 2011). Ground samples were stored in pre-combusted glass vials with acid-washed polyethylene caps and purged with N_2 gas to exclude airborne oxygen and prevent lipid peroxidation prior to storage at −80°C.

Isotopic determinations

Sub-samples of each whole ground fish were analyzed on a Micromass Isochrom Continuous Flow Stable Isotope Mass Spectrometer coupled to a Carlo Erba Elemental Analyzer (CHNS-O EA1 108). Standards were Peedee Belemnite for carbon, air for nitrogen, and Canyon Diablo triolites for sulfur. Prior to statistical comparison of stable isotope signatures among juvenile weakfish from different size classes, normalization for lipid content and ontogenetic shifts was required. Fractionation during lipid synthesis results in differences between $\delta^{13}C$ of lipids and other tissues (DeNiro & Epstein 1977, Post et al. 2007). Previous work (Litvin et al. 2011) demonstrated that lipid content is low in YOY *Cynoscion regalis* <60 mm SL (4.59 ± 0.89%, mean ± SD) and begins to increase rapidly between 60 and 100 mm SL. Therefore, carbon isotope values of all juveniles >60 mm SL were adjusted based on the C:N ratio of the sub-sample selected for isotopic determination (Post et al. 2007). Normalization for ontogenetic shifts

in trophic level was required due to the expected enrichment of stable isotope values, 1.0‰ $\delta^{13}C$, 3.4‰ $\delta^{15}N$, and 0.5‰ $\delta^{34}S$, associated with trophic transfer (Peterson & Fry 1987). The estimated trophic level for the smallest size class of weakfish was approximately 0.15 and 0.30 lower than the medium and larger size classes, respectively (Grecay 1990, Nemerson 2001). To account for these differences, stable isotope values were adjusted by 0.15‰ $\delta^{13}C$, 0.51‰ $\delta^{15}N$, and 0.08‰ $\delta^{34}S$ for medium, and 0.30‰ $\delta^{13}C$, 1.02‰ $\delta^{15}N$, and 0.15‰ $\delta^{34}S$ for large juvenile weakfish in the subsequent statistical comparisons (Litvin & Weinstein 2004).

TAG concentration determination by thin layer chromatography/flame ionization detection

A 50 ± 5 mg subsample of ground tissue was folded into a 70 mm round of Whatman® 541 ashless filter paper and extracted 3 times, first in 4.0 ml of 2:1 (v/v) dichloromethane:methanol for 15 h at 5°C (vial head-space purged with N_2), then in 3.0 ml of fresh solvent mixture for 3 h, followed by a final 3 h extraction in 2 ml of fresh solvent mixture. The 3 sequential extracts were combined and stored at −80°C under N_2 for no more than 4 d to avoid esterification of fatty acids by methanol in the extraction solvent (Parrish 1987). Nonadecane ($C_{19}H_{40}$: 1.000 mg total, 50 µg µl^{-1}) internal standard (for 50 mg samples reconstituted to 0.5 ml, see below, or adjusted to preserve the identical final concentration) in chloroform was added to each extract, and back extraction in 0.1 M aqueous KCl solution at 5°C (Folch et al. 1957) was used to remove non-lipid materials. Back-extracted samples were concentrated by evaporating to dryness in a 38°C water bath under a stream of N_2 gas and then reconstituted in 0.5 to 1.5 ml of dichloromethane, depending on sample size and lipid content.

To determine TAG concentrations, we used a modified method of Lochmann et al. (1995), in which lipid extracts were spotted on Iatron Chromarod III® silica-coated rods and partially developed in 3 successive HPLC grade solvent systems to separate lipid classes. Flame ionization detector (FID) scanning using an Iatroscan® Mark V with a Hewlett Packard® HP3690 integrator was used for data acquisition. Blanks, a synthetic standard (tripalmitin), and 1 replicate for every 7 samples were utilized to determine TAG concentrations and ensure accuracy. Conversion of FID peak areas to extract TAG concentrations (mg g^{-1} dry weight) was performed using a segmented third-order polynomial

calibration model with separate curves generated for the standard on each chromarod used.

Data analysis

In assessing the effect of habitat utilization on the physiological condition of YOY weakfish, we accounted for the potential discrepancy between the region where an individual was collected and the region where it may have recently resided for a significant period through the application of canonical discriminant analysis classification to the isotopic signatures of YOY *C. regalis*. We reasoned that any discrepancy between the isotopic signature of a juvenile and the range of $\delta^{13}C$, $\delta^{15}N$, and $\delta^{34}S$ values expected for the region where the individual was captured indicated recent residency in an alternate region (Hobson 1999, Litvin & Weinstein 2004). Expected values were based on the isotopic signatures of small YOY *C. regalis* collected in each region ('baseline weakfish', Litvin & Weinstein 2004), which we conjectured would exhibit the greatest site fidelity and therefore reflect the isotopic signature-associated residency within a given region (Deegan & Garritt 1997, Weinstein et al. 2000, Litvin & Weinstein 2003). Canonical discriminant analysis was utilized to extract patterns of isotopic signatures as a function of region in baseline weakfish (see Fig. S1a in the Supplement at www.int-res.com/articles/suppl/m510 p087_supp.pdf) and to validate the ability of the analysis to identify their region of collection based on ^{13}C, $\delta^{15}N$, and $\delta^{34}S$ values (reclassification success rate of 85%, see Litvin & Weinstein 2004 for further details of the method). Comparisons of physiological condition (see below) were based both on the region (OUB, OMB, OLB, UBM, MBM, or LMB) in which YOY *C. regalis* were collected ('region of collection') and the region to which they were assigned by the discriminant analysis classification based on their isotopic signatures ('region of residence').

TAG contents (g) for whole fish were extrapolated from concentrations within extracted subsamples and individual dry weights and converted to energy equivalents (kJ) using a published energy conversion value (39.57 kJ g^{-1}, Brett & Groves 1979) to estimate total energetic content in the form of TAG ('TAG energy content'). Previous work (Litvin et al. 2011) demonstrated that TAG concentration is at or near 0 in smaller YOY *C. regalis* and begins to increase rapidly between 60 and 100 mm SL. This expected change in TAG concentration with length in juvenile weakfish precluded the direct comparison of TAG

energy content among individuals of different lengths. To normalize this measure, the relationship between TAG energy content and the length of juvenile weakfish (642 individuals with detectable TAG content) were accounted for by nonlinear piecewise regression fitted as a function of the natural log of juvenile weakfish SL (Wilkinson 1990, Post & Lee 1996, Post & Parkinson 2001, Litvin et al. 2011):

$$\text{Log}(\text{ECSL}_{\text{TAG}}) = b_0 + b_1\text{Log}(\text{SL}) \quad \text{if } \text{Log}(\text{SL}) < I \quad \text{(1a)}$$

$$\text{Log}(\text{ECSL}_{\text{TAG}}) = b_0 + b_1 + b_2\,(\text{Log}(\text{SL}) - I)$$
$$\text{if } \text{Log}(\text{SL}) > I \quad \text{(1b)}$$

where ECSL_{TAG} is the predicted TAG energy content at standard length SL, b_0 is the intercept of the first regression, b_1 is the slope of the first regression, b_2 is the difference in the slopes between the 2 regressions, and I is the estimated inflection point between the 2 segments.

Normalized physiological condition (NPC) was determined by comparing the TAG energy content for each individual to the predicted value at its SL, determined via the piecewise regression analysis:

$$\text{NPC} = \text{Log}(\text{EC}_{\text{TAG}}) - \text{Log}(\text{ECSL}_{\text{TAG}}) \quad \text{(2)}$$

where EC_{TAG} is the TAG energy content of a juvenile weakfish, and ECSL_{TAG} is the predicted TAG energy content at standard length SL from Eq. (1) (see Table S1 and Fig. S2 in the Supplement for nonlinear piecewise regression results). Thus, our metric of physiological condition removed the effects of size on TAG energy content of weakfish. NPC is a residual from an overall population relationship, with positive values reflecting individuals with energy reserves higher then would be expected at given length and negative values indicating the inverse. Juveniles with no detectable TAG were included by assigning them values slightly lower than the detection limit of the TLC/FID method (0.049 mg ml^{-1} extract).

The relative benefit of TAG reserves (TAG benefit), in terms of ameliorating over-winter starvation (Shuter & Post 1990, Hurst & Conover 2003), was estimated for fish captured at the mouth of Delaware Bay prior to migration to their offshore wintering grounds (Wilk 1979) in 1999, 2001, and 2002. We estimated the relative benefit of TAG to YOY *C. regalis* in terms of rate of utilization (i.e. individual metabolic rate), which was assumed to scale as a function of body weight$^{3/4}$ (Schmidt-Nielsen 1984, Post & Evans 1989, Shuter & Post 1990, Brown & West 2000):

$$\text{TAG benefit} = \text{TAG}_M\,(\text{TD}_M{}^{3/4})^{-1} \quad \text{(3)}$$

where TAG_M is the mass of TAG content in mg and TD_M is the total dry mass of an individual in g. To fur-

ther determine the relative role of TAG reserves and body size in mediating potential over-wintering survival (Sogard 1997, Biro et al. 2004) for emigrating YOY *C. regalis*, we evaluated a morphometric index of relative mass, Fulton's K:

$$K = 100(W\,\text{SL}^{-3}) \quad \text{(4)}$$

where W is the wet total body weight (mg), and SL is measured in mm.

For YOY *C. regalis* collected within Delaware Bay between 1999 and 2001, NPC was compared among regions of collection and residence within each and across all years. For individuals collected at the bay mouth, NPC, TAG benefit, and Fulton's K were compared among years and regions of residence, pooled across all years. Because not all parametric statistical assumptions could be met, a non-parametric approach was adopted utilizing Mann-Whitney 2-sample tests with serial Bonferroni adjustments (Rice 1989).

RESULTS

By applying canonical discriminant analysis classification to the isotopic signatures of YOY *Cynoscion regalis* (Fig. S3 in the Supplement), we were able to reclassify individuals used in this study to their region of residence (Litvin & Weinstein 2004), i.e. areas likely occupied for extended periods, regardless of where they were captured (see 'Materials and methods'; Table 1). The classification results for fish collected in 1999, 2000, and 2001 throughout open bay and marsh habitats (Fig. S1b) were generally similar to those reported by Litvin & Weinstein (2004), with the majority of individuals classified to either their site of collection or an adjacent region. In 1999 and 2002, the vast majority of YOY *C. regalis* collected at the mouth of Delaware Bay (BM), just prior to emigration, were classified to either the open waters of the lower Bay (OLB: 85%) or lower Bay salt marshes (LBM: 9%). However, in 2001, stable isotope signatures indicated that the majority of the fish preparing to emigrate from Delaware Bay (BM) were recent arrivals from salt marsh habitats (UBM + MBM + LBM: 56%, Table 1).

There was considerable variability in values of normalized physiological condition (NPC; range −6.90 to +4.32) across all YOY *C. regalis* collected in this study. Trawling was not conducted in open bay regions in 1999 and 2000, thus differences in NPC based on region of collection (though not region of residence, see 'Materials and methods') were re-

Table 1. Year of collection, location, size, and size class (small [<60 mm standard length, SL], medium [60–100 mm SL], and large [>100 mm SL]) of young-of-the-year weakfish *Cynoscion regalis* utilized in the physiological condition study and their canonical discriminant function regional classification (region of residence) based on their carbon, nitrogen, and sulfur isotope signatures. Region of collection/residence (see 'Materials and methods'): upper bay marshes (UBM), mid-bay marshes (MBM), lower bay marshes (LBM), open waters of the upper bay (OUB), mid-bay (OMB), and lower bay (OLB), and the mouth of Delaware Bay (BM)

Year	Region of collection	Mean SL (mm)	Min	Max	SD	Size class			Region of residence						Total
						Small	Medium	Large	OUB	UBM	OMB	MBM	OLB	LBM	
1999	UBM	68	24	135	24.52	9	18	2	0	20	8	0	0	1	29
	MBM	72	33	125	18.13	5	22	2	0	11	0	7	3	8	29
	LBM	88	27	200	58.55	24	6	18	0	0	2	2	14	30	48
	BM	149	99	194	25.2	0	1	34	0	0	4	1	26	4	35
2000	UBM	90	80	110	7.176	0	54	6	1	57	0	2	0	0	60
	MBM	99	80	155	17.17	0	15	7	0	13	0	8	1	0	22
	LBM	151	97	175	19.16	0	1	15	0	0	0	1	11	4	16
2001	UBM	100	85	126	10.35	0	9	8	0	15	0	2	0	0	17
	MBM	99	74	154	19.36	0	13	11	0	12	0	5	0	7	24
	LBM	142	93	170	20.75	0	1	17	0	0	0	2	11	5	18
	OUB	85	77	112	11	0	12	2	0	14	0	0	0	0	14
	OMB	128	79	179	28.6	0	9	20	0	9	0	1	12	7	29
	OLB	142	99	186	23.1	0	1	84	0	1	2	9	61	12	85
	BM	165	98	240	32.9	0	3	85	0	5	5	22	34	22	88
2002	BM	169	86	221	22.7	0	3	185	1	1	2	3	164	17	188

stricted to comparisons among marshes. In those years, YOY *C. regalis* from the LBM region had significantly higher NPC (Fig. 2a,b) then those from the MBM and UBM regions in terms of region of collection or region of residence. For YOY *C. regalis* assigned an open bay region of residence based on their isotopic signatures, in 1999 (Fig. 2a) those assigned to the OLB region had significantly higher NPC than individuals from the MBM, UBM, and OMB regions, while in 2000 (Fig. 2b) the NPC of juveniles assigned to the OLB region were significantly lower than those with a UBM region of residence. In 2001, YOY *C. regalis* were collected throughout all 6 bay regions. Individuals collected in the OMB and OLB regions possessed significantly lower mean NPC than those from marsh regions (Fig. 2c), which, unlike in 1999 and 2000, did not significantly differ in NPC. In this year, significant differences based on region of residence were limited to those assigned to the OLB having lower NPC relative to YOY *C. regalis* with a UBM region of residence (Fig. 2c).

For YOY *C. regalis* collected in 1999, 2001, and 2002 prior to emigration at the mouth of Delaware Bay, significant differences among region of residence, pooled over all years, were limited to higher Fulton's *K* in juvenile weakfish assigned to the OLB relative to those assigned to the MBM region (p < 0.001, Fig. S4 in the Supplement). When pooled by collection year, individuals collected in 1999 had significantly higher NPC and Fulton's *K*, but not TAG benefit, than those collected in 2001 or 2002 (Fig. 3). The mean NPC of juvenile *C. regalis* collected at the mouth of the bay in 2001 and 2002 was not significantly different, although C. *regalis* from 2001 had significantly lower Fulton's *K*, yet higher TAG benefit, relative to 2002 (Fig. 3).

DISCUSSION

In this study, we present an approach for the evaluation of habitat suitability for YOY *Cynoscion regalis*, an ontogenetic shifter, in the context of the habitats utilized by individuals during their period of estuarine residency. By using stable isotope signatures from the tissues of YOY fish in combination with canonical discriminant analysis to infer movements, we were able to discern patterns of habitat residency in the Delaware Bay estuary (Litvin & Weinstein 2004). In addition, we developed a powerful tool to assess physiological condition among YOY *C. regalis* by normalizing for the expected changes in TAG, their specific form of long-term energy reserves, with growth (Litvin et al. 2011). While analysis of energetic reserves as an indicator of condition and potential over-wintering survival has been employed for a range of species (e.g. Schultz & Conover
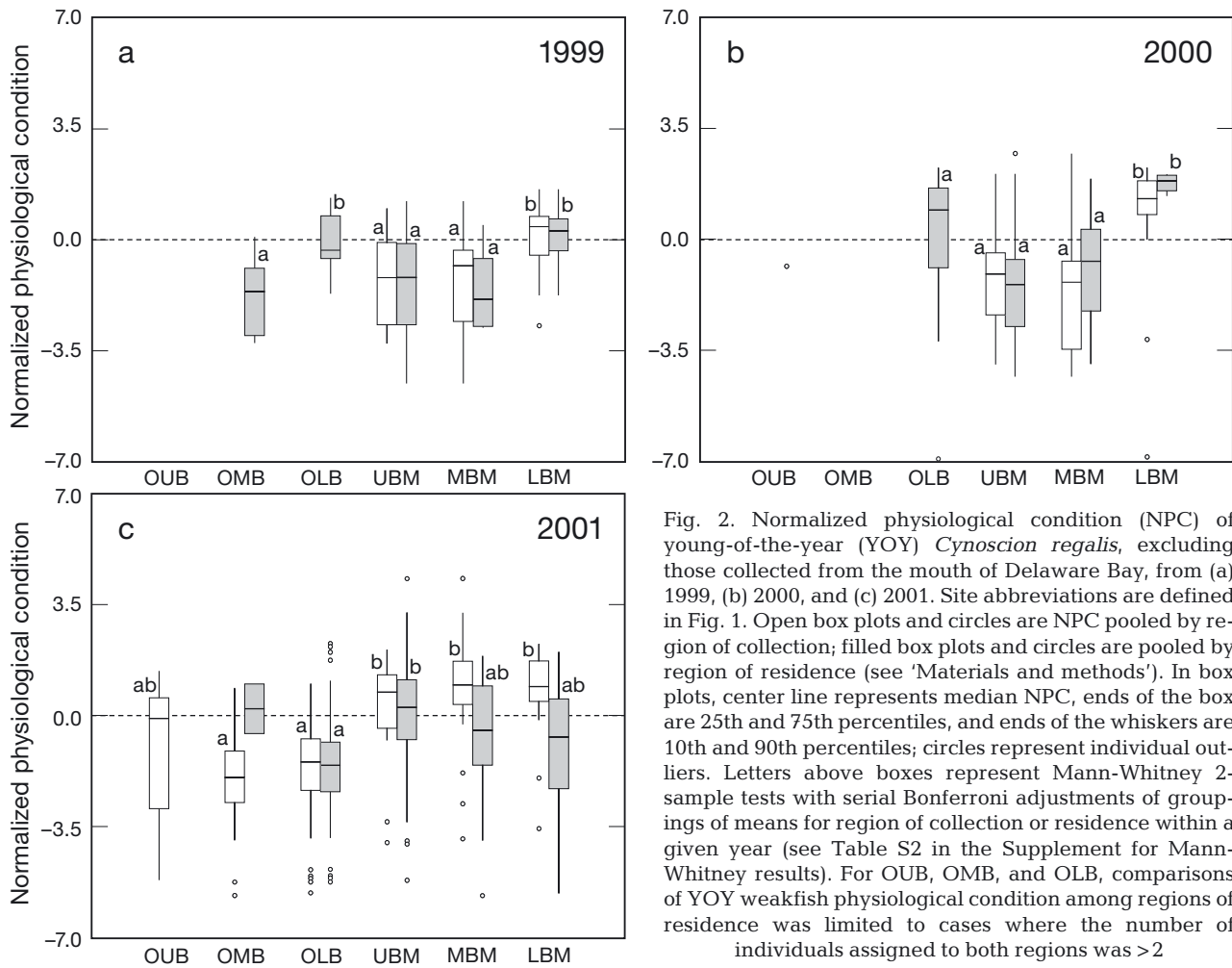
Fig. 2. Normalized physiological condition (NPC) of young-of-the-year (YOY) *Cynoscion regalis*, excluding those collected from the mouth of Delaware Bay, from (a) 1999, (b) 2000, and (c) 2001. Site abbreviations are defined in Fig. 1. Open box plots and circles are NPC pooled by region of collection; filled box plots and circles are pooled by region of residence (see 'Materials and methods'). In box plots, center line represents median NPC, ends of the box are 25th and 75th percentiles, and ends of the whiskers are 10th and 90th percentiles; circles represent individual outliers. Letters above boxes represent Mann-Whitney 2-sample tests with serial Bonferroni adjustments of groupings of means for region of collection or residence within a given year (see Table S2 in the Supplement for Mann-Whitney results). For OUB, OMB, and OLB, comparisons of YOY weakfish physiological condition among regions of residence was limited to cases where the number of individuals assigned to both regions was > 2

1997, Fullerton et al. 2000, Hurst & Conover 2003, Dibble & Meyerson 2012), the examination of the specific form of long-term energy reserves provides a demonstrably more sensitive measure of relative physiological condition (Jobling et al. 1998, Norton et al. 2001, Lochmann & Ludwig 2003, Weinstein et al. 2009, 2010). Although measures of physiological condition can be influenced by reproductive cycles, disease, parasite infestation, and other factors, our use of large samples and sexually immature individuals helped limit the variability of this metric to ecological processes and habitat-related factors (Shulman 1974, Evans 1998).

The spatial distribution of YOY *C. regalis* with low measures of NPC in our study implies heterogeneity in the suitability of habitats within Delaware Bay (Håkanson 1989, Kerrigan 1994, Sutton et al. 2000, Weinstein et al. 2009, 2010). Most notably, across all years, YOY *C. regalis* from the lower bay salt marshes consistently had comparable or significantly

elevated NPC measures compared to all other regions, particularly mid- and upper bay salt marshes (Fig. 2, Table S2). This was true regardless of whether habitat utilization patterns were couched in terms of collection location or regional assignment based on isotopic signatures. In addition, with the exception of those with LBM as their habitat of residence in 2001, YOY *C. regalis* from lower bay marshes were the only group to consistently have positive (i.e. >0) median NPC values across all years (Fig. 2), indicating higher than expected physiological condition relative to the average individual characterized in this study. Overall, our data suggest that lower Delaware Bay marshes are superior habitats for young weakfish.

Tradeoffs between maximizing growth and mortality in young *C. regalis* due to variability in physio-chemical factors, food resource availability, and predation across Delaware Bay have previously been highlighted (Lankford & Targett 1994, Grecay & Tar-
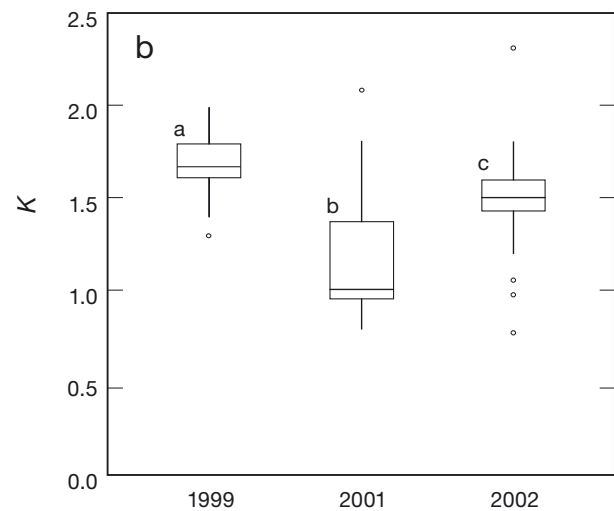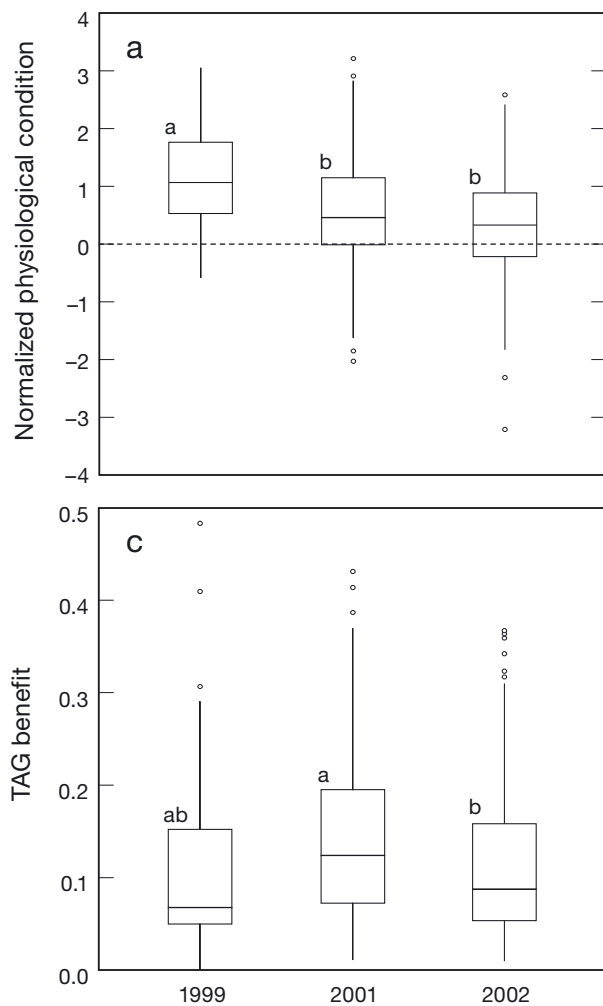
Fig. 3. (a) Normalized physiological condition (NPC), (b) Fulton's *K* (*K*), and (c) triacylglycerol (TAG) benefit (see 'Materials and methods') of young-of-the-year *Cynoscion regalis* collected at the mouth of Delaware Bay in 1999, 2001, and 2002. In box plots, center line represents median, ends of the box are 25th and 75th percentiles, and ends of the whiskers are 10th and 90th percentiles; circles represent individual outliers. Letters above boxes represent Mann-Whitney 2-sample tests with serial Bonferroni adjustments of groupings of means (see Table S3 in the Supplement for Mann-Whitney results)

gett 1996, Paperno et al. 2000) and provide possible mechanisms for the spatial disparity in physiological condition that we have observed. These studies noted that small weakfish collected in the open waters of the lower Delaware Bay had fuller stomachs, greater weight at length and length at age, and exhibited higher growth rates than individuals collected in mid- and upper bay waters. The observations were attributed to the influence of increased turbidity, lower illumination, and suboptimal physiochemical conditions in the latter regions. In addition, work in or near tidal salt marsh creeks included in this study (Dennis Creek, Mad Horse Creek, and Mill Creek, a *Phragmites*-dominated system near Alloway Creek, Fig. 1), characterized the lower bay marshes as a region where juvenile weakfish had elevated feeding success (Nemerson & Able 2004).

Apart from the drivers mentioned above, the near monocultures of an invasive variety of *P. australis* (Saltonstall 2002) in meso-oligohaline salt marshes of

Delaware Bay likely contributed to the lower physiological condition of YOY *C. regalis* from marshes in those regions of the Bay. *P. australis* drives changes in salt marsh structure and hydrology, resulting in the restriction of access to food resources and changes in food web structure (Meyerson et al. 2009). This leads to negative impacts on the condition (Weinstein et al. 2009, 2010) and abundance of fish within the invaded systems, particularly juveniles (Dibble et al. 2013).

While the preponderance of studies suggests that the lower bay is superior habitat for YOY *C. regalis* in terms of growth and condition, mortality rates are lower for YOY fish, including *C. regalis*, in the mid- and upper Delaware Bay (Paperno et al. 2000, Nemerson & Able 2004). These findings suggest that the spatial variability in individual physiological condition of YOY *C. regalis* we have observed was the function of (1) habitat quality in terms of food availability, physiochemical suitability, and lower abun-

dance of predators (Miller et al. 1985, Lankford & Targett 1994, Paperno et al. 2000, Nemerson & Able 2004) and (2) the competing demands of energy for growth and energy reserves which drive allocation of energy from growth to energy reserves in larger YOY fish (Sogard 1997, Post & Parkinson 2001, Hurst & Conover 2003, Litvin et al. 2011). The observed spatial and temporal differences in physiological condition reflect the outcome of these interacting factors and suggest that the superior condition exhibited by YOY weakfish in lower bay marshes is likely a result of high resource availability and suitable physio-chemical conditions out-weighing the disadvantages, in terms of acquisition (or expenditure) of energy, that elevated risk of predation represents (Biro et al. 2003, 2005, Mogensen & Post 2012).

Stable isotope signatures in individuals captured within the estuary during the summer and early fall in 1999, 2000, and 2001 inferred that YOY *C. regalis* exhibited substantial site fidelity during part of their estuarine residency (Litvin & Weinstein 2004). Consequently, the physiological condition of these individuals can be viewed as the product of residency in relatively few habitats. In contrast, the condition of fish collected at the mouth of Delaware Bay in 1999, 2001, and 2002 represents the integrated quality of all habitats utilized prior to emigration and the selective pressure to first minimize size-dependent predation and then acquire sufficient energy reserves to survive the over-wintering period (Shuter & Post 1990, Sogard 1997, Schultz & Conover 1999, Post & Parkinson 2001). The stable isotope signatures in individuals collected in 1999 and 2002 (i.e. region of residence classification) also suggested that the vast majority (>85%) of YOY *C. regalis* exhibited what we have come to refer to as 'saltatory' behavior (Litvin & Weinstein 2004), i.e. after exiting their initial settlement habitats, they did not move directly downstream to the bay mouth. Rather, they moved varying distances down estuary and resided in open waters for extended periods before arriving at the bay mouth (Chao & Musick 1977, Weinstein & Brooks 1983).

A remarkably different pattern was observed at the bay mouth in 2001. In this year, isotopic signatures indicate that >50% of those fish collected appeared to inhabit marshes for their entire period of estuarine residency, after which time they moved directly to the bay mouth and presumably offshore. While the increase in proportion of YOY *C. regalis* captured prior to emigrations from Delaware Bay with isotopic signatures reflecting marsh residency might reflect a population level change in the sequence of habitats utilized in 2001, several lines of evidence from the late summer and fall collections from that year suggest that there was no deviation from the anticipated saltatory behavior: (1) over 75% of the individuals collected in the open waters of the mid- and upper bay in September of that year were assigned to a marsh region of residence, suggesting that they had already begun their expected movements out of marsh creeks and down the estuary, (2) the majority of fish collected in the lower bay region were assigned as such, indicating that they either initially settled in this region or arrived from up-bay and spent sufficient time in the lower estuary to acquire the *in situ* stable isotopic signatures, while the balance had recently arrived from other regions in the bay, both expected elements of saltatory behavior, and (3) data from the existing monitoring program that provided individuals for this study indicate that YOY *C. regalis* resided throughout the open Delaware Bay from July through early October 2001 (J. Balletto pers. comm.). However, some YOY *C. regalis* collected at the mouth of Delaware Bay may have utilized shallow coastal regions as juvenile habitat (Wuenschel et al. 2013) and then entered the mouth of the bay while migrating to offshore over-wintering areas. Although evidence from Litvin & Weinstein (2004) suggests that YOY weakfish isotope signatures in open waters of the lower Delaware Bay are partially driven by marsh-derived resources, which would make them distinct from juvenile weakfish utilizing purely marine-derived production, no isotope data are available from YOY weakfish residing in shallow coastal and marine habitats for comparison. Future studies would benefit from YOY *C. regalis* isotope data from adjoining shallow coastal regions or the utilization of additional tracer methods, such as otolith microchemistry (Thorrold et al. 1998).

The physiological condition results provide insight into what may have driven this change in relative utilization of marsh versus open bay regions over the period of estuarine residency for YOY *C. regalis* preparing to migrate offshore. In 2001, the NPC values of young weakfish collected in open bay regions were among the lowest recorded in this study. In addition, the majority of YOY *C. regalis* with negative NPC and characterized as having a salt marsh region of residence were actually captured in open bay regions. While it was difficult to discern how long individuals resided in an open bay region (Litvin & Weinstein 2004), together these results suggest that open bay waters were particularly unsuitable for young fish in 2001. Although the specific factors that negatively affected the condition of YOY

C. regalis from open waters of the bay in 2001 are un-known, our previous work with bioenergetic models suggested that the value of open bay regions for the production of young weakfish through the summer and early fall was considerably lower in 2001 than 1999, potentially due to physiochemical constraints associated with higher temperatures and lower salin-ity in 2001 (Weinstein et al. 2012). While our study and that of Weinstein et al. (2012) did not examine mortality rates per se, our results suggest that sub-optimal conditions may have led to higher mortality rates in open bay regions in 2001, particularly for those individuals settling in the open bay or exhibit-ing saltatory behavior, i.e. leaving the marsh in mid-to late summer, at relatively small sizes (<100 mm SL) and with little energy reserves (Litvin & Weinstein 2004, Litvin et al. 2011). In both cases, YOY *C. regalis* surviving to emigrate in the late fall would ultimately acquire the majority of their biomass within the open bay, acquiring isotopic signatures indicative of those regions (Litvin & Weinstein 2004). Relatively higher mortality rates experienced by fish in 2001, in the aforementioned groups, might also explain the dif-ferences among years in the relative utilization of marsh and open bay regions (Litvin & Weinstein 2004, this study), for YOY *C. regalis* emigrating from Delaware Bay.

Regardless of the mechanism, there is clear inter-annual variability in the condition (NPC and TAG benefit) of YOY *C. regalis* preparing to emigrate from Delaware Bay, an observation that parallels their changes in habitat utilization during the period of estuarine residency. The degree to which the dif-ferences in condition predict the likelihood of pre-venting over-wintering mortality due to starvation are less clear. Winter survival depends both on body size, which governs mass-specific metabolic rates, and energy stores in conjunction with the duration and severity of the over-wintering period (Sogard 1997, Biro et al. 2004, Mogensen & Post 2012). Nor-malized physiological condition results revealed that, at a given length, young weakfish emigrating from Delaware Bay in 2001 had equal or slightly smaller energetic reserves compared to 1999 and 2002. Con-versely, young *C. regalis* collected in 2001 had signif-icantly depressed *K* values, i.e. they possessed less mass at a given length. This observation suggests that, at a given length, YOY *C. regalis* captured in 2001 had higher mass-specific metabolic costs which would render their lipid reserves less valuable in pre-venting over-winter mortality (Post & Evans 1989, Shuter & Post 1990, Biro et al. 2004, Mogensen & Post 2012). However, TAG benefit, the expected value of

energetic reserves in terms of individual metabolic rate (rather than length as in NPC and *K*, Schmidt-Nielsen 1984, Brown & West 2000), values indicated that YOY *C. regalis* captured in 2001 were likely as prepared for the energetic demands associated with over-wintering as those captured in 1999 and 2002 (Post & Evans 1989, Shuter & Post 1990, Mogensen & Post 2012). This observation suggests that young *C. regalis* have the ability to direct the allocation of en-ergy to reserves (TAG) versus structural biomass in order to maximize over-winter survival (Post & Evans 1989, Shuter & Post 1990), even as they continue to increase in length. As energetic reserves are more costly to produce than structural biomass (Brett & Groves 1979), this plasticity in energy allocation strat-egy suggests that YOY *C. regalis* are able to maintain high TAG benefit even in years where physiological suitability is low or ecological processes limit resource availability within Delaware Bay.

CONCLUSIONS

For ontogenetic shifters, i.e. species exhibiting multiple habitat, diet, and behavioral shifts during their early life history (Adams et al. 2006), a growing body of work calls for the evaluation of nursery func-tion in the context of the habitats that are functionally connected through their movements over the period of estuarine residency (Beck et al. 2001, 2003, Wein-stein et al. 2005, Sheaves et al. 2006, Sheaves 2009, Weinstein et al. 2014, Nagelkerken et al. in press).

Our approach, on a broad spatial scale, achieves this for YOY *Cynoscion regalis* in Delaware Bay by considering their physiological condition in the con-text of habitat utilization patterns inferred from iso-topic analysis. With this approach, we demonstrated that during the period of estuarine residency, both the habitats utilized by YOY *C. regalis* and large-scale inter-annual variability can affect their condi-tion and preparedness for the rigors of migration and over-wintering. However, we caution that for species in seasonal environments, such as *C. regalis*, metrics of condition examining energetic reserves, particu-larly lipid stores, must be considered in the context of energetic tradeoffs with somatic growth and the rel-ative value of these reserves in mitigating the poten-tial for over-winter starvation (Post & Evans 1989, Shuter & Post 1990, Mogensen & Post 2012).

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