

# Mummichog *Fundulus heteroclitus* responses to long-term, whole-ecosystem nutrient enrichment

Konner C. Lockfield<sup>1</sup>, John W. Fleeger<sup>1\*</sup>, Linda A. Deegan<sup>2</sup>

<sup>1</sup>Department of Biological Sciences, Louisiana State University, Baton Rouge, Louisiana 70803, USA

<sup>2</sup>The Ecosystems Center, Marine Biological Laboratory, Woods Hole, Massachusetts 02543, USA

**ABSTRACT:** The effects of eutrophication on coastal plants and sessile animals are becoming well known, but responses of mobile species are less well studied. Here, we link variation in abundance, biomass, body size, growth rate, and resource utilization in mummichogs *Fundulus heteroclitus* >40 mm in length to experimental nutrient enrichment in Plum Island Sound, Massachusetts, USA. To mimic cultural eutrophication, dissolved fertilizer was released into replicate saltmarsh creeks on each rising tide throughout entire growing seasons. In the summer of the sixth year of enrichment, we released coded-wire tagged mummichogs into nutrient-enriched (n = 3733 fish) and reference (n = 3894 fish) creeks and recaptured them over the next 2 mo. We found increased abundance (by 37%), biomass (58%), body size (8%), and herbivory (115%, measured as photosynthetic gut pigment content) in nutrient-enriched creeks, although body condition was unaffected. However, individual growth rates were 43% lower in nutrient-enriched creeks. Nutrient enrichment stimulated primary production, causing a bottom-up enrichment of the food web which fostered increased biomass and body size. However, the reduction in growth rate indicates an adverse consequence of long-term nutrient enrichment. This negative effect occurred in the absence of increased hypoxia in these highly tidally (4 m amplitude) flushed study creeks. The mummichog is an important predator/grazer in salt marshes, and nutrient-induced alterations in biomass or resource utilization will directly or indirectly affect lower trophic levels, including benthic algae, thereby impacting the ecosystem-wide response to eutrophication.

**KEY WORDS:** *Fundulus heteroclitus* · Mark and recapture · Eutrophication · Decimal coded-wire tags · Growth rate · Salt marsh

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## INTRODUCTION

An accelerated global nitrogen cycle has more than doubled the flow of nitrogen from terrestrial to coastal marine ecosystems (Vitousek et al. 1997, Galloway et al. 2008, Canfield et al. 2010), contributing to increased nutrient loads in estuaries (Deegan et al. 2012). As a result, cultural eutrophication has become widespread, and nearly 70% of North American estuaries have been classified as moderately to highly eutrophic (NOAA 1999). Eutrophication leads to degraded environmental conditions including the loss of submerged vegetation, harmful algal blooms,

changes in primary producer communities, dietary changes in consumers, habitat loss, excess carbon production, and oxygen depletion (Deegan 2002, Valiela et al. 2004, Powers et al. 2005, Diaz & Rosenberg 2008, Conley et al. 2009). Estuarine salt marshes provide important ecological and economic services including nutrient removal, storm protection for coastal cities, carbon sequestration, and habitat provisioning for numerous species of fish, birds and invertebrates (Barbier et al. 2011). Many of the services that may be disrupted or altered by eutrophication support higher trophic levels (e.g. including mobile species associated with fisheries).

\*Corresponding author. Email: zoflee@lsu.edu

Many studies detail the responses of plant and benthic communities to eutrophication, and effects on abundance, community structure, species composition, diet, and growth allocation are becoming well documented (Khan & Ansari 2005, Darby & Turner 2008, Fleeger et al. 2008, McFarlin et al. 2008, Turner et al. 2009, Gedan et al. 2011, Johnson 2011, Fox et al. 2012). However, less is known about the responses of nekton (Breitburg 1992, Deegan 2002, Essington & Paulsen 2010). Eutrophication may have highly disparate effects on nekton. One alternative is that the abundance or production of nekton may be reduced by nutrient-enrichment effects on habitat quality or by oxygen depletion (Eby et al. 2005, Valiela et al. 2004). Another alternative is that increases in nekton abundance from elevated primary production and stimulated food webs may accompany eutrophication in the absence of hypoxia (Nixon & Buckley 2002, Breitburg et al. 2009).

Although nutrient enrichment may increase nekton abundance in the short term, long-term ecological impacts, especially in the absence of hypoxia, are poorly understood. For example, increased abundance associated with eutrophication may lead to indirect effects through density-dependent increases in intraspecific competition (Rose et al. 2001). Weisberg & Lotrich (1986) showed that, with no increase in food availability, a doubling of population density in mummichog *Fundulus heteroclitus* led to a 50% decrease in growth rate and that a 4-fold increase in population size led to increased mortality, indicating that increased abundance may initiate cascading effects on populations. However, nutrient enrichment may also alter food resources, and resource utilization and population responses should therefore both be examined in order to elucidate the mechanisms by which nekton respond to eutrophication.

Mummichog is a small killifish (15 to ~120 mm total length, TL) that comprises a high proportion of the numbers and biomass of nekton communities in US Atlantic coast salt marshes (Kneib & Stiven 1982, Kneib 1986, Allen et al. 1994, Deegan et al. 2007). Mummichogs are opportunistic omnivores. Juveniles feed on plant material, benthic microalgae, detritus, and small benthic invertebrates, while adults (~40 mm TL and greater) consume macroalgae, grass shrimp *Palaeomonetes pugio*, amphipods, snails,

and smaller fish (including juvenile mummichogs) (Kneib & Stiven 1978, Allen et al. 1994, Currin et al. 2003). Mummichogs contribute to top-down regulation of benthic algal and benthic invertebrate communities and may have profound effects on ecosystem structure and function (Kneib 1986, Allen et al. 1994, Sardá et al. 1998, Deegan et al. 2007, Johnson et al. 2009). Furthermore, the mummichog is considered a sentinel of environmental health in estuaries (Weis et al. 2001, Finley et al. 2009).

We report here the results of an ecosystem-scale manipulation experiment and a tag and recapture study of mummichogs conducted in tidal creeks experiencing long-term nutrient enrichment. To rigorously quantify responses to nutrient enrichment at a single point in time, estimates of abundance, body size, biomass, individual growth rate, resource utilization (i.e. herbivory), and body condition were made over a 2 mo period in the summer of the sixth year of nutrient enrichment.

## MATERIALS AND METHODS

### Study site and nutrient enrichment

Our research is part of the TIDE project (Trophic cascades and Interacting control processes in a Detritus-based aquatic Ecosystem) conducted in the Plum Island Estuary (PIE), Massachusetts, USA (Fig. 1, 42.45° N, 70.52° W) (Deegan et al. 2007, 2012). PIE's salt marshes are typical of New England (Niering &

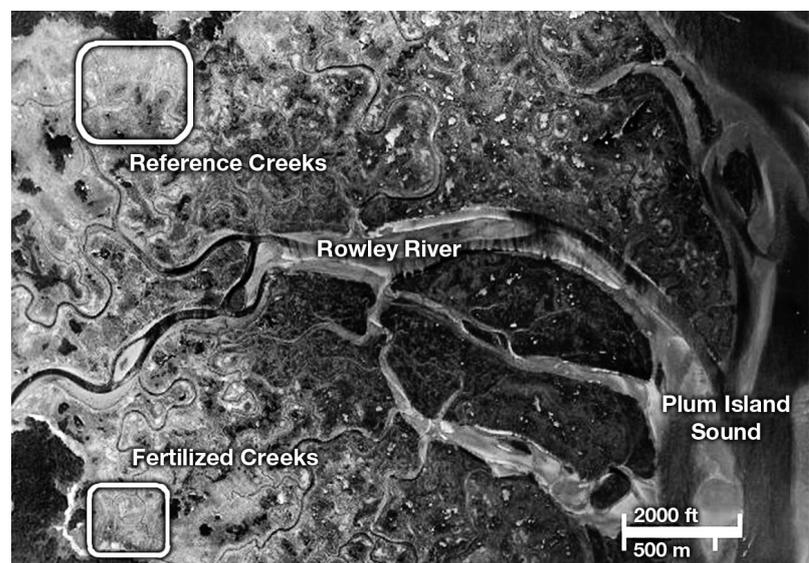


Fig. 1. Aerial photo of the study site, located in the Rowley River drainage which drains into the Plum Island Sound in northeastern Massachusetts, USA

Table 1. Physical characteristics of study creeks. Creek dimensions and measurements from Johnson et al. (2007). Each creek was divided into 2 similar creek reaches for fish collections

Creek	Total watershed area (m <sup>2</sup> × 10 <sup>4</sup> )	Linear distance (m)	Distance from Rowley River (km)	Distance from Plum Island Sound (km)	Volume (l × 10 <sup>6</sup> )	Cross-sectional area (m <sup>2</sup> )
Reference 1	6.01	260	1.28	3.74	1.37	5.27
Reference 2	5.32	230	1.43	3.89	2.04	8.89
Fertilized 1	5.91	300	1.31	4.43	3.73	12.42
Fertilized 2	6.59	335	1.31	4.43	3.59	10.73

Warren 1980), and are characterized by ubiquitous 3 to 4 m wide bands of *Spartina alterniflora* along creek low marsh edges and mosquito ditches. The high marsh consists of expansive areas of *Spartina patens* and permanently flooded saltmarsh ponds. Tidal amplitudes reach ~4 m during spring and ~2 to 3 m during neap tides, and all creek water drains into Plum Island Sound at low tide. Mummichogs have access to the flooded marsh on spring high tides, and move locally between interconnected creeks, ditches, ponds, and small isolated pools that retain creek water (Sweeney et al. 1998, Corman & Roman 2011, Able et al. 2012).

Four first-order saltmarsh creeks were selected because of their similarities in physical characteristics (e.g. size, substrate, tidal amplitude, and physiognomy, Table 1) as well as vegetation, fauna, and plant and animal zonation (Johnson et al. 2007). Since 2004, 2 of these creeks have been nutrient enriched daily during entire growing seasons (from approx. May 1 to September 15) at target concentrations in flooding creek water of 50 to 70  $\mu\text{mol NO}_3^- \text{l}^{-1}$  and 4  $\mu\text{mol PO}_4^{3-} \text{l}^{-1}$  (Deegan et al. 2007). These concentrations are consistent with those in estuaries experiencing moderate to high eutrophication (NOAA 1999, EPA 2002, Deegan et al. 2012). The other 2

creeks have served as unmanipulated references (Fig. 2) with background concentrations of ~3.5  $\mu\text{mol NO}_3^- \text{l}^{-1}$  and ~0.9  $\mu\text{mol PO}_4^{3-} \text{l}^{-1}$  (Deegan et al. 2007). No change in the patterns of dissolved oxygen concentration has been observed in TIDE reference or nutrient-enriched creeks over the course of nutrient manipulation (L. A. Deegan unpubl. data).

#### Abundance and density estimates

Each nutrient-enriched and reference creek was divided into 2 reaches of approximately equal length (Fig. 2) to examine patterns at a finer spatial scale and to coordinate with routine fish monitoring using flume nets (see below). To estimate abundance, biomass, body size and growth rates, mummichogs were captured, tagged and released daily in each creek reach from July 7 to 17 (Table 2), and then recaptured from July 27 to September 15, 2009.

A total of 7828 fish were captured for tagging on ebbing tides using standard minnow traps. The 2-piece traps were torpedo-shaped, 49.1 cm in length and 22.9 cm in diameter, with 2.5 cm openings on both ends. The trap's 0.6 mm mesh most efficiently retains mummichogs >40 mm TL (Kneib & Craig 2001, L. A. Deegan unpubl. data). No population information was collected during initial capture. After transport to a nearby field laboratory, fish were anesthetized with clove oil, measured ( $\pm 1$  mm TL), individually marked with sequential coded-wire tags (Northwest Marine Technology), and held at least 2 h in aerated tanks to allow for recovery. The size range of tagged fish was 31 to 113 mm TL with a median length of 54 mm (Fig. 3). Fish that died during the recovery period were enumerated and removed. Mortality was 2.5% (Lockfield 2011), and a total of 7627 tagged fish were re-

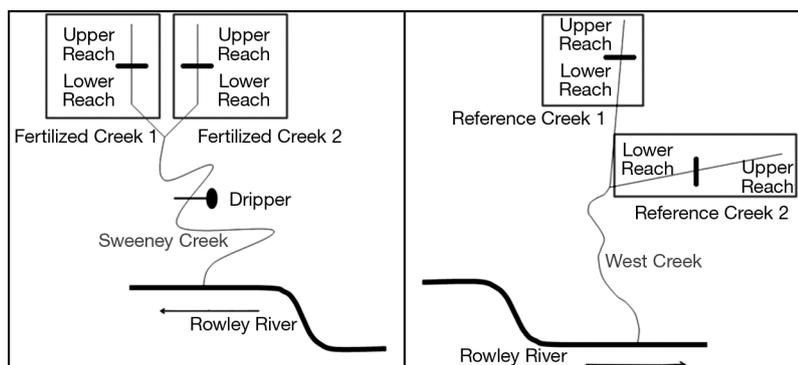


Fig. 2. Schematic of TIDE experimental creeks, which were divided into upper and lower reaches for each creek. The dripper is the fertilizer application point for the nutrient-enriched creek

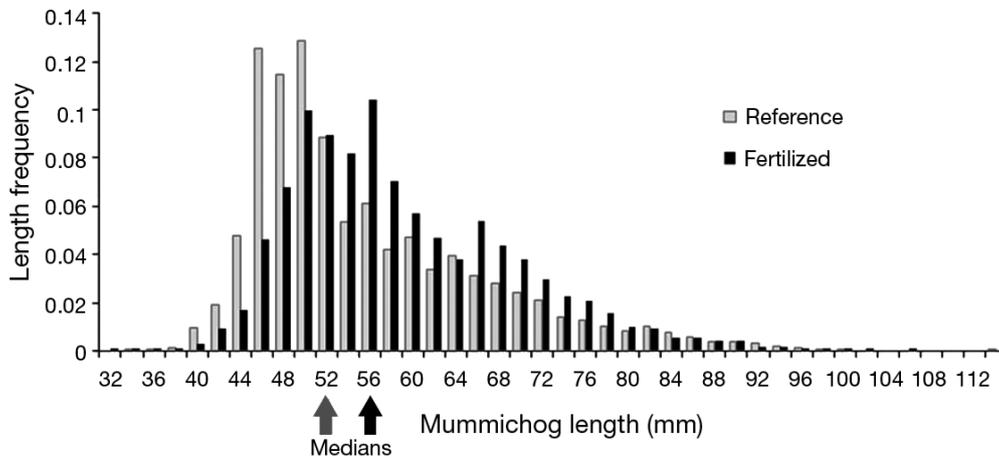


Fig. 3. Mummichog length-frequency distributions in reference ( $n = 4003$ ) and nutrient-enriched ( $n = 3825$ ) creeks of fish tagged for release. Arrows indicate the median length in the reference and nutrient-enriched creeks. Mortality of tagged fish was 2.5%; 3894 tagged fish were released into reference and 3733 tagged fish were released into nutrient-enriched creeks

Table 2. Number of fish tagged and released each day during the mark and recapture study; dates are given as mo/d/yr

Date	Nutrient treatment	Replicate	Reach	No. of fish released
7/7/09	Reference	1	Upper	523
7/8/09	Reference	1	Lower	277
7/8/09	Reference	2	Upper	615
7/9/09	Reference	1	Lower	558
7/9/09	Reference	2	Lower	503
7/10/09	Fertilized	1	Upper	530
7/10/09	Fertilized	2	Lower	555
7/13/09	Fertilized	1	Lower	518
7/13/09	Fertilized	2	Upper	498
7/14/09	Fertilized	1	Upper	465
7/14/09	Fertilized	2	Lower	266
7/14/09	Fertilized	2	Upper	163
7/15/09	Fertilized	1	Lower	338
7/15/09	Fertilized	2	Upper	400
7/16/09	Reference	1	Upper	467
7/16/09	Reference	1	Lower	256
7/16/09	Reference	2	Lower	400
7/17/09	Reference	2	Upper	295
Total				7627

leased; 3733 into nutrient-enriched and 3894 into reference creeks (Table 2). Tagged fish were released at high tide into the same creek reach where they were captured. After a minimum of 10 d from the last release, fish were recaptured and examined in the field for tags by passing fish through a Northwest Marine Technology V-Detector.

Marked and unmarked mummichogs were enumerated upon capture in standard minnow traps during the first 2 wk of the recapture period to estimate abundance in each creek reach using the Lincoln-

Peterson method (Seber 1973). Between 12 and 20 minnow traps were placed evenly across each creek reach and fished for varying periods of time on ebbing tides, and each creek reach was sampled every 1 to 3 d. Marked fish were removed from the population for growth analysis. Non-marked fish were returned to the population. Recapture rates were calculated as the percentage of recaptured fish from the number of tagged fish released into each creek reach. Prior work at our study site (Sweeney et al. 1998) and with coded-wire tags in mummichogs (Able et al. 2006, Kneib 2009) indicate assumptions were reasonably met (i.e. a closed population, an equal probability of capture of marked and unmarked fish, equal mortality of marked and unmarked fish, and complete mark retention). Abundance from each minnow-trap collection was estimated and averaged to generate a creek-reach mean (mummichogs creek reach<sup>-1</sup>) and 95% confidence interval following Able et al. (2006) and Kneib (2009). However due to a low resampling efficiency in the upper reach of fertilized Creek 1 (<5% of the marked fish were recaptured), abundance in only 7 creek reaches was estimated (Table 3). High variation in resampling efficiency appears to be common with mummichogs (Kneib 2009), and the investigator travel time to the upper reach of fertilized Creek 1 was the greatest among the reaches, reducing available sampling time on each visit. Abundance for each creek (mummichogs creek<sup>-1</sup>) as a whole was estimated by combining data from both reaches of the same creek.

As part of TIDE's long-term, routine monitoring program, flume nets were deployed monthly to esti-

Table 3. Recapture rates, abundance estimates and 95% confidence intervals of each creek reach derived from the mark and recapture study. Not applicable (NA)

Creek	Replicate	Reach	Recapture rate (%)	Abundance estimate	95% Confidence Interval
Reference	1	Upper	17.1	13315	8576–18054
Reference	1	Lower	17.1	17371	12552–22190
Reference	2	Upper	12.8	22069	16674–27464
Reference	2	Lower	14.6	14196	10569–17823
Fertilized	1	Upper	NA	NA	NA
Fertilized	1	Lower	8.5	27113	19302–34924
Fertilized	2	Upper	11.2	27744	21255–34233
Fertilized	2	Lower	11.7	25398	17006–33790

mate the density of mummichogs utilizing the flooded marsh during nighttime spring high tides. Flume nets were built on the high marsh platform at the *Spartina alterniflora*-*S. patens* interface (i.e. flume nets were placed 2 m from the marsh edge and included *S. alterniflora* and *S. patens*). Two replicate flume nets (2 m in width, 5 m in length and with 4.76 mm mesh sides) were fished in each creek reach on one night during the first 2 wk of the mummichog recapture period, and data were used to compare with mark-recapture results. Mummichogs were enumerated, measured ( $\pm 1$  mm TL), and individually weighed (wet weight,  $\pm 0.09$  g). Previous research in PIE indicates that flume nets retain juvenile mummichogs  $\sim 20$  mm TL and greater (L. A. Deegan unpubl. data). Densities (mummichogs  $m^{-2}$ ) for 2 size classes ( $\geq 20$  and  $\geq 40$  mm TL) were calculated for each creek reach ( $n = 2$ ) by dividing the number of fish trapped of the appropriate size range by the area sampled by the flume net.

Mark-recapture abundance (mummichogs creek $^{-1}$ ) estimates were converted to density (mummichogs  $m^{-2}$ ) using the watershed area (defined as the marsh area covered by water during spring high tides) for each creek (Table 1). The watershed area of each creek reach was not known with confidence, and creek-reach density was not calculated by mark-recapture methods (but was estimated from flume net data collected in each reach). Error terms and degrees of freedom in comparisons among creeks were based on creek-level replication (2 nutrient-enriched and 2 reference creeks). All error terms throughout the text are standard deviations based on variation between the 2 replicate creeks unless otherwise noted. *t*-tests compared fish densities in nutrient-enriched ( $n = 2$ ) and reference creeks ( $n = 2$ ) estimated from mark-recapture data and from flume-net data. Independent population estimates in each

creek reach were available from the mark and recapture study (as abundance of fish  $> 40$  mm TL in the watershed) and from flume-net samples (as density of fish  $\geq 40$  mm TL utilizing the flooded marsh) from the same time period. They were compared with Spearman's rank correlation coefficient ( $n = 7$ ).

### Body size, biomass and growth rate

Mummichog length-frequency distributions were derived from tagged fish (Fig. 3). Length distributions from nutrient-enriched ( $n = 3825$  fish) and reference ( $n = 4003$  fish) creeks were asymmetric (i.e. skewed to the right), and distributions were compared using a 2-sample Kolmogorov-Smirnov test.

Biomass (mg dry wt  $m^{-2}$ ) was also estimated from tagged fish. The length for each fish was converted to wet weight from a length-weight regression (where  $\log_{10}$  wet weight =  $2.874 \times \log_{10}$  length - 4.7432;  $R^2 = 0.8751$ ) determined from measurements of 450 fish collected during the recapture period. A wet to dry conversion factor (0.234) was used to estimate dry weight. Biomass in each creek was determined by multiplying the mean dry weight individual $^{-1}$  in a creek by the density (mummichogs  $m^{-2}$ ) estimated by mark-recapture for that creek. A *t*-test was used to compare biomass in nutrient-enriched ( $n = 2$ ) and reference treatments ( $n = 2$ ).

Individual growth rates were determined on tagged fish captured from throughout the recapture period (333 tagged fish were recovered in nutrient-enriched, and 570 were recovered in reference creeks). Each fish was processed by recording its length and wet weight as above, and the coded-wire tag was recovered from the dorsal musculature and read. Archived data were accessed to retrieve the initial length of each recovered fish. Growth rate was calculated by the equation:

$$GR = (L_1 - L_0) / (T_1 - T_0) \quad (1)$$

where GR is the growth rate of each individual fish,  $L_0$  is the initial length,  $L_1$  is the recovered length,  $T_0$  is the Julian date marked, and  $T_1$  is the date recovered (Teo & Able 2003, Hagan et al. 2007). Growth rate was analyzed by 3 methods. (1) A *t*-test employing fish of all sizes was used to compare average growth rates between nutrient-enriched ( $n = 2$ ) and reference treatments ( $n = 2$ ). (2) Data

from fish of all sizes were fitted to a growth model to test for a difference between growth coefficients ( $k$ ) for all sizes. This method eliminates bias that may be present if fish size differed among the sampling units because older, larger fish grow slower than younger, smaller fish (Teo & Able 2003). Growth rates in creeks with and without nutrient enrichment were compared using a model selection process; data were fit to the Gompertz, Von Bertalanffy and logistic growth models. All 3 models yielded similar results but the highest goodness of fit was achieved with the Gompertz model. To test for an effect of nutrient treatment, the 95% confidence intervals of the calculated difference of the Gompertz growth coefficients ( $K_{\text{DIFF}}$ ) were analyzed. A difference in growth rate was accepted if the 95% confidence intervals of  $K_{\text{DIFF}}$  between the nutrient-enriched and reference creeks did not include 0. (3) To more finely examine variation in growth rate associated with variation in body size, individual growth rates were calculated separately for sizes greater than or equal to and less than the median length (54 mm TL) of tagged mummichogs.

Linear regression was used to test for density-dependent effects on mummichog growth rate. A standardized growth rate, obtained by dividing the individual growth rate by the length cubed of the same fish, was used to account for age-biased growth. Density of mummichogs  $\geq 40$  mm TL from flume-net samples from each creek reach (creek-reach density data were unavailable from the mark-recapture study) was used as the independent variable, and mean standardized growth rate from the same creek reach was used as the dependent variable ( $n = 8$ ).

### Condition

Fulton's condition factor was also measured on recaptured mummichogs ( $n = 903$ ). Condition factor was calculated following Nash et al. (2006) and Mustac & Sinovic (2010):

$$K = (W_g / L_{\text{mm}}^3) \times 100\,000 \quad (2)$$

where  $K$  is condition,  $W_g$  is the weight in grams, and  $L_{\text{mm}}$  is the total length in millimeters. A  $t$ -test was used to compare condition factor among the nutrient-enriched ( $n = 2$ ) and reference creeks ( $n = 2$ ). Linear regression was used to test for density-dependent effects on condition by comparing fish density (mummichogs  $\geq 40$  mm TL from flume-net samples) with mean fish condition among the creek reaches ( $n = 8$ ).

### Herbivory

Photosynthetic gut pigment content was measured as a proxy of herbivory in selected mummichogs collected during the recapture period from nutrient-enriched ( $n = 48$  fish with a range of 42 to 83 mm TL and a mean TL of  $60.0 \pm 9.4$  mm) and reference creeks ( $n = 128$  with a range of 30 to 91 TL and a mean TL of  $52.8 \pm 9.6$  mm). Fish collected in standard minnow traps fished for  $\leq 30$  min on the falling tide were selected for this analysis. Fish were placed on dry ice in the field, and stored at  $-80^\circ\text{C}$  until processed. Each fish was thawed and the stomach was removed after measuring fish length as above. Stomach contents were rinsed into a 50 ml tube, acetone was added to achieve a 75% acetone:water ratio, and samples were refrigerated overnight (16 to 20 h). The next day, after reaching room temperature, tube contents were centrifuged, and the fluid decanted and filtered with  $0.22 \mu\text{m}$  diameter nylon filters. Pigment concentrations were measured using a Turner model 10 fluorometer before and after acidification, and values were converted into  $\mu\text{g}$  chlorophyll  $a$  (chl  $a$ ) fish $^{-1}$  and  $\mu\text{g}$  phaeopigment fish $^{-1}$  and then standardized by fish length cubed for statistical analysis. The ratio of chl  $a$ :phaeopigment for each fish (Fleeger et al. 1999) was also calculated.  $t$ -tests without creek-level replication (fish from replicate creeks were pooled because of an unbalanced sample size per creek) were used to compare standardized photosynthetic gut pigment content and the ratio of chl  $a$ :phaeopigment in nutrient-enriched and reference creeks.

### RESULTS

One tagged and recaptured mummichog was 39 mm TL at the time of release; all other recaptured fish were  $>40$  mm at the time of release. Minnow traps used to collect fish for tagging and for recapture rarely captured fish  $<40$  mm TL (33 out of the 7828 fish tagged were  $<40$  mm TL). Thus, data derived from the mark-recapture study most effectively assessed abundance and growth rate of mummichogs  $>40$  mm TL.

### Abundance and density

A total of 903 released fish were recaptured. Recapture rates varied from 8.5 to 17.1% among creek reaches, and overall 12.8% were recaptured (Table 3). About 80% of the fish were recovered in

the same reach where released; 16% were recovered in the adjacent reach. Although 3.7% of the mummichogs moved to a nearby study creek, no mummichogs moved between the nutrient-enriched and reference creeks. The mean TL at the time of release for recaptured fish was  $56.4 \pm 10.7$  in reference creeks and  $59.0 \pm 9.9$  mm in nutrient-enriched creeks. Recaptured mummichogs in reference creeks exhibited a mean TL of  $59.4 \pm 10.2$ , and recaptured fish in nutrient-enriched creeks had a mean TL of  $62.1 \pm 9.7$  mm. The initial range in TL (i.e. when tagged) of the mummichogs we recaptured was 39 to 98 mm, and length at the time of recapture ranged from 42 to 98 mm.

Estimates of mummichog abundance were based on successive recaptures derived from mark-recapture data, and means varied from 13 315 to 27 744 mummichogs per creek reach,  $\pm 3600$ – $8000$  (95% confidence intervals) (Table 3). Mean whole-creek density was  $0.59 \pm 0.07$  mummichogs  $m^{-2}$  in reference creeks, while fertilized creeks averaged  $0.81 \pm 0.04$  mummichogs  $m^{-2}$ . This 37% higher abundance in the nutrient-enriched creeks was marginally significant ( $df = 2$ ,  $t = 4.07$ ,  $p = 0.055$ ).

Flume-net derived estimates of the density of mummichogs  $\geq 40$  mm TL from the high marsh in fertilized creeks averaged  $0.35 \pm 0.16$  compared to  $0.15 \pm 0.14$  mummichogs  $m^{-2}$  in reference creeks, but densities did not differ statistically ( $df = 2$ ,  $t = -1.60$ ,  $p = 0.251$ ). Flume-net derived mean density estimates of mummichogs  $\geq 20$  mm TL were  $0.39 \pm 0.47$  in reference compared to  $0.85 \pm 0.39$   $m^{-2}$  in fertilized creeks. This difference also was not significant ( $df = 2$ ,  $t = -1.57$ ,  $p = 0.258$ ). The abundance estimated from the mark-recapture study (mummichogs  $> 40$  mm TL creek reach $^{-1}$ ) and density of mummichogs (mummichogs  $\geq 40$  mm TL  $m^{-2}$ ) estimated from flume nets followed similar trends among the creek reaches. These 2 independent estimates were positively correlated and marginally significant (correlation coefficient = 0.71;  $p = 0.055$ ).

### Body size, biomass, and growth rate

The Kolmogorov-Smirnov test indicated that mummichog length distributions in tagged fish were significantly different in reference and nutrient-enriched creeks (Fig. 3; Kolmogorov-Smirnov  $K_s = 8.97$ ,  $p < 0.001$ ). Nutrient-enriched creeks had a higher proportion of larger fish than reference creeks.

Mummichog biomass was significantly higher in fertilized creeks ( $df = 2$ ,  $t = 5.47$ ,  $p = 0.031$ ). Biomass in

reference creeks averaged  $272.72 \pm 12.71$ , and biomass averaged  $445.23 \pm 40.34$  mg dry wt  $m^{-2}$  in nutrient-enriched creeks.

Across all sizes, mean linear mummichog growth rates ( $0.103 \pm 0.085$  mm  $d^{-1}$  in reference creeks and  $0.072 \pm 0.065$  mm  $d^{-1}$  in fertilized creeks) were significantly faster in reference creeks ( $df = 2$ ,  $t = 6.44$ ,  $p = 0.023$ ). For mummichogs  $< 54$  mm TL (the median length of tagged fish), growth rate averaged 0.123 in reference and 0.083 mm  $d^{-1}$  in nutrient-enriched creeks. For mummichogs  $\geq 54$  mm TL, the mean growth rate was 0.080 in reference and 0.066 mm  $d^{-1}$  in nutrient-enriched creeks.

Growth rate was inversely related to initial length for recaptured mummichogs (based on linear regression, where growth rate =  $-0.0025 \times$  initial length + 0.2358;  $R^2 = 0.1088$ ,  $p < 0.001$ ). Mummichog growth data were therefore fitted to a Gompertz growth model to remove this length-growth rate bias. Reference creeks had a Gompertz growth coefficient of  $0.0041 \pm 0.0003$  and fertilized creeks had a growth coefficient of  $0.0029 \pm 0.0004$ . The calculated difference,  $K_{DIFF}$  (=0.0012), had 95% asymptotic confidence intervals that did not include 0 ( $-0.0021$ ,  $-0.0005$ ); therefore, we concluded that the growth coefficients of the 2 treatments were different and that faster growth rate occurred in the reference creeks. Finally, standardized growth rate decreased as the density of mummichogs increased among the creek reaches (Fig. 4). This relationship was significant (based on linear regression, where standardized growth rate =  $-0.1149 \times$  density + 0.0875;  $R^2 = 0.7927$ ,  $df = 7$ ,  $p = 0.003$ ).

### Condition

Mean condition factor did not differ between reference ( $1.32 \pm 0.23$ ) and nutrient-enriched creeks ( $1.27 \pm 0.13$ ) ( $df = 2$ ,  $t = 1.55$ ,  $p = 0.262$ ). Furthermore, condition did not vary with mummichog density (based on linear regression, where condition =  $-0.1738 \times$  density + 1.344,  $R^2 = 0.2345$ ,  $df = 7$ ,  $p = 0.224$ ).

### Herbivory

Mean gut pigment content ( $\mu\text{g chl } a \text{ fish}^{-1}$ ) was  $5.20 \pm 10.30$  in reference and  $21.91 \pm 28.21$  in nutrient-enriched creeks. Standardized chl *a* gut content (data not shown) differed between nutrient-enriched and reference creeks ( $t = -3.71$ ,  $p < 0.001$ ). Phaeopigment

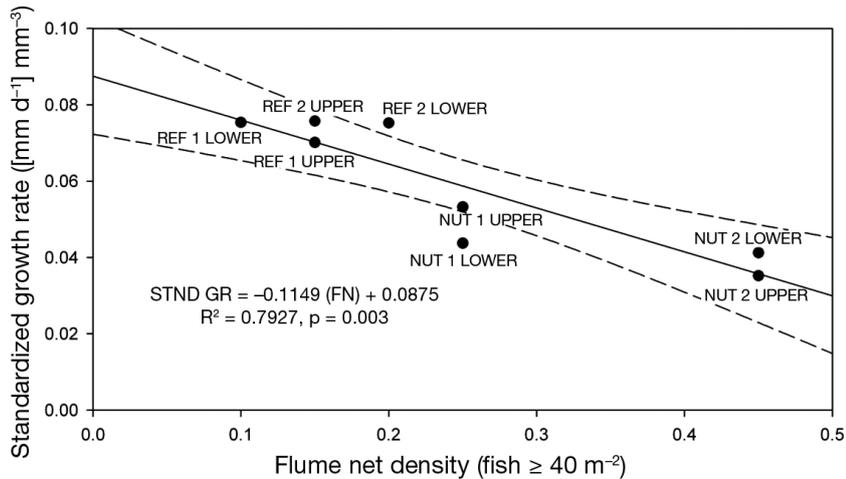


Fig. 4. Relationship between mummichog density (mummichogs  $\text{m}^{-2}$  from flume-net [FN] samples) and standardized growth rate. Standardized growth rates are equal to growth rate expressed as  $\text{mm d}^{-1}$  divided by fish length cubed. The solid line is the best fit linear regression line and the dotted lines are the 95% confidence intervals ( $n = 8$ ). Symbols are coded to identify specific creek reaches (see Table 3)

gut content was consistently lower than chl *a* in the same fish, and averaged  $2.47 \pm 5.54$  in reference creeks and  $4.07 \pm 4.79 \mu\text{g fish}^{-1}$  in nutrient-enriched creeks. The ratio of chl *a*:phaeopigment was significantly higher ( $t = -2.56$ ,  $p = 0.014$ ) in nutrient-enriched creeks and averaged  $1.23 \pm 1.80$  in reference and  $2.64 \pm 3.38$  in nutrient-enriched creeks.

## DISCUSSION

Mummichog responses in the sixth year of creek-level nutrient enrichment were complex, and positive and negative impacts were both observed. Population biomass and individual body size were higher with nutrient enrichment, although individual growth rates were lower during the 2 mo summer study period, without change in fish condition. Nutrient enrichment also altered resource utilization as indicated by our proxy (gut photosynthetic pigment content) for herbivory, which indicated a greater use of algal resources in nutrient-enriched creeks. It is unlikely that migration contributed to, or diluted, the observed differences among creeks because mummichogs are well known to exhibit high site fidelity (Sweeney et al. 1998, Hagan et al. 2007, Able et al. 2006). Fewer than 4% of mummichogs moved from one creek to another creek nearby, and none moved between the reference and nutrient-enriched creeks, a distance of about 1.5 km.

The median length of the fish we tagged was 54 mm TL, and recaptured tagged fish ranged in

length from 42 to 98 mm. Previous research on mummichogs indicates this size range includes juveniles (i.e. young-of-the-year) and mummichogs in the second year of life (Teo & Able 2003, Hagan et al. 2007). Although mummichogs are known to experience high summer growth rates (Teo & Able 2003), the growth potential during our recapture period likely differed in the 2 age classes. On average, juveniles spawned in the spring or early summer should grow faster in the first half of the summer and more slowly in the second half as they reach maturity and begin to reproduce. Second-year fish grow more slowly (Teo & Able 2003), and, as adults, likely grow at a more similar rate throughout the growing season.

Although the 2 mo study period represents about a third of the growing season and about 10% of the lifespan of mummichog, this length of time has been shown to be effective at identifying differences in growth rate across marsh landscapes (Kneib 2009). Furthermore, routine monitoring by the TIDE project based on length-frequency distributions taken monthly during the summer over several years indicates broadly similar growth rates,  $\sim 0.1 \text{ mm d}^{-1}$ , and that growth rate is consistent throughout the summer period for second-year mummichogs (J. A. Nelson & L. A. Deegan unpubl. data). Our research indicated that growth rates were lower in nutrient-enriched creeks compared to reference creeks in both age classes by a similar amount (for fish  $< 54 \text{ mm}$ , mean individual growth in the nutrient-enriched creek was less by  $0.0402 \text{ mm d}^{-1}$  and for fish  $\geq 54 \text{ mm}$ , the difference was less by  $0.0140 \text{ mm d}^{-1}$ ). These observations suggest that our methods yielded findings consistent with patterns of growth throughout the growing season in our experimental creeks and across the size range of mummichogs studied. However, it is possible that differences in growth rates associated with nutrient enrichment occurred during or just prior to our study, and thus growth rates may be indicative of the particular period in time during which the study was conducted.

The increased individual body size and higher population biomass of mummichogs in the nutrient-enriched creeks can be traced to a bottom-up stimulation of the food web induced by nutrient enrichment. Nitrogen and phosphorous enrichment stimulates benthic algae (Elser et al. 2007) which in

turn stimulates infaunal and epibenthic invertebrates (Posey et al. 1999, 2002, Johnson 2011, Johnson & Short 2012). Benthic algae and infaunal and epifaunal invertebrates all serve as food resources for mummichogs (Allen et al. 1994). Mummichogs consumed more benthic algae in nutrient-enriched creeks as measured by photosynthetic gut pigment content. Johnson & Fleeger (2009) found that nutrient enrichment led to an increase in the biomass and body size of some infaunal invertebrates, and Johnson (2011) and Johnson & Short (2012) found that nutrient enrichment stimulated the abundance and biomass of epifaunal amphipods, isopods, and snails. The mummichog is an opportunistic omnivore and a highly flexible diet should allow it to take advantage of a stimulation of several components of the food web.

Individual growth rates, however, revealed that environmental quality at the time of the study was reduced by long-term nutrient enrichment. Mummichog growth rates based on length were significantly lower (by 43%) in fertilized creeks. However, fish condition, based on individual length and weight, was equivalent in all creeks. High condition factor values are generally associated with more robust fish (Nash et al. 2006), and condition values in PIE were similar to or higher than those found in other studies with mummichogs (McMullin et al. 2009), suggesting all experimental creeks provided a high-quality habitat for mummichogs. If bottom-up effects led to an increased quality or supply of food as anticipated, condition would be expected to be higher in the nutrient-enriched creeks. However, the allocation of biomass in fishes to length or body mass varies with environmental conditions such as food supply and season (Rikardsen & Elliott 2000). For example, fish on a low-quality diet may maximize an energy storage strategy over a growth maximization strategy (and thus allocate more growth to body mass over increases in length, Post & Parkinson 2001). Furthermore, life history constraints in mummichogs may dictate a tradeoff between growth in terms of length (increased length may contribute to a reduction in predation) balanced against lipid storage needed to survive the winter. Fish in nutrient-enriched creeks may therefore have differed in their absolute growth rate and/or the way they allocated growth. The high condition factor but low growth rate in mummichogs in nutrient-enriched creeks could therefore have been a function of growth allocation. Alternatively, reductions in growth rate may have occurred due to a recent reduction in habitat quality before a change in condition could be manifested. Below, we discuss

some of the ways that nutrient enrichment may reduce environmental quality or affect mummichog abundance, diet, or behavior and contribute to reduced or altered growth. These effects took place in the absence of nutrient-induced oxygen depletion in our tidally flushed study creeks.

Density-dependent effects via intraspecific competition may have contributed to the lower growth rate in nutrient-enriched creeks. Mummichogs were present in higher abundance and biomass in fertilized creeks, which could lead to increased competition for food. Weisberg & Lotrich (1986) found that a doubling of the population density of mummichogs led to a 50% reduction in growth rate due to reductions in the amount of food per fish. Growth rates would slow in the nutrient-enriched creeks if the negative effects of increased competition outweighed the positive effects of nutrient enrichment on resource quantity and quality. The magnitude of higher abundance (37%) and lower growth rate (43%) in nutrient-enriched creeks indicates a density-dependent response similar to that found by Weisberg & Lotrich (1986), and suggests little, if any, net resource benefit to mummichogs was gained from nutrient enrichment at the time of the study. Strong support for the importance of intraspecific competition as a cause of the decreased growth rates comes from our observation that mummichog growth rate decreased significantly with increasing mummichog density among the creek reaches (Fig. 4). However, fish condition did not vary with mummichog density, as would be predicted if intraspecific competition caused variation in growth rate. A monitoring program with a focus on long-term trends in fish size, biomass and growth is being conducted in TIDE creeks and should improve our understanding of the mechanism of and the longer-term nutrient-enrichment effects on mummichogs (J. A. Nelson & L. A. Deegan unpubl. data). Our mark-recapture study complements their data in that it takes an intensive and in-depth, but snapshot look at mummichog responses.

The gut contents of mummichogs collected in all creeks contained relatively large amounts of photosynthetic pigment. Visualization-based studies of gut contents, isotope composition studies and density manipulations with mummichogs suggest the source of pigment was benthic algae (Allen et al. 1994, McMahan et al. 2005, Deegan et al. 2007). We also found that gut pigment content increased by 115% in similarly sized fish from nutrient-enriched creeks where mummichogs exhibited a higher chl *a*: phaeopigment ratio. A nutrient-stimulated increase

in algal productivity or an increase in nutritional quality would be expected to increase the availability or attractiveness of algae as a food for mummichogs, leading to increases in herbivory. However, if consumption of animal prey was concomitantly reduced with increased herbivory in the nutrient-enriched creeks, the result could be a slower growth rate due to the lower dietary quality or protein content of plant tissue. Such changes in diet and behavior could have contributed to a slower growth rate in the nutrient-enriched creeks. Herbivorous fish have been found to be regulated by the supply of algae in a bottom-up fashion (Flecker et al. 2002), but pathways responsible for food-web stimulation to omnivores are more complex, variable, and difficult to identify (Bruno & O'Connor 2005). Unfortunately, available data shed little light on the relative importance of contributions of algal and animal components to mummichog diet, and the variation in those contributions due to nutrient enrichment is also uncertain (e.g. animal contributions to mummichog diet were not examined here). Alternatively, it is possible that the observed increase in gut photosynthetic pigment content was due to increased incidental ingestion of algae while foraging for small, cryptic animal prey. In nutrient-enriched creeks, increased cover may have been provided by more productive benthic algae increasing incidental ingestion while foraging. However, this seems unlikely because benthic algal biomass was not affected in mudflat or creek-wall habitats in nutrient-enriched creeks in the year our study was conducted, and an increase in marsh-edge, *Spartina alterniflora* habitat algal biomass (Mitwally & Fleeger 2013) may have been mitigated by nutrient-induced habitat loss (see below). Additional study of nutrient-enrichment effects on resource utilization in mummichogs is needed.

Long-term nutrient-enrichment effects on the marsh landscape have been accumulating, and resulting habitat degradation may have contributed to a reduction in mummichog growth rate at the time of our study. Deegan et al. (2012) found the marsh-edge, *Spartina alterniflora* habitat was decreased in TIDE's nutrient-enriched creeks. Nutrient enrichment altered the allocation of biomass in *S. alterniflora* (less was allocated to the sediment-stabilizing roots) and increased microbial decomposition rates of root material, which together decreased soil strength (Deegan et al. 2012). As a result, fractures formed in the soil surface and large sections of the marsh edge collapsed into the adjoining creek channel before our study was conducted. A survey taken at regularly

spaced distances along the creek edge in 2009 found that 8.9% of the observations in reference creeks were of an unvegetated muddy substrate (i.e. 91.1% of the bottom was vegetated by *S. alterniflora*), while 24.8% of the nutrient-enriched creeks was unvegetated (Deegan et al. 2012). Many studies (Baltz et al. 1993, Peterson & Turner 1994, Deegan 2002, Minello et al. 2003) have shown the importance of a vegetated creek-marsh edge for saltmarsh nekton, although the high marsh has also been shown to be important in New England marshes for mummichogs (MacKenzie & Dionne 2008). If the *S. alterniflora*-dominated low marsh is an important habitat facilitating increased growth rates or increased feeding opportunities compared to that in the collapsed marsh edge of the nutrient-enriched creeks, or is a significant access point to the high marsh for mummichogs, this observed habitat alteration could contribute to lower growth rates in mummichogs.

The mummichog is a high-level grazer and predator in salt marshes (Deegan et al. 2007), and nutrient-induced alterations in biomass or resource utilization may therefore have important repercussions to saltmarsh food webs via direct or indirect effects. For example, Deegan et al. (2007) found that benthic algal biomass was increased by the combination of nutrient enrichment and fish removal in the second year of TIDE fertilization. Our findings indicate that direct herbivory by mummichogs contributed to this interactive effect. The magnitude of eutrophication is often measured by algal abundance or biomass (Ferreira et al. 2011). The increase in mummichog biomass, coupled with the observed increase in consumption of benthic algae with nutrient enrichment, suggests that mummichogs may slow the rate of increase in algal biomass and therefore the observed pace of eutrophication in nutrient-enriched creeks. This finding is similar to that of Pascal et al. (2013) for benthic invertebrates in TIDE's nutrient-enriched creeks. However, if negative impacts to fitness occur over the long-term affecting populations, mummichog grazing rates may be reduced. This would lead to an accelerated increase in benthic algal biomass, contributing to an increased rate of eutrophication. The abundance, behavior, and growth of infauna, epifauna, and grass shrimp would also vary with changes in mummichog abundance or predation rate (Kneib 1986, Cross & Stiven 1999, Carson & Merchant 2005, Deegan et al. 2007). Therefore, the mummichog should be considered a keystone species that affects the persistence and resilience of saltmarsh ecosystems, with the potential to modify the ecosystem-wide response to eutrophication.

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