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Ontogenetic Habitat Shifts of the Atlantic Tomcod (*Microgadus tomcod*) Across an Estuarine Transition Zone

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Abstract Tomcod (*Microgadus tomcod*) in the St. Lawrence estuarine transition zone (ETZ) undergo an ontogenetic habitat shift. Older age classes, characterised by a male-dominated sex ratio, disperse downstream over the summer months to occupy the colder more saline waters of the estuary. Significant differences in length and mass along the salinity gradient were observed in September with upstream fish of any given age class generally exhibiting greater growth. These differences were not seen in early summer. Benthic amphipod δ^{34}S signatures were strongly correlated with salinity and served to demonstrate that tomcod δ^{34}S signatures were not in isotopic equilibrium in the more saline waters of the ETZ. Seasonal distributional patterns, growth dynamics and isotopic disequilibrium all indicate that the observed habitat shift may occur on an annual basis, following winter aggregation in warmer, less saline waters. Tomcod located in the downstream parts of the ETZ, predominantly males, were significantly more sexually developed than upstream tomcod for a given age. On the other hand, greater growth early in life is insured by occupying warmer, upstream waters during the summer months.

Keywords Atlantic tomcod · Estuarine life cycle · Ontogenetic habitat shift · Sulphur stable isotopes

Introduction

The estuarine transition zone (ETZ), the dynamic frontal region where freshwater of continental origin first mixes with saltwater, is characterised by estuarine recirculation, tidal stratification and mixing and strong gradients, both horizontal and vertical, in temperature, salinity and various biological properties (Vincent and Dodson 1999). The estuarine fishes that inhabit this highly variable environment are considered to be physiologically plastic and are generally characterised as powerful osmoregulators (Barton 2007). The eurytopic strategy involves the physiological ability to exploit the various estuarine gradients and readily respond to fluctuations in salinity as well as other environmental variables and may be considered as the fundamental life-history strategy of marine and freshwater species exploiting estuaries (Attrill and Rundle 2002).

There are at least two important behavioural variations of the fundamental eurytopic strategy. First, there is increasing evidence that alternative life-history phenotypes co-exist within populations, such that part of the population adopts a sedentary phenotype and another

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adopts a migratory phenotype (Jonsson and Jonsson 1993). Although originally documented for salmonid fishes, this phenomenon, also known as partial migration, appears to be taxonomically widespread, being observed in moronids, cyprinids and gasterosteids (Kitamura et al. 2006; Brodersen et al. 2008; Kerr et al. 2009). For example, a portion of a population of the estuarine-dependant white perch resides in the natal freshwater habitat whereas another portion migrates downstream to exploit the brackish waters of the upper estuary (Kerr et al. 2009). Second, the ontogenetic niche shift is a strategy involving a change in habitat and/or diet that serves to segregate different segments of the life cycle in different habitats (Werner and Gilliam 1984). As an example, optimal growth temperature is inversely proportional to size for immature cod (*Gadhus morhua*) (Björnsson et al. 2001), flounder (*Pleuronectes platessa*) and plaice (*Platichthys flesus*) (Fonds et al. 1992), such that these species shift to colder waters as they grow. Estuarine fishes may, thus, potentially adopt different behavioural strategies to cope with or exploit the steep physical and biological gradients that characterise the ETZ.

In this paper, we assess the relative importance of these strategies in the life history of the estuarine-dependant Atlantic tomcod (*Microgadus tomcod*), an anadromous gadid which numerically dominates the fish community of the St. Lawrence middle estuary (Fig. 1). Tomcod spawn in mid-winter approximately 140 km upstream of the estuary in tributary rivers (Scott and Crossman 1974; Bergeron et al. 1998). Sexual maturity occurs in this population at age 2 for males and at age 3 for females. Upon hatching in early spring, young of the year are transported to the species' principal feeding habitat located within the estuary that encompasses the ETZ. Little is known about the ecology of the species in the ETZ. The tomcod is also a dominant component of the Hudson River estuary (Dew and Hecht 1994) where it serves as an indicator species of ecosystem health (Yuan et al. 2006; Carlson et al. 2009).

Specifically, we aimed to document how tomcod exploits the estuarine gradient and to what extent different behavioural strategies influence the growth and maturity of the species. To do so, we documented the distribution of different tomcod age classes across the salinity gradient of the St. Lawrence estuarine transition zone. Here, we use salinity as the principal tracer of the estuarine transition zone gradients. In the case of the ontogenetic habitat shift, we expected to find evidence of the differential distribution of age classes across the salinity gradient. In the case of partial migration, we expected a discontinuous distribution within age classes across the salinity gradient, with one contingent occupying fresher, warmer, upstream waters and a second contingent occupying colder, more saline downstream waters.

As this distribution is based on a series of 'snapshots' in time provided by bottom trawl catches, we also required a means to determine if fish caught at a particular salinity had in fact occupied that range over a seasonal or annual period of time. The stable isotope of sulphur ($\delta^{34}S$) was thus used as a tracer of salinity (Fry 2002; Rubenstein and Hobson 2004). Organic sulphur found in fishes comes directly from two essential amino acids, methionine and cystine. Sulphur ($\delta^{34}S$) at the base of the food chain (e.g. sulphate) is greatly enriched in ^{34}S in the marine environment compared with freshwater (Fry 2002; Godbout et al. 2010). $\delta^{34}S$ is also conservatively transferred up the food chain with little fractionation between prey and predator (McCutchan et al. 2003).

The $\delta^{34}S$ of resident fish or invertebrates should therefore reflect the local $\delta^{34}S$ signature and hence the salinity in which an organism feeds for a period of time (Moon and Gatlin 1991; Rubenstein and Hobson 2004).

We first determined the relationship between salinity and the $\delta^{34}S$ signature of a sedentary food source, benthic amphipods. Although no single amphipod species is known to occur throughout the whole ETZ salinity gradient (Sars 1895; Bousfield 1973; Bourget 1997), Amphipoda is a highly diverse group with taxa distributed throughout the estuary, represented by both benthic and pelagic species (Brunel et al. 1998). Their widespread nature accounts for their prevalence in the diet of many estuarine fishes, including tomcod (Scott and Crossman 1974; Lambert and Fitzgerald 1979; Winkler et al. 2003). Unlike largely pelagic taxa, few, if any, benthic amphipod taxa are known to undertake long migrations along the ETZ salinity gradient. Because benthic amphipods are the most likely representatives of the order to lead a sedentary life style, they were targeted for isotopic analysis to obtain an integrated $\delta^{34}S$ signature characterising local salinity. We then related tomcod's isotopic signature to that of the benthic amphipods, and hence determined if different contingents of the same age group are feeding in different parts of the salinity gradient. Finally, we used measures of growth, condition and sexual development to assess the impact of spatial distribution on the growth and maturation of the species.

Materials and Methods

Study Area and Sampling Techniques

The St Lawrence middle estuary encompasses the ETZ which is approximately 180 km long, stretching between the eastern Point of Orleans Island and the city of Rivière-du-Loup on the south shore of the middle estuary (Fig. 1). The zone is 17 km wide on average (Lecomte and Dodson

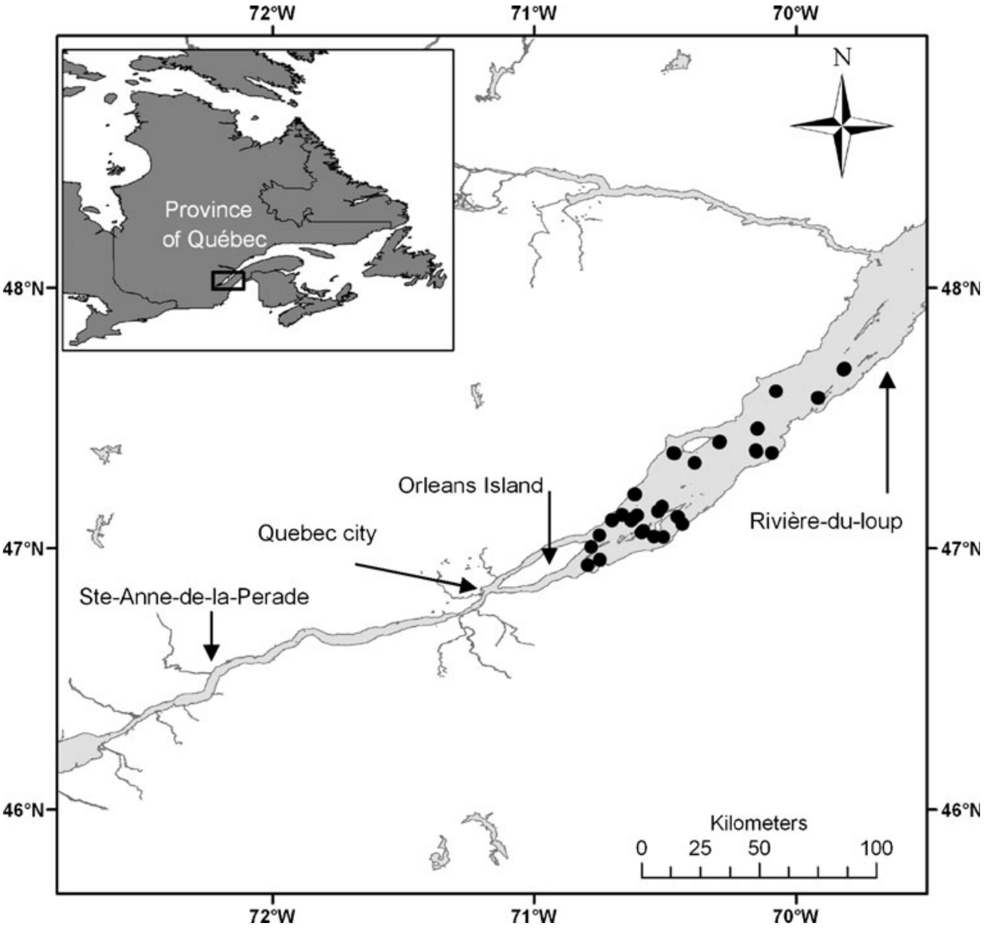

Fig. 1 The St. Lawrence middle estuary, St. Lawrence River, Québec (Canada) The estuarine transition zone is located between Orleans Island and the city of Rivière-du-Loup. The *black dots* represent sites sampled during the three sampling surveys. Main tomcod spawning site, at Ste-Anne-de-la-Pérade, is also shown

2005). Mean annual flow at Quebec City is 12,600 $m^3 s^{-1}$. This flow coupled with daily tides (6.9 m) generates currents up to 3.5 ms^{-1} (Frenette et al. 1995). The bathymetry of this estuary is highly heterogeneous; deep channels characterise the north shore (15 to 100 m deep), while large bays and shoals are found along the south shore (Lecomte and Dodson 2005).

The ETZ was sampled over 2 years (June 2006, June 2007 and September 2007; the September 2006 sampling was cancelled due to equipment failure), resulting in three sampling surveys) (Fig. 1) using the *RV Lampsilis*, a 25-m catamaran. Tomcod were sampled with a commercial bottom fishing trawl (9.9 m wide×2.3 m high for the mouth opening, first net mesh size of 8.9 cm, 1.3 cm for the interior net). Amphipods were sampled with a Wildco benthic dredge (Wildlife Supply Company, Buffalo, NY) custom modified with a 1-mm nylon mesh net, or with a 42-kg Peterson grab where bed features or strong currents prevented dragging.

A total of 28 sampling stations distributed across the ETZ at depths ranging from 5 to 50 m were planned per sampling survey, although fewer were sampled due to weather conditions and/or inappropriate bottom contours for trawling. At each station, the bottom trawl was fished for 5 min to provide sufficient numbers of tomcod for demographic analyses. Four length (l) classes were established a priori ($l \leq 10$, $10 < l \leq 15$, $15 < l \leq 20$ and $l >$ 20 cm) and sorted on board immediately following capture. Ten individuals were retained for subsequent analyses from each of the four length classes at each sampling station of the three sampling surveys. For any length class containing more than ten individuals, ten fish were chosen haphazardly. During June sampling surveys, young of the year tomcod were too small to be sampled but were large enough in September to be retained by the bottom trawl. All amphipod samples from the 2006 campaign were frozen immediately with the substrate. Catches from the 2007 surveys were sorted and identified on board to insure that they contained sufficient specimens to replicate the 2006 survey catches and then immediately frozen in demineralised water.

Temperature, depth and salinity profiles were recorded for all stations at every sampling survey with paired YSI-6600 (YSI Inc., Yellow Springs, OH) and Sealogger SBE-19 CTD (Sea-Bird Electronics Inc., Bellevue, WA) instruments. As Atlantic tomcod is demersal, only bottom salinity and temperature were retained for the analyses. The two variables are highly correlated ($n=38$, $r=-0.944$).

Laboratory Procedures

All Atlantic tomcod retained following on-board sorting were immediately frozen (−20°C) until treated in the laboratory. Sex of the older individuals was visually determined, but for young individuals captured in June, gonads were viewed under a dissecting microscope. Each fish was measured (total length, ±0.01 mm) and weighed (total mass, ±0.01 g). Liver and gonads were extracted and weighed (±0.001 g). The relation between liver mass and body mass over the salinity gradient was employed as an indicator of energy storage and hence condition (Love 1970; Holdway and Beamish 1984). Sexual development in relation to salinity was evaluated by using the relation between gonad mass and total mass.

Otoliths (sagittae) were extracted from all individuals conserved from the three sampling surveys for biological measurements. A subsample ($N=877$) of the total number of individuals captured was aged. Tomcod otoliths were cut in two transversal halves near the nucleus of the otolith with a low-speed saw (AP01—low-speed saw—Buehler Isomet®) equipped with a toothless and water lubricated blade. The exposed surfaces were polished with 3M Imperial wet or dry, 2500A and 1200A, lapping paper. Otoliths were analysed using a dissecting scope equipped with a digital camera. Pictures of all otoliths analysed were digitally recorded for validation by an external reader. Two readers read independently all otoliths to corroborate age estimates. Results were compared, and mismatch were re-examined. When there was still no concordance, the problematic otoliths were removed from the analysis. Since there was considerable overlap in body lengths between ages sampled at different salinities, it was not possible to develop a length-age key. Thus, we used only the 877 specimens with a confirmed age in all subsequent morphological comparisons.

A subsample of 120 tomcod was prepared for the stable isotope analyses. Individuals of different age classes were chosen from the most contrasting estuarine habitats (upstream and downstream stations) to maximise the effect of the salinity gradient. Individuals older than 2 years were excluded from this analysis because they may have migrated to freshwater and spawned at least once, thus affecting the overall mean of their δ^{34}S signature. A piece of dorsal muscle was extracted from the fish, dried at 70°C in a drying chamber for 24 to 48 h, crushed to a powder and stored in glass bottles until analysis.

All amphipod samples were identified in the laboratory to the taxonomic level allowing for discrimination between pelagic and benthic taxa (Brunel et al. 1998). Taxa retained for δ^{34}S analysis included *Calliopius laeviusculus*, *Gammarellus homari*, *Gammarus fasciatus*, *Gammarus oceanicus*, *Gammarus tigrinus*, *Ischyrocerus latipes*, *Monoculodes latimanus*, *Paramphithoe hystrix*, *Psammonyx* sp. (Sars 1895; Holmes 1905; Bousfield 1973; Bourget 1997; Brunel et al. 1998).

Samples (30 mg of tissue from tomcods and amphipods) were sent in Eppendorf tubes for isotopic analysis by ISO-Analytical (Unit D, Phase 3, The Quantum, Marshfield Bank Business Park, Crewe, CW2 8UY, UK).

Statistical Analysis

We tested the null hypotheses that tomcod are distributed across the estuary independently of salinity and age and that sex ratio does not vary as a function of salinity. To test these hypotheses, we used a multinomial logistic regression model to test the effect of salinity and its interaction with sex and year on the probability of observing tomcod of different age classes. A binary logistic regression model was used to study the effect of salinity alone on the probability of observing males relative to females (proc logistic: SAS 2009 Version 9.2; SAS Institute, Cary NC, USA). Higher order powers of salinity (quadratic, cubic etc.) were tested to account for possible non-linear relationships between salinity and the probability of observing different age groups or sexes. In order to avoid overfitting and because the interpretation of the parameters becomes difficult as the order of the polynomial increases, we initially fitted a first-degree model and tested whether the parameters were significant. For sake of parsimony, we then added a higher degree term into the model only if it was significant.

In addition, we tested the null hypotheses that the estuarine gradient has no effect on body length, body mass, the length–mass relationship, the hepatic-mass–body-mass relationship and the gonad-mass–body-mass relationship. To do so, we used ordinary least-squares multiple regression models including salinity as a continuous independent variable and age, sex and sampling year (in the case of June samples) as qualitative independent variables (proc mixed: SAS 2009 Version 9.2; SAS Institute, Cary NC, USA). June samples and September samples were analysed separately because of the seasonal change in growth and environmental conditions. Length and mass were log transformed to meet assumptions of the regression analysis.

To examine the relationship between δ^{34}S of amphipods and salinity, we used ordinary least-squares regression analysis after logarithmic transformation of both dependent and independent variables. An ANCOVA was used to test for statistical difference in the relationship between δ^{34}S and salinity among the three sampling surveys.

In order to test the null hypothesis that tomcod adopt a eurytopic strategy and may freely forage across the salinity gradient, we first compared the δ^{34}S signatures (log transformed) of tomcod sampled at upstream (least saline) and downstream (most saline) stations (proc glm; SAS 2009 Version 9.2; SAS Institute, Cary NC, USA). Significant differences between stations located upstream and downstream along the salinity gradient served to reject the null hypothesis (see "Results"). After demonstrating that δ^{34}S values of benthic amphipods were significantly correlated with bottom salinity (see "Results"), we compared, using paired *t* tests, observed δ^{34}S signatures of tomcod with values predicted according to the relationship between the δ^{34}S signatures of benthic amphipods and salinity. The *p* value of each test was calculated from the bootstrap method as described by Efron and Tibshirani (1993) with 10,000 replicates. For each replicate, a sample of bootstrap individuals was selected with equal probability and with replacement from each of the original tomcod and amphipod samples with sample sizes identical to their original values. New predicted values were derived from the bootstrap amphipod sample. Then the average of the difference between the bootstrap tomcod δ^{34}S signatures values and their corresponding predicted values was calculated each time and, finally, the original difference was subtracted to obtain the distribution under the null hypothesis. The *p* values correspond to the proportion of those values that are more extreme than the original difference. Considering that there is no fractioning between trophic levels for sulphur stable isotopes (Hesslein et al. 1991; Hesslein et al. 1993; McCutchan et al. 2003), we considered that the benthic amphipod–salinity relationship provides the predicted δ^{34}S of an individual fish that consumes sedentary benthic amphipods found at the salinity of the sampling site (Hesslein et al. 1993). Significant differences between observed and predicted values are interpreted as a lack of isotopic equilibrium between the fish and their prey at a given salinity.

Results

Distribution of the Species

In both June and September, tomcod age classes were not randomly distributed along the estuarine gradient. In June, the multinomial logistic regression conducted to measure the effect of salinity on the occurrence of different age classes, taking into account sampling year and sex, revealed no significant interaction terms (sex–year, year–salinity, year–sex or sex–year–salinity). The model was thus simplified to include only the main effects (Table 1). The significant effects of year and sex on the distribution of age classes are of little interest in the present analysis. They arise simply because fish were older in 2007 than in 2006 and females were older than males. More importantly, salinity influences the distribution of the three age classes, the relationship being cubic. Salinity discriminates between the occurrences of fish aged 1 and 2, 1 and 3 as well as between fish aged 2 and 3 (Table 1). Model parameters indicate that the probability of observing age 1 tomcod decreases with increasing salinity whereas for older tomcod age classes it increases with increasing salinity (Fig. 2).

In September, 2007, the multinomial logistic regression conducted to measure the effect of salinity on the probability of observing the four age classes (including young of the year (YOY)), taking into account the sex of fish, revealed no significant interaction term (sex×salinity: chi-square=3.340, *df*=3 and *p*=0.3421). The model was thus simplified to include only the main effects. The significant effect of sex on age is again of little interest in the present analysis, indicating only that females were older than males. Again, the far more significant result is the variation in age as a function of salinity. In September, the effect of salinity was linear. Salinity discriminates between the distributions of fish aged 0 and 1 and that of fish aged 2 and 3 (Table 2). Model parameters indicate that the probability of observing age 0 and 1 tomcod decreases with increasing salinity whereas the opposite tendency is observed for age 2 and 3 tomcod (Fig. 3).

Salinity had a significant effect on the probability of occurrence of males relative to females. The effect of salinity was linear and significantly influenced the sex ratio (chi-square=6.39, *df*=1 and *p*=0.0115). Sex ratio was strongly male biassed at higher salinities, with the sex ratio (M/F) increasing by 1.9% for each unit increase in salinity (Fig. 4).

Table 1 Multinomial logistic ANOVA table summarizing the major effects influencing the distribution of Atlantic tomcod age classes along the salinity gradient, June, St. Lawrence middle estuary

Effect	*df*	Chi-square	*p*
Sex	2	25.372	**<0.0001**
Year	2	29.291	**<0.0001**
Salinity	2	34.824	**<0.0001**
Salinity^2	2	17.259	**0.0002**
Salinity^3	2	12.298	**0.0021**
Global salinity (age 1 vs age 2)	3	68.524	**<0.0001**
Global salinity (age 1 vs age 3)	3	87.107	**<0.0001**
Global salinity (age 2 vs age 3)	3	28.297	**<0.0001**

The global salinity effect, combining the linear, squared and cubic salinity effects are presented for the age class. Pairwise age class comparisons for salinity effects are corrected for multiple comparisons (Bonferroni critical, *p*=0.05/3=0.0167). Bold probability values indicate significant differences following correction for multiple comparisons

p probability

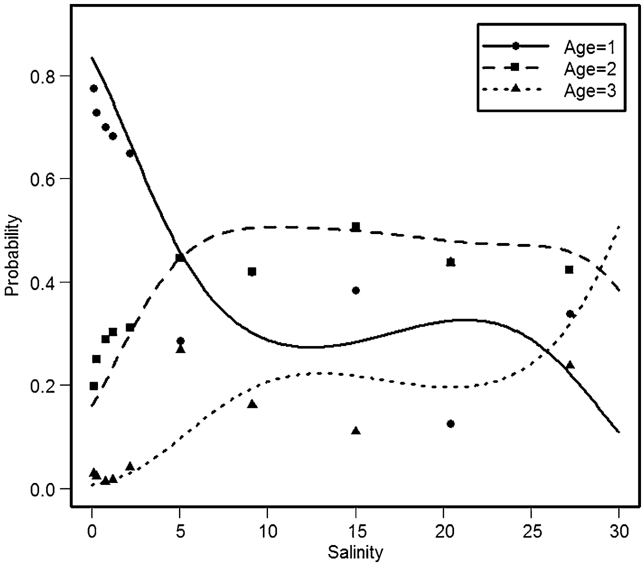

Fig. 2 The probability of observing tomcod aged 1, 2 and 3 as a function of salinity based on the parameters of the logistic regression, June 2006 and 2007

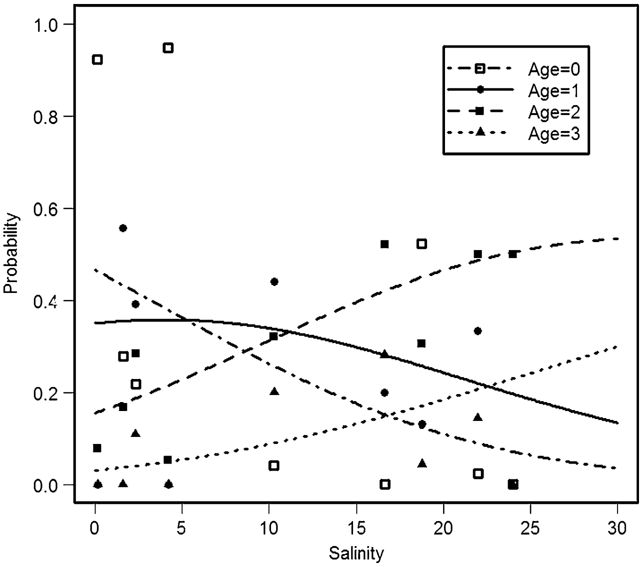

Fig. 3 The probability of observing tomcod aged 0, 1, 2 and 3 as a function of salinity based on the parameters of the logistic regression, September 2007

Growth, Condition and Sexual Development

Descriptive statistics of length and mass by age and by sampling survey are presented in Table 3. There was evidence that the growth of tomcod varied along the salinity gradient on a seasonal basis. In June, we observed no significant interaction between age and salinity for body length (salinity×age interaction: $F=2.46$, $df=2{,}634$ and $p=0.0884$) or body mass (salinity×age interaction: $F=2.11$, $df=2$, 634 and $p=0.122$). Moreover, there was no global salinity effect on either body length ($F=0.23$, $df=1$, 634 and $p=0.883$) or body mass ($F=0.23$, $df=1$, 634 and $p=0.629$). Only the age of the fish was significantly related to its length or mass, as would be expected. In September, however, body length showed a significant salinity×age interaction ($F=17.01$, $df=3$, 223 and $p<0.0001$) as did body mass ($F=19.38$, $df=3$, 223 and $p<0.0001$). For both variables, regression parameter estimates and contrasts indicated that whereas the length and mass of the 0 age class increased with increasing salinity, length and mass of the 1-, 2- and 3-year-old age classes decreased with increasing salinity (Table 4).

Table 2 Multinomial logistic ANOVA table summarizing the major effects influencing the distribution of Atlantic tomcod age classes along the salinity gradient, September, St. Lawrence middle estuary

Effect	*df*	Chi-square	*p*
Sex	3	9.180	0.0270
Salinity	3	33.329	<0.0001
Salinity (age 0 vs age 1)	1	4.918	0.0266
Salinity (age 0 vs age 2)	1	24.901	**<0.0001**
Salinity (age 0 vs age 3)	1	20.078	**<0.0001**
Salinity (age 1 vs age 2)	1	10.693	**0.0011**
Salinity (age 1 vs age 3)	1	10.059	**0.0015**
Salinity (age 2 vs age 3)	1	87.107	0.2984

Pairwise age class comparisons for salinity effects are corrected for multiple comparisons (Bonferroni critical $p=0.05/6=0.008$). Bold probability values indicate significant differences following correction for multiple comparisons

p probability

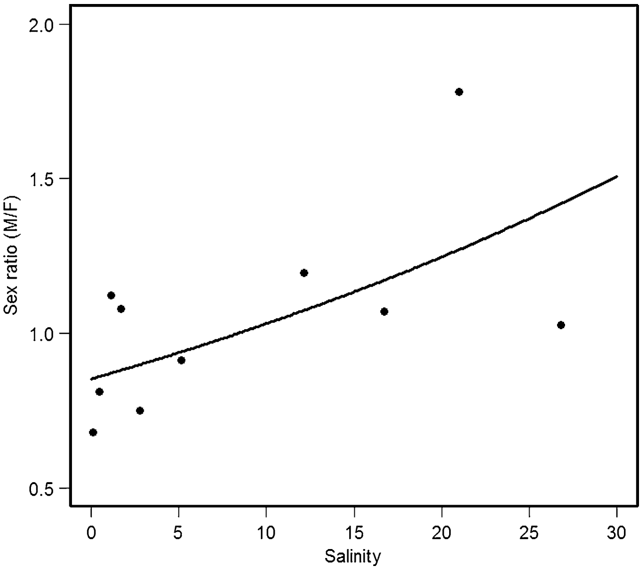

Fig. 4 Logistic regression model estimates of sex ratio as a function of salinity

Table 3 Descriptive statistics for length (mm) and mass (gm) of age 0, 1, 2 and 3 Atlantic tomcod captured during the three sampling surveys in the St. Lawrence estuary

Age	Variable	Survey								
		June 2006			June 2007			Sept 2007		
		N	Mean	SD	*N*	Mean	SD	*N*	Mean	SD
0	Length							64	85.86	11.60
	Mass								5.34	2.47
1	Length	115	114.30	21.51	217	117.38	17.73	72	149.57	19.73
	Mass		12.83	9.87		12.89	6.57		30.51	15.15
2	Length	73	159.21	22.75	158	161.97	25.31	71	166.84	23.74
	Mass		33.95	20.62		37.20	25.28		43.37	24.18
3	Length	23	190.61	28.20	60	190.35	32.10	24	179.12	29.38
	Mass		60.98	29.03		62.5	37.37		52.37	35.50

N sample size, *SD* standard deviation

For all surveys, there was little evidence that length–mass relationships varied along the salinity gradient. In June, the regression analysis revealed a significant three-way interaction indicating that in early summer the slope of the length–mass relationship varied according to age and salinity (slope×salinity×age: $F=6.24$, $df=2$, 634 and $p=0.002$). The three age classes sampled in June were thus analysed separately. Only the length–mass relationship of age 2 tomcod sampled in June showed a significant relationship with salinity (Table 5). In this case, the slope of the relationship increased and the intercept decreased with increasing salinity. In September, no relationship was observed with salinity (slope×salinity: $F=0.13$, $df=1$, 215 and $p=0.721$), indicating that the slope of the length–mass relationship did not vary along the salinity gradient and this conclusion applied to all age classes as the triple interaction is not significant (slope×salinity×age: $F=1.65$, $df=3{,}215$, $p=0.179$).

There was no evidence that the liver-mass–body-mass relationship varied along the salinity gradient. The slope of this relationship did not differ as a function of age and salinity in either June (slope×salinity×age: $F=1.05$, $df=2$, 634 and $p=0.351$) or September (slope×salinity×age: $F=0.45$, $df=3$, 215 and $p=0.715$). In general then, there is little evidence that the condition of Atlantic tomcod, as expressed by either the length–mass relationship or the liver-mass–body-mass relationship, varies across the salinity gradient.

Gonad development was observed during the September sampling survey for age 1, 2 and 3 fish. Tomcod occupying more saline waters exhibited a greater degree of gonad

Table 4 Ordinary least-squares multiple regression analysis relating body length and body mass of Atlantic tomcod to salinity: estimates of regression parameters and contrasts

	Body length					Body mass				
	Estimate	SE	*t*	*F*	*p*	Estimate	SE	*t*	*F*	*p*
Effect										
Salinity (age 0)	0.0113	0.0022	5.08		<0.0001	0.0394	0.0074	5.33		<0.0001
Salinity (age 1)	−0.0058	0.0017	−3.44		0.0007	−0.0243	0.0057	−4.25		<0.0001
Salinity (age 2)	−0.0072	0.0018	−4.06		<0.0001	−0..234	0.0059	−3.97		<0.0001
Salinity (age 3)	−0.0069	0.0035	−1.95		0.0522	−0.0274	0.0117	−2.33		0.0207
Contrasts										
Salinity (age 0 vs age 1)				37.54	<0.0001				46.38	<0.0001
Salinity (age 0 vs age 2)				42.36	<0.0001				44.05	<0.0001
Salinity (age 0 vs age 3)				19.03	<0.0001				23.15	<0.0001
Salinity (age 1 vs age 2)				0.27	0.6006				0.01	0.9162
Salinity (age 1 vs age 3)				0.06	0.8041				0.06	0.8137
Salinity (age 2 vs age 3)				0.01	0.9355				0.09	0.7642

September, 2007, St. Lawrence estuary. Error degrees of freedom=223

SE standard error of the estimate

Table 5 The relationship between salinity and the length–mass relationship of Atlantic tomcod, June 2006 and 2007 by age class

Month	Age class	Estimate	SE	*df*	*t* value	*p*
June	1	0.0038	0.0044	1, 328	0.86	0.3881
June	2	0.0157	0.0053	1, 227	2.96	0.0034
June	3	−0.0216	0.0130	1, 79	−1.66	0.1000

The estimate (ordinary least-squares multiple regression model) is the interaction of length–mass and salinity with its standard error (SE), *t* value and probability level (*p*)

df degrees of freedom

development. An increase in salinity significantly increased the slope of the gonad-mass–body-mass relationship for all ages and both sexes (gonad-mass–body-mass × salinity interaction: $F=6.83$, $df=1$, 144 and $p=0.009$).

Stable Isotope Analyses

There was a highly significant relationship between the δ^{34}S signature of the benthic amphipods and the salinity measured at the sampling stations (Regression: $F=704.78$, $df=1$, 44, $R^2=0.94$, $p<.0001$; Fig. 5), with no significant effects of date or interactions between date and salinity (ANCOVA: date effect, $F=0.46$, $df=1{,}40$ and $p=0.634$; interaction date × salinity, $F=0.48$, $df=2$ and 30 $p=0.621$). When comparing isotopic signatures of tomcod sampled at the upstream and downstream end of the salinity gradient (Table 6), only age 1 tomcod sampled in June 2006 exhibited a similar δ^{34}S signature between upstream and downstream habitats. Upstream δ^{34}S signatures of all other age classes were always significantly lower than downstream δ^{34}S signatures (Table 6). Thus, with the exception of the June 2006 specimens, tomcod δ^{34}S signatures tended to reflect the salinity gradient. However, tomcod signatures did not always conform to local δ^{34}S signatures as revealed by comparisons with the δ^{34}S signatures of benthic amphipods captured at the same salinity (Table 6). The signatures of all tomcod sampled at upstream stations, with the exception of age 0^+ tomcod and, marginally, of age 1 tomcod in September, were in equilibrium (Table 6). All comparisons of tomcod sampled at downstream stations revealed observed values significantly smaller than predicted values (Table 6). Overall, for ages 1 and 2, fish achieved only 66.2% of their predicted isotopic equilibrium value (100 × observed δ^{34}S/predicted δ^{34}S) in the downstream stations, while they averaged close to 100% (98.2%) in the upstream section.

Discussion

The distribution of Atlantic tomcod in the St. Lawrence estuarine transition zone and the variation in somatic growth, sex ratio, sexual development and stable isotope signatures as a function of salinity lead us to reject the null hypothesis of a pure eurytopic life-history strategy. Few or no differences in the aforementioned characteristics should have been observed if tomcod freely exploited the salinity gradient. On the contrary, the majority of ages 0 and 1 tomcod were found upstream, in warm, low salinity waters, whereas older age classes were distributed further downstream in colder, more saline waters. This pattern was clearly sex biassed as the occurrence of males relative to females significantly increased with increasing salinity.

Isotope analyses revealed that age groups were composed of contingents that occupied and fed in both low and high salinity waters, consistent with the hypothesis of partial migration. However, the existence of discrete sedentary and migratory ecotypes was not evident as we did not observe a discontinuous distribution of age classes across the salinity gradient in either June or September. The continuous distribution of age classes across the salinity

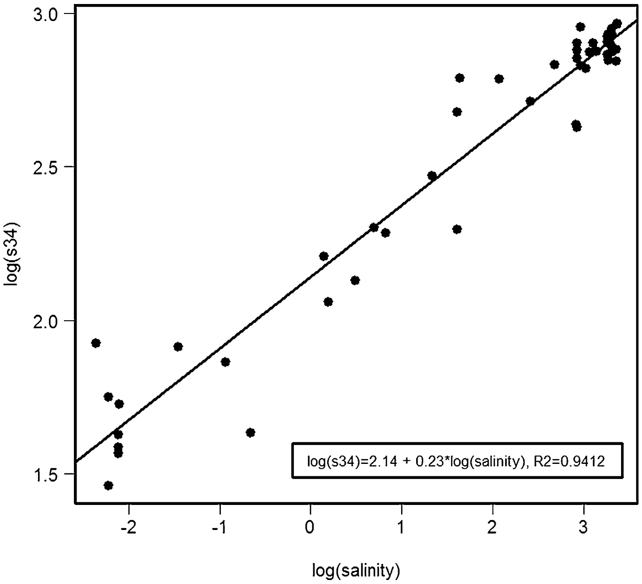

Fig. 5 Relation between sedentary benthic amphipod's isotopic signature (δ^{34}S), and sampling stations' logarithmic salinity (Log_e (Salinity)) as measured during June 2006, June 2007, and September 2007 cruises

Table 6 Results of the isotopic δ^{34}S disequilibrium analyses

Cruise	Group	Number	Tomcod		Predicted		t[a]	p[b]	Equilibrium[c]
			Mean δ^{34}S(‰)	SE	Mean δ^{34}S(‰)	SEp			
June 2006	Age 1 upstream	10	8.41[d]	0.41	8.71	0.26	−0.60	0.5392	Yes
	Age 1 downstream	10	9.41[d]	0.69	17.83	0.47	−10.17	<.0001	No
June 2007	Age 1 upstream	10	7.50[d]	0.26	7.25	0.27	0.68	0.4853	Yes
	Age 1 downstream	10	11.45[e]	0.41	16.41	0.24	−10.45	<.0001	No
	Age 1 upstream	10	8.17[d]	0.36	7.18	0.50	1.587	0.0324	Yes
	Age 1 downstream	10	13.61[e]	0.40	16.41	0.24	−6.04	<.0001	No
Sept 2007	Age 0^{+} upstream	10	8.43[d]	0.29	5.24	0.27	8.08	<.0001	No
	Age 0^{+} downstream	10	13.74[e]	0.348	16.85	0.253	−7.24	<.0001	No
	Age 1 upstream	10	8.34[d]	0.27	9.50	0.25	−3.15	0.002	Marginal[f]
	Age 1 downstream	10	9.61[e]	0.33	17.50	0.27	−18.54	<.0001	No
	Age 2 upstream	10	8.75[d]	0.46	9.78	0.39	−1.72	0.0503	Yes
	Age 2 downstream	10	12.39[e]	0.56	17.50	0.27	−8.23	<.0001	No

Tomcod mean δ^{34}S (m1) corresponds to the mean of the measured δ^{34}S calculated for each group

SE standard error corresponding to the measured δ^{34}S mean, *predicted mean δ^{34}S* (m2) predicted value calculated using the amphipod model with the salinity of the sampling station of the measured group, *SEp* bootstrap standard error associated to this predicted mean value

[a] t value is equal to $(m1-m2)/\sqrt{(SE^2+SEp^2)}$

[b] p value obtained with 10,000 replicates of the bootstrap method corrected for multiple comparisons (critical $p=0.05/12=0.004$)

[c] 'No' indicates predicted δ^{34}S value is significantly different from the measured δ^{34}S value following Bonferroni correction for multiple comparisons

[d] No significant difference

[e] Significant differences (t test, $p<0.01$) between upstream and downstream mean-observed δ^{34}S values, pairwise comparisons by age and by sampling survey

[f] Marginal statistical significance

gradient, with older age classes occupying more saline waters, appears to be more consistent with a hypothesis of ontogenetic niche shifts (Knudsen et al. 2006). In fact, the two competing hypotheses may be confounded if different age groups exhibit varying degrees of partial migration, with age 1 tomcod being predominantly non-migratory and older fish being increasingly migratory. The documentation of individual life-time tracks obtained from otoliths using non-trophic techniques (e.g. strontium–calcium ratios) will be needed to discriminate between these two hypotheses.

The distributional pattern of age classes was more pronounced during the September sampling survey. In June, the probability of observing 1-, 2- and 3-year-old fish remained relatively stable over a wide range of intermediate salinities (from approximately 8 to 25), suggesting that the more pronounced distributional pattern of 2- and 3-year-old tomcod observed in September may develop throughout the summer months as ages 2 and 3 tomcod disperse downstream. If such is the case, it implies that all age classes congregate at the upstream end of the salinity gradient during winter. Older age classes may then disperse downstream during the summer months. In support of this interpretation, significant differences in length and mass along the salinity gradient were only observed in September, with upstream fish of any given age class (with the exception of age 0 tomcod) exhibiting greater lengths and masses. In June, no such differences were observed within age classes. If the distributional pattern of age classes is maintained over the life cycle of the cohorts, one would expect to see significant differences in mass and length retained throughout the year such that 1-, 2- and 3-year-old tomcod captured upstream in June should exhibit greater masses and lengths than those same age classes captured downstream, which was clearly not the case.

The analysis of δ^{34}S values of different age groups collected at opposing ends of the salinity gradient indicate that tomcod do not freely forage over the entire gradient. All year classes, with the exception of age 1 tomcod in 2006, living in the upstream, lower salinity, habitats had δ^{34}S values indistinguishable from the local prey δ^{34}S values predicted from the amphipod–salinity relationship, suggesting that this portion of the population remains associated with this range of salinity. This contrasted with the downstream, more saline, habitats where all year classes exhibited δ^{34}S significantly lower than expected had they been at equilibrium with local benthic prey. This result would be expected from the pattern of downstream movement during summer inferred from the size distributions (see above).

However, inference of isotopic disequilibrium also requires a consideration of the time period needed to reach isotopic equilibrium, which is a function of rates of growth and metabolism (e.g. Hesslein et al. 1993; Herzka 2005). A simple growth and metabolism model (Hesslein et al. 1993) serves to illustrate this relationship. Let us assume that age 1 tomcod settle in June 2006 in higher salinity waters, that they eat the high δ^{34}S (δX_n=17.6‰, Table 6) food associated with these waters and grow there until September 2007. Average body mass values (age 1 tomcod=12.8 g in June, 2006, age 2 tomcod=43.4 g in September, 2007 (Table 3)) indicate an average gain in new body mass of 30.6 g over 465 days (thus a relative growth rate, k=0.0026 days^{-1}). The growth/metabolism model,

$$\delta X(t) = \delta X_n + (\delta X_0 - \delta X_n)e^{-(k+m)t} \tag{1}$$

assuming no metabolic turnover (m=0), projects an isotopic signature of 15.2‰, which is substantially higher than the observed δ^{34}S in September (12.4‰). It is difficult to speculate about what the value of m should be in the field during this growth period as diet-switching studies estimating m from isotopic changes are typically done in the laboratory (Herzka 2005). However, inclusion of a non-zero metabolic rate would result in a still higher projected δ^{34}S. For example, a value of m=0.0021 days^{-1} (near the value of k) would suffice to bring the September fish to their expected equilibrium value of 17.6‰.

Approximately equal m and k in young fish have been observed in flounder (*Paralichthys dentatus*, Buchheister and Latour 2010), goby (*Rhinogobius* sp., Maruyama et al. 2001) and salmon (*Oncorhynchus nerka*, Sakano et al. 2005). It is, therefore, reasonable to assume that if tomcod settle in the high saline habitats without further seasonal upstream movements in less saline habitats, they should be at isotopic equilibrium with the local prey within the time scale of the present study. The lack of isotopic equilibrium at downstream sampling sites thus indicates that fish resided in these waters for a shorter period of time and were captured before the requisite time for equilibrating with downstream δ^{34}S (Rasmussen et al. 2009). This would support our inference that all age classes congregate in fresher waters early in the year and that the majority of ages 2 and 3 tomcod disperse to downstream waters throughout the summer months.

We found, using benthic amphipods, a strong gradient in δ^{34}S along the salinity gradient, which confirms previous results (Fry 2002, Godbout et al. 2010). This strong relationship was observed during three sampling surveys (June 2006, 2007 and September 2007) with no indication of significant differences in the relationship among time periods, indicating that this is a robust approach to delineate the trophic residency of a demersal species such as tomcod along the salinity gradient. This approach to tracking habitat use along a salinity gradient necessarily assumes on-going feeding by the target organism. This contrasts with non-trophic techniques, such as the quantification of elemental ratios based, for example, on differential precipitation of strontium and calcium from water with increased salinity (Tzeng 1996; Kerr et al. 2009). Used in tandem, these two approaches should complement each other in revealing over which periods of time or areas fish movement is decoupled from feeding.

Even though the incidence of 2- and 3-year-old fish increased downstream, tomcod aged 1, 2 and 3 all exhibited greater body size (length and mass) in warmer, less saline, upstream waters following the summer growing season. Given the warmer temperatures of upstream waters, such differences in growth performance are to be expected. Interestingly, this was not the case for YOY tomcod, as body length and mass increased in downstream waters. This observation complements those of Laprise and Dodson (1989, 1990) who noted that whereas larger pre-metamorphic YOY tomcod were located upstream of smaller tomcod in June, larger post-metamorphic YOY tomcod were located downstream of smaller tomcod in July. These authors suggested that the downstream movement of larger YOY tomcod was related to the dynamics of the retention mechanism with large YOY tomcod more apt to be advected downstream (Laprise and Dodson 1990). Whatever the cause, the present observations suggest that although this situation persists until September, it does not persist through to the following summer. There is no difference in length of age 1 tomcod between upstream and downstream samples obtained during the June sampling surveys. This may be related to growth compensation of smaller YOY in the warmer upstream waters and/or passive upstream migration of YOY tomcod during winter within the deep landward residual currents of the estuary (Laprise and Dodson 1989, 1990).

Tomcod located in the downstream parts of the ETZ, predominantly males but also females, were significantly more sexually developed than upstream tomcod for a given age. This is most likely related to a reallocation of somatic resources to the gonads during autumn cooling. This physiological phenomenon is widespread among different fish families, including gadids (Santic et al. 2009), galaxids (for example, *Galaxias maculatus* (Boy et al. 2009)) and gasterosteids (for example, *Gasterosteus aculeatus* (Huntingford et al. 2001)). For these species, a decline in lipid mass is correlated with an increase in gonad weight before the reproductive period. Moreover, the moment when this reallocation is made is correlated with temperature. For winter spawners, autumn cooling slows metabolism and feeding, after which lipid reserves are invested in gonads for sexual development (Santic et al. 2009). We speculate that the first individuals to be affected by autumn cooling are those residing in downstream waters, resulting in accelerated sexual development, particularly among males, compared with tomcod associated with warmer upstream stations, predominantly females. Given that males may also benefit from improved growth at the head of the ETZ, there may be some reproductive advantage for males to achieve maturity as early as possible and to arrive before females on the spawning grounds. Male tomcod far outnumber females on the spawning grounds at the beginning of the reproductive season (Mailhot, Y., Ministère des Ressources Naturelles et Faune, Trois-Rivières, Quebec, personal communication).

In conclusion, the behavioural repertoire of the Atlantic tomcod permits this species to fully exploit the range of physical gradients characteristic of the estuarine transition zone. The ontogenetic habitat shift of older age classes appears to be associated with accelerated sexual development, particularly in males, whereas the predominance of younger age classes in upstream waters favours somatic growth.

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