

Tracking seasonal migrations of redfish (*Sebastes* spp.) in and around the Gulf of St. Lawrence using otolith elemental fingerprints

Steven E. Campana, Alexandra Valentin, Jean-Marie Sévigny, and Don Power

Abstract: Large concentrations of beaked redfish (*Sebastes mentella* and *Sebastes fasciatus*) overwinter in the Cabot Strait and the approaches of the Gulf of St. Lawrence each year. Synoptic research vessel surveys indicate that redfish are distributed more widely in the summer than in the winter, particularly within the Gulf. Significant differences in the trace element composition of the otolith ("otolith elemental fingerprint") were observed among summer aggregations, indicating that the aggregations maintained some degree of separation while in the Gulf. *Sebastes mentella* and *S. fasciatus* were readily distinguished based on otolith elemental fingerprints. Using the elemental fingerprints of the summer samples as a natural tag, we found that *S. mentella* tended to move out of the Gulf in the winter. Aggregations of *S. mentella* found in the east during the summer were not found in our winter collections. The elemental fingerprints of *S. mentella* from the Saguenay Fjord were clearly distinct from redfish further east in the Gulf of St. Lawrence, indicating that this group had been separated from other redfish for much of their life. The implications of our findings extend not only to the fisheries management of redfish, but also to the extent of movement expected of deep-water fish species.

Résumé : Chaque année, de grands rassemblements de sébastes (« beaked redfish », *Sebastes mentella* et *S. fasciatus*) passent l'hiver dans le détroit de Cabot et les abords du golfe du Saint-Laurent. Des inventaires synoptiques faits par des navires de recherche indiquent que les sébastes ont une répartition plus étendue en été qu'en hiver, particulièrement dans le golfe. On observe des différences significatives dans la composition en éléments en traces des otolithes (« signature des éléments dans les otolithes ») dans les regroupements d'été, ce qui indique que ces regroupements maintiennent un certain degré de séparation pendant leur séjour dans le golfe. *Sebastes mentella* et *S. fasciatus* se distinguent clairement d'après la signature des éléments en traces dans leurs otolithes. En utilisant la signature des éléments des échantillons d'été comme étiquettes naturelles, nous découvrons que *S. mentella* a tendance à quitter le golfe pendant l'hiver. Les regroupements de *S. mentella* trouvés dans l'est durant l'été ne se retrouvent pas dans nos récoltes d'hiver. Les signatures des éléments des *S. mentella* du fjord du Saguenay sont nettement distinctes de celles des sébastes vivant plus à l'est dans le golfe du Saint-Laurent, ce qui indique que les sébastes du Saguenay ont été séparés des autres sébastes pour une grande partie de leur vie. Les conséquences de nos observations affectent non seulement la gestion des pêches de sébastes, mais elles concernent aussi l'importance des déplacements attendus chez les espèces de poissons d'eau profonde.

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Introduction

The migration patterns of marine fish populations are less understood than the spawning migrations of anadromous fish such as salmon, but the influence on their population dynamics may be just as important. In response to spawning, feeding, or predator avoidance cues, marine fish migrations can extend over scales as small as a few kilometres in the

case of flatfish moving offshore to overwinter (MacDonald et al. 1984) to thousands of kilometres for bluefin tuna crossing the North Atlantic (Lutcavage et al. 1999). The extent and timing of these often-annual migrations are generally both consistent and predictable within a given population, suggesting an evolutionary advantage. However, the exact nature of the survival advantage, as well as the migratory route and destination, are often poorly understood, in

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part due to the technical limitations associated with tracking the movements of millions of fish deep beneath the ocean's surface.

Although our understanding of marine fish migrations in the surface layers of the ocean requires improvement, it is immensely better than our understanding of the movements of deep-sea fishes. Excluding diel vertical migrations, which have been well documented (Gauthier and Rose 2002), large-scale seasonal migrations have not been reported in deep-sea fishes (Beamish et al. 2005). The absence of reports could be due to the sedentary nature of deep-sea fishes, but a more likely cause is the lack of study. Deep-sea fishes are very difficult to track in situ, largely because of the difficulties involved in bringing deepwater fishes to the surface for tagging (Starr et al. 2000). In the handful of studies reporting deep-sea migrations, reproduction and (or) feeding have been suggested as proximal causes in most (Kuo and Tanaka 1984; Duarte et al. 2001).

Acadian redfish (*Sebastes fasciatus*) and deepwater redfish (*S. mentella*) are members of a species complex of beaked redfish that form large aggregations in cold, deep water off the eastern coast of Canada, particularly in the Gulf of Maine, along the Scotian Shelf, off the shelf edge of Newfoundland, and into the Gulf of St. Lawrence (Atkinson 1987). The species can be exceedingly difficult to identify, requiring either dissection of the swimbladder musculature or genetic assay or both for confident identification (Ni 1981; Gascon 2003; Valentin et al. 2006). Hybridization of the sympatric species has also been reported (Rubec et al. 1991; Desrosiers et al. 1999; Roques et al. 2001). *Sebastes fasciatus* and *S. mentella* are common in the Gulf of St. Lawrence, where they often form large sympatric aggregations that are the targets for a year-round mixed-species commercial fishery (Atkinson 1987; Gascon 2003).

Unlike many marine fishes, redfish are internally fertilized and ovoviviparous, mating in late fall or early winter and extruding their live young in late spring and early summer (Atkinson 1987; St-Pierre and de Lafontaine 1995). The locations of mating and extrusion are not necessarily the same. Although extruded larvae of both species are known to be numerous in the Gulf of St. Lawrence and the intraspecific distribution of these larvae is known to be heterogeneous (Sévigny et al. 2000), the population structure of redfish in the Gulf is unknown. Population genetic studies of redfish in the Gulf of St. Lawrence and their approaches based on microsatellite DNA assays are also equivocal, suggesting weak structure in *S. fasciatus* and negligible structure in *S. mentella* (Roques et al. 2001; A. Valentin, unpublished data).

Many of the fish species in the Gulf of St. Lawrence are known to migrate to the warm, deep waters of the Laurentian Channel (near the mouth of the Gulf) to overwinter, presumably to avoid near-freezing water temperatures and ice cover over much of their summer habitat (Templeman 1962; D'Amours et al. 1994; Campana et al. 1999). It is unlikely that *Sebastes* spp. need to migrate to avoid cold temperatures, as temperature at their typical depth ranges of 150–300 m (for *S. fasciatus*) and 350–500 m (for *S. mentella*) are reasonably constant all year round (Atkinson 1984). However, based on a comparison of summer and winter research

surveys and the historical distribution of the fishing fleet, there is some indication that redfish change their distribution between summer and winter, moving to the southeast for the winter (Morin et al. 1994; Gascon 2003). A substantial proportion of the biomass of Gulf of St. Lawrence *Sebastes* spp. apparently overwinters in a relatively circumscribed area in the Laurentian Channel close to the Cabot Strait. However, the line separating the two redfish management units that encompass the Gulf of St. Lawrence and Laurentian Channel areas bisects what appears to be a continuous distribution in the overwintering area (Morin et al. 1994). Both mixed-population catches and distributions of populations outside of management units can introduce serious error into the stock assessment of any fish species, thus degrading efforts at optimal management (Wood et al. 1989).

Conventional tagging studies are seldom carried out on deepwater species such as redfish because of the difficulties in bringing them to the surface without fatal decompression of the swimbladder, compounded by low recapture rates (Starr et al. 2000). Therefore, we used the trace element composition of the otolith as a more highly resolved natural tag. The otolith is well suited to this application because it grows without resorption throughout the life of the fish (Campana and Neilson 1985) and it accretes trace elements from the environment in a temperature-sensitive manner (Campana 1999). Thus the elemental composition of the whole otolith ("elemental fingerprint") serves as an environmentally induced natural tag of fish that have spent at least part of their lives in different habitats, independent of genetic identity. Recent studies have demonstrated not only that the elemental fingerprint of species such as cod is population-specific, but also that otolith growth and environmental shifts over periods of up to a year have a negligible effect on the whole-otolith fingerprint (Campana et al. 1999, 2000). Given the slow growth and extended life span of redfish (up to 75 years) (Campana et al. 1990), the elemental fingerprint of redfish otoliths would be expected to be even more stable. By using the whole-otolith elemental fingerprint of redfish on summer grounds as a short-term natural tag, it should be possible to track and identify those same groups of fish on the overwintering grounds with no more assumptions than those associated with genetic markers (Campana et al. 1999).

In this paper, we start by using the results of synoptic research vessel surveys to document the distribution and density of redfish on their summer grounds in the Gulf of St. Lawrence and Laurentian Channel. We then apply otolith elemental fingerprints as natural tags to test the hypothesis that redfish move out of the Gulf of St. Lawrence to overwinter in the Laurentian Channel, where they potentially mix with another redfish population. We conclude by assessing the implications of the findings for migration theory and fisheries management.

Materials and methods

Sample collection

The density and distribution of redfish in the Gulf of St. Lawrence and the Laurentian Channel were surveyed as part of three separate stratified random surveys in July and

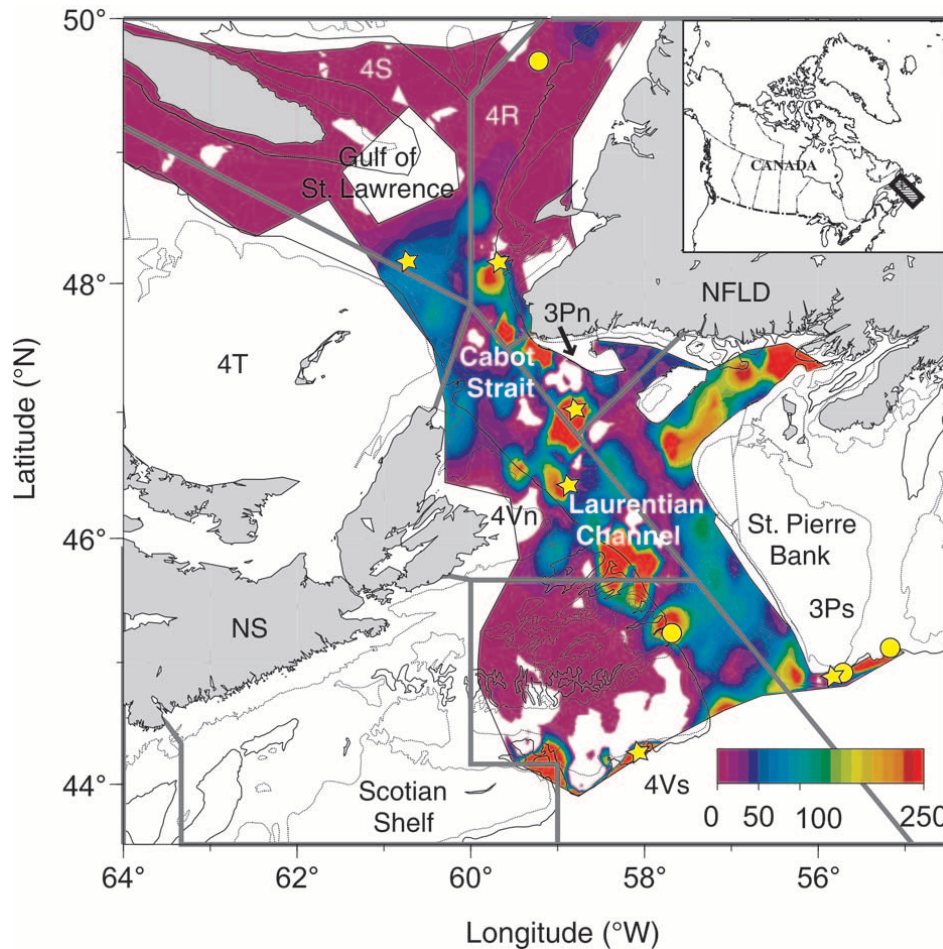
Table 1. Summary of redfish samples analyzed by species and season.

Sample label	Season	Date	Latitude (N)	Longitude (W)	Depth (m)	<i>S. mentella</i>			<i>S. fasciatus</i>		
						N	Length, cm (SE)	Otolith weight, mg (SE)	N	Length, cm (SE)	Otolith weight, mg (SE)
3PN1	Summer	3 Aug. 2002	46°53.3'	58°50.0'	434	30	33.5 (0.4)	281 (7)	31	28.6 (0.4)	218 (8)
4S44	Summer	7 Aug. 2002	48°03.6'	60°34.2'	447	32	34.7 (0.4)	316 (10)			
4R48	Summer	7 Aug. 2002	48°07.3'	59°46.0'	315	30	33.6 (0.5)	289 (10)			
3PS1	Summer	30 July 2002	45°08.2'	55°10.2'	202	31	34.7 (0.4)	348 (11)			
4VS13	Summer	13 Aug. 2002	44°13.8'	58°02.8'	515	31	34.7 (0.4)	348 (11)			
4VS36	Summer	3 Aug. 2002	45°16.3'	57°42.2'	217	31	33.8 (0.4)	293 (9)			
4VN77	Summer	27 July 2002	46°22.8'	58°55.4'	348	31	33.8 (0.4)	293 (9)			
4R107	Summer	12 Aug. 2001	49°45.5'	59°10.8'	217	2	36.5 (0.5)	348 (11)			
3PS4*	Summer	30 July 2002	44°56.4'	55°39.9'	203	2	36.5 (0.5)	348 (11)			
3PS4*	Summer	31 July 2002	44°53.1'	55°44.1'	306	1	43.0 (0)	458 (0)			
3PS4*	Summer	31 July 2002	44°48.7'	55°40.8'	623	11	37.3 (1.6)	335 (41)			
3PS4*	Summer	31 July 2002	44°51.0'	55°46.7'	485	2	36.5 (2.5)	397 (119)			
4VN2	Winter	9 Nov. 2002	45°42.8'	57°53.0'	425	31	35.1 (0.4)	311 (9)			
4VN5	Winter	9 Nov. 2002	45°47.1'	58°07.0'	245	32	34.3 (0.5)	312 (10)			
4VN12	Winter	10 Nov. 2002	46°58.3'	59°37.2'	431	31	35.8 (0.5)	357 (12)			
4S35	Winter	11 Nov. 2002	48°19.5'	60°50.5'	429	31	35.8 (0.5)	357 (12)			
4R51	Winter	12 Nov. 2002	48°19.1'	59°58.9'	392	32	34.3 (0.4)	314 (10)			
4R53	Winter	12 Nov. 2002	48°17.8'	59°44.3'	248	32	33.0 (0.3)	296 (9)			
3PN77	Winter	13 Nov. 2002	47°08.3'	58°24.0'	390	31	34.3 (0.5)	319 (11)			
3PS133	Winter	15 Nov. 2002	45°32.0'	56°49.2'	394	48	29.4 (0.1)	204 (3)			
3PS138	Winter	18 Nov. 2002	44°51.9'	56°01.8'	448	48	29.4 (0.1)	204 (3)			
Saguenay	Winter	Jan.-Feb. 2003	48°07'	69°40'		48	29.4 (0.1)	204 (3)			
Total						407			208		

Note: N, number of fish used in the analysis. SE, standard error.

*Pooled as one sample.

Fig. 1. Map of study area contoured to show the relative distribution of *Sebastes* spp. in the summer of 2002 (kg/standardized set). Yellow circles show summer collection sites for *S. fasciatus*; yellow stars show summer collection sites of *S. mentella*. The 100 and 200 m bathymetric contours are shown.



August of 2002 (Table 1). The mean distance between survey samples was 20–30 km, although some areas were surveyed at 5 km intervals. Standardized catch weight per set was contoured using Delauney triangles in the spatial analysis program ACON (available at <http://www.mar.dfo-mpo.gc.ca/science/acon/index.html>).

To characterize the otolith elemental fingerprint of the major redfish aggregations in and around the Gulf of St. Lawrence, samples of primarily adult redfish (25–45 cm) were collected with otter trawls aboard research vessels in the summers of 2001 and 2002 from previously documented major aggregations (Gascon 2003). Sets in which the catch exceeded 100 kg were considered to be representative of each of the major aggregations (Table 1; Fig. 1). A minimum of 30 redfish was selected from each set for a total of 110 *S. fasciatus* and 170 *S. mentella*. The specimens were frozen immediately after capture. After thawing in the laboratory, the fork length, weight, and sex were recorded. The sagittal otolith pair was then removed from each fish and stored dry in paper envelopes until the time of elemental analysis. The species identity of individual fish was unknown at the time of collection (when fin clips were taken) but was subsequently assigned on the basis of the genotype at 13 microsatellite loci (A. Valentin, unpublished data). The

otolith elemental fingerprints of these nine summer samples were considered as our reference collection against which our winter samples were subsequently compared.

Winter aggregations of both species of redfish were sampled in the fall and winter of 2002 (Table 1). A total of nine sets were sampled for otoliths, yielding 98 *S. fasciatus* and 189 *S. mentella*. An additional 48 *S. mentella* were collected by handline from the Saguenay Fjord in the winter of 2003. Sample processing was as described for the summer samples.

Elemental analysis

Before elemental analysis, all otoliths were decontaminated using a modification of the protocol described in Fowler et al. (1995). Briefly, this involved a 5-min sonification of each otolith in an acid-washed 50 ml polypropylene vial containing Super Q water (distilled, millipore-filtered, reverse-osmosis water), followed by a 1-min scrubbing with an acid-washed toothbrush, triple rinsing in Super Q water, a 3-min sonification in Super Q, and a final triple rinse in Super Q. Decontaminated otoliths were air-dried in acid-washed polypropylene caps under a Class 100 laminar-flow, positive-pressure fume hood for 24 h before weighing to the nearest 0.1 mg. Decontaminated otoliths were subsequently stored

dry in sealed, acid-washed polypropylene vials to await assay. Blank vials were similarly prepared for blank corrections and calculations of limits of detection. At all stages of the decontamination process, otoliths were exposed only to acid-washed plastic materials, and all steps other than sonification were carried out in the laminar-flow fume hood.

Decontaminated otoliths were dissolved in subboiling, redistilled nitric acid and brought to 0.1% w/v with Super Q water. A suite of seven trace elements (Li, K, Mg, Mn, Sr, Cd, and Ba) was assayed with inductively coupled plasma mass spectrometry (ICP-MS), of which five were suitable for quantification by isotope dilution. Isotope dilution was the preferred method of quantification owing to superior accuracy and precision in otolith assays (Campana et al. 1995). The enriched isotopes used in the spiking procedure were ^6Li , ^{25}Mg , ^{67}Zn , ^{86}Sr , and ^{136}Ba , whereas the remaining more abundant isotopes were used for quantification. The remaining elements were referenced to an internal standard (In) for assay by conventional ICP-MS and quantified using matrix-matched external standards. Because of concerns over possible isobaric interferences or proximity to detection limits, significant assay results for B, Cu, Zn, Pb, and U were not carried forward to the statistical analyses.

An additional three elements (Ca, Na, and Sr) were assayed with inductively coupled plasma emission spectrometry (ICP-ES) after a 300-fold dilution of the original dissolved otolith. Quantification was through matrix-matched external standards. Fe was also assayed, but mean concentrations were too close to detection limits to be useful.

Differences in otolith elemental composition among groups of fish may be statistically significant, but they will not necessarily be large. Two protocols were adopted to minimize the possibility for artifactual differences and to reduce the variance: (i) the assay sequence was systematically randomized across sample sites to insure that instrument drift did not artifactually inflate the assay results of one sample site over another, and (ii) a pooled sample solution, consisting of aliquots of solution of 150 otoliths, was analyzed at regular intervals throughout the ICP-ES and ICP-MS analytical sequences. Analytical batches were subsequently normalized to the mean pooled-sample concentration (element by element). The effect of this normalization was to remove the effect of instrument drift and interbatch differences from all assays and therefore reduce the variance of the assays.

Limits of detection (calculated as 3 standard deviations (SD) of the blank; $\mu\text{g}\cdot\text{g}^{-1}$) for the elements of interest were as follows: 0.1 for Ba, 0.003 for Cd, 154 for Ca, 0.005 for Cu, 0.02 for Li, 0.09 for Mg, 0.01 for Mn, 7.0 for K, 0.8 for Na, and 0.6 for Sr.

Statistical analysis

The two redfish species were analyzed independently of each other. The within-group distributions of Li, Mg, and Mn concentrations were skewed and thus were ln-transformed prior to statistical analysis. To insure that differences in fish size or age among samples were not confused with site-specific differences, the effect of otolith weight was statistically removed from those elemental concentrations in which a significant size effect was evident (Campana 1999). The effect of otolith weight was removed from the elemental concentration of Na, K, Li, Mn, Mg, and Sr in each

species by subtracting the product of the otolith weight and the common, within-group slope (from an analysis of covariance (ANCOVA)) from each observed concentration. The main effect in the ANCOVA was sample location, with otolith weight as the covariate. The interaction term between location and otolith weight was also tested for significance; elements with a significant interaction term were evaluated with and without size detrending to insure that statistical artifacts did not confound the analysis.

Each otolith was characterized by a suite of several elements; therefore multivariate statistics were used to distinguish among samples. Multivariate analysis of variance (MANOVA) was used to test for significant differences among samples, whereas discriminant function analysis (DFA) was used to prepare two-factor elemental fingerprints for illustrative purposes. Discriminant analysis was not used to classify the samples of unknown stock affinity (those collected in the winter). Principal component analysis (PCA) was also used to display the multivariate fingerprint, but unlike in DFA, this type of analysis does not attempt to maximize the distance between groups of fish.

Stock composition analysis of each sample location in the winter collection was carried out using the maximum likelihood based stock mixture analysis described in Campana et al. (1999). The reference groups for all stock mixture analyses were the species-specific, set-by-set summer samples of redfish. Conceptually, the stock composition analysis uses the multivariate distribution of the elemental fingerprints in each reference (summer) sample to estimate the proportion of each reference population in the unknown (winter) mixture. As long as all of the possible groups contributing to the winter group mixture have been represented in the summer samples, the analysis will produce an unbiased estimate of group proportions, with no more assumptions than those associated with genetic markers (Wood et al. 1987, 1989; Campana et al. 1999). The product of the analysis was the proportions of each summer reference sample in each winter sample. Note that the true spawning origin of each summer samples was unknown. Therefore, the classification of the winter samples is in terms of summer groups (samples), not of spawning populations. This approach is well suited to determining the relative movement of redfish collected in winter compared with where they were in the summer.

Results

Redfish distribution in the summer was concentrated in deep water along the shelf edge in the outer Gulf of St. Lawrence and approaches (Fig. 1). Relatively few redfish were collected west of 61°W . Redfish aggregations tended to be discontinuous, except on the outer Scotian Shelf and along St. Pierre Bank.

Although some of the collection sets included redfish of both species, most sets selected were dominantly or exclusively one species or the other (Table 1). Fish length differed slightly but significantly among sets and species ($p < 0.05$). The mean (± 1 standard error (SE)) fork length of *S. fasciatus* in summer and winter was 30.3 ± 0.3 cm and 29.8 ± 0.3 cm, respectively, whereas that for *S. mentella* was 34.4 ± 0.2 cm in both winter and summer (excluding the fish from the Saguenay Fjord). *Sebastes mentella* from the winter

Fig. 2. Examples of the relationship between elemental concentration and otolith weight in *Sebastes mentella* collected in the Gulf of St. Lawrence. There was a significant relationship in the case of (a) Na but not (b) Ba. Each symbol type denotes a different sample location. The common within-group slope from the analysis of covariance is shown and was removed statistically from all elements with a significant relationship.

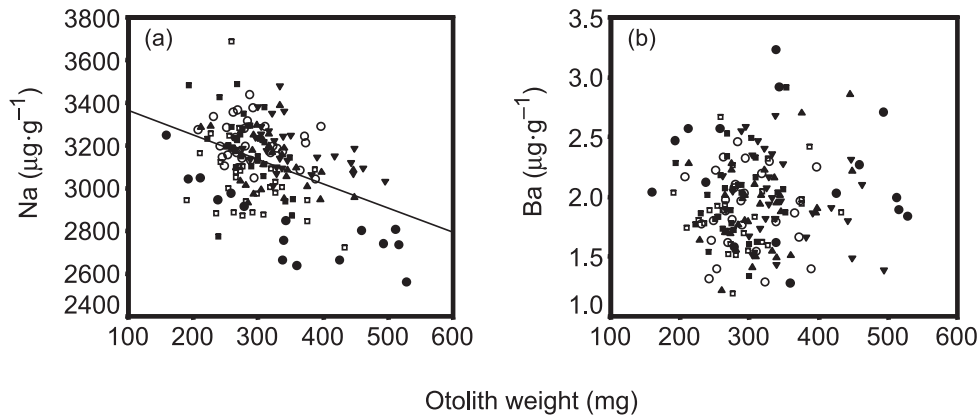


Table 2. Differences in elemental concentration among species and sample locations in the summer reference collections based on analysis of covariance with otolith weight as the covariate.

Species	Element	Slope parameter	Otolith weight × location	Location
<i>S. fasciatus</i>	Cd		ns	ns
	Na	-0.326	0.02	<0.01
	K	-0.328	0.01	<0.01
	ln Li	-0.00248	<0.01	<0.01
	Sr		ns	ns
	ln Mn	-0.00179	ns	<0.01
	ln Mg	-0.0010	ns	<0.01
	Ba		ns	<0.01
<i>S. mentella</i>	Cd	5.00×10^{-6}	ns	ns
	Na	-1.059	ns	<0.01
	K	-0.09	0.04	<0.01
	ln Li		ns	0.02
	Sr	1.486	ns	0.01
	ln Mn	-0.00259	ns	<0.01
	ln Mg	-0.00092	ns	ns
	Ba		ns	<0.01

Note: Where significant, the common within-group slope that was used to statistically remove the effect of otolith weight from elemental concentration is shown. ns, not significant.

Saguenay Fjord collection were significantly smaller at 29.4 ± 0.1 cm ($p < 0.05$), whereas those from summer 3PS4 were significantly larger at 37.4 ± 1.2 cm ($p < 0.05$) than any of the other summer sets.

All of the elements except Ba and Cd showed a significant relationship between concentration and fish length or otolith weight (Fig. 2). To insure that differences in fish size among sample locations did not confound any real differences in elemental concentration, the effect of otolith weight was statistically removed from the elemental concentrations through ANCOVA where significant (Table 2). In most but not all cases, the interaction term between location and otolith weight was not significant, making the common within-group slope of the ANCOVA the best measure of the size-specific effect. Where the interaction term was significant but limited to a single location, the common within-group

slope was still used for detrending. However, stronger interactions were not detrended. In all cases, relative differences among detrended samples tended to be ranked similarly to those based on the original data.

Analysis of the summer (reference) samples of each species indicated that the concentrations of most elements differed substantially among locations (Fig. 3). All elements but Cd differed significantly among locations within at least one species (Table 2). Elements such as Ba (both species) and K (*S. mentella* only) showed a generally increasing gradient moving out of the Gulf of St. Lawrence, whereas elements such as Li, Mn, and Sr differed substantially among locations, but with no obvious gradient (Fig. 3). Although there was only one location where both redfish species were analyzed (3PS4) there seemed to be little overall correspondence in elemental concentration between the species at that

Fig. 3. Variation in mean ($\pm 95\%$ confidence interval) elemental concentration between species and summer locations. Concentrations for all elements except Ba and Cd have been weight-detrended; however, the differences among locations changed relatively little as a result of the detrending. Solid symbols, *Sebastes mentella*; open symbols, *S. fasciatus*. Sample sites have been ordered from northwest (left) to southeast (right).

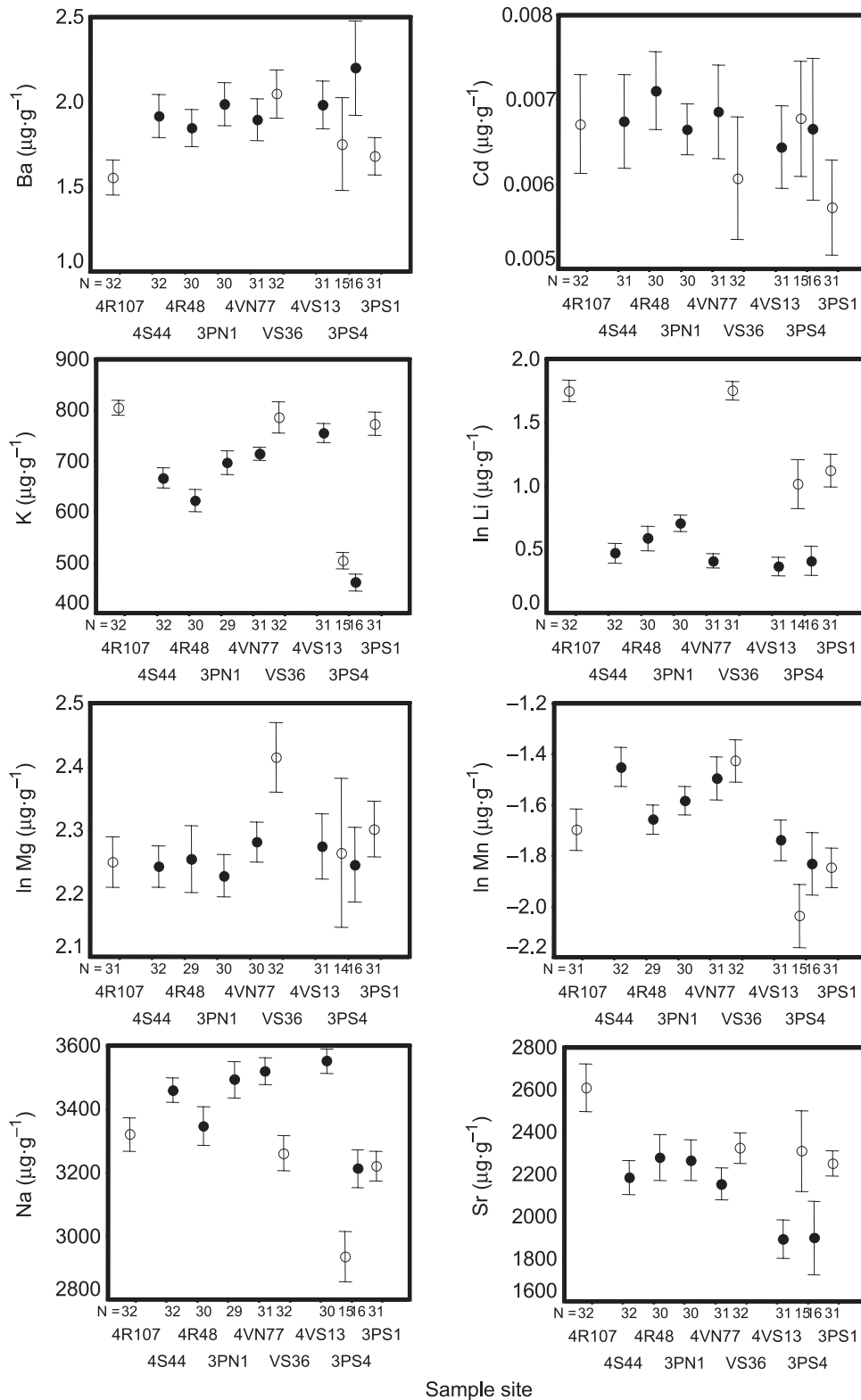
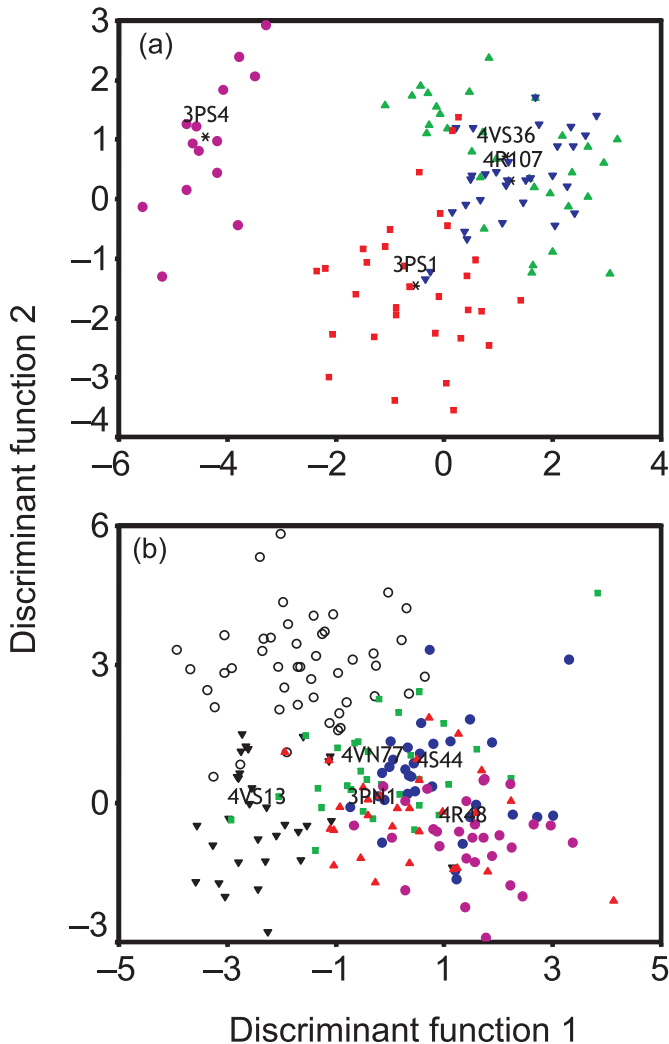


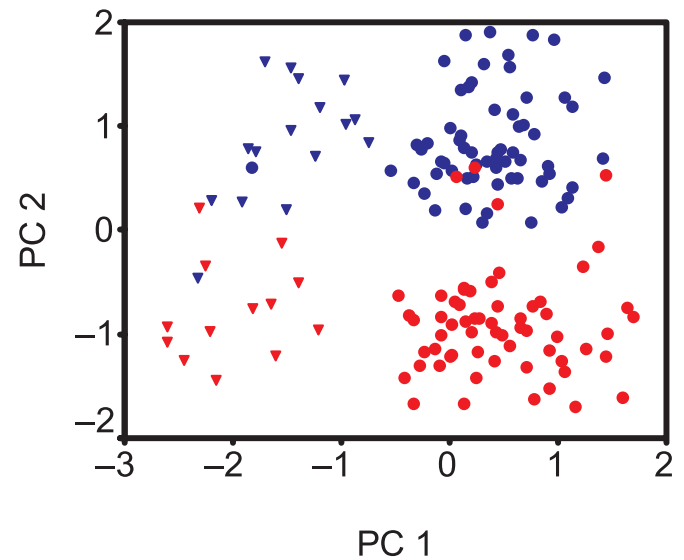
Fig. 4. The elemental fingerprints of (a) *Sebastes fasciatus* and (b) *S. mentella* as markers of summer samples in a discriminant analysis. Each data point represents a fish, and each colour represents a sample location. The centroids of each location are located below each label. Winter Saguenay samples (open circles) do not lie in the discriminant space defined by the summer samples of *S. mentella*, indicating that none of the summer samples represents the source group for the Saguenay sample.



site, perhaps because this sample comprised several closely spaced but independent sets (Table 1).

Although it may be possible to use the concentration of a single element to distinguish between and track groups of redfish, it is preferable to use a multivariate approach, which uses all elements at once. A MANOVA demonstrated that the differences among summer sample locations were highly significant within each species ($p < 0.001$). DFA proved to be an excellent way to visualize those differences (Fig. 4). Four elements entering into the stepwise DFA (Li, Mn, Sr, and K) were common to both species, with Ba also entering into the DFA for *S. mentella*. In both species, the first two discriminant functions explained more than 90% of the variance. The DFA for *S. fasciatus* showed that two of the summer samples (3PS1 and 3PS4) were easily distinguished from all others in discriminant space, whereas the remaining

Fig. 5. Plot of the first two principal components (PC) of otolith elemental composition for locations containing both *Sebastes fasciatus* (in red) and *S. mentella* (in blue) in summer (▼) and winter (●). The two species tend to be easily identifiable based only on otolith elemental composition, irrespective of season.

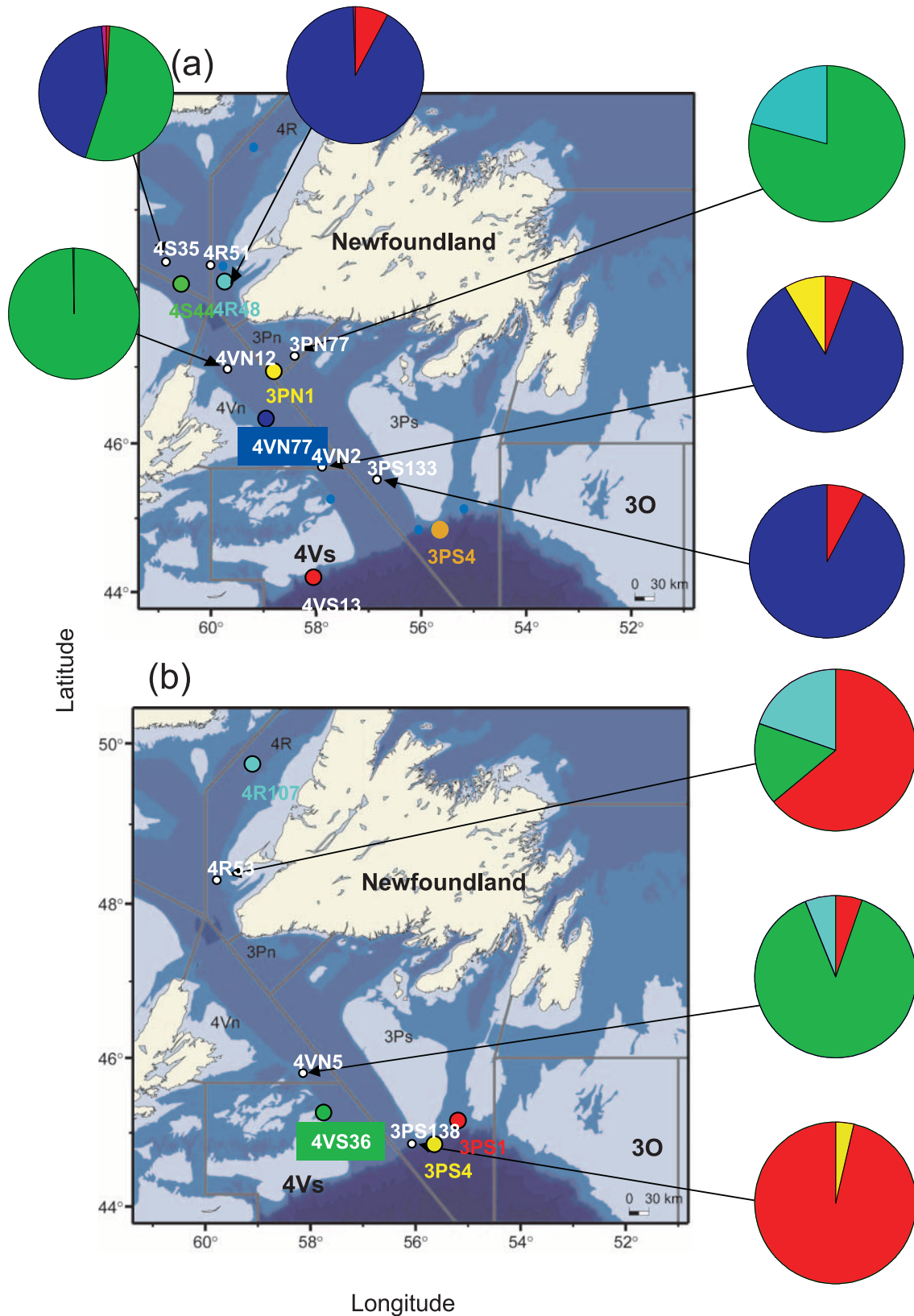


two samples were similar to each other (Fig. 4). When the discriminant scores for the winter samples were overlaid on the summer scores for *S. fasciatus* (using a DFA where only the summer samples were entered as reference groups), all of the winter samples seemed to be well represented by the space described by the summer samples (not shown). In other words, there was no reason to believe that the source groups for the winter samples included groups other than those represented by the existing summer samples.

A comparable DFA for *S. mentella* also showed that sample 3PS4 was isolated in discriminant space (not shown). When the DFA scores for the winter samples were overlaid on the summer scores, none of the winter samples lay in the discriminant space defined by sample 3PS4. Because this result implies that sample 3PS4 could not have been a source group for any of the winter samples, the DFA was repeated without using sample 3PS4 as a reference group. The resulting DFA showed clear and significant separation between two of the groups and overlapping but significant separation among all groups except 4VN77 and 3PN1 ($p < 0.05$) (Fig. 4). The discriminant space defined by these summer samples appeared to describe that of the winter samples very well, with the exception of the Saguenay redfish. The discriminant scores of the Saguenay redfish lay well outside the summer discriminant space, indicating that there were no appropriate source groups for the winter Saguenay redfish among any of the summer samples (Fig. 4).

The objective of this study was to differentiate among locations within a species, not to discriminate between species. However, given the difficulties in differentiating between species, elemental differences between species collected at the same location could help with the species identification. *Sebastes fasciatus* and *S. mentella* collected at similar locations (winter samples 4R53 vs 4R51 and 4VN2 vs 4VN5; summer sample 3PS4) in the same season were easily identified based only on a PCA of the otolith elemental composi-

Fig. 6. Stock mixture analysis of winter collections of (a) *Sebastes mentella* and (b) *S. fasciatus* of unknown origin classified using the otolith elemental fingerprints of summer collections as reference sources. The locations of the summer reference collections are shown as large coloured circles, the winter collections are indicated by small open circles. The proportional stock composition of each unknown winter collection is shown as a pie chart, with each colour referring to a specific summer source location.



tion (Fig. 5). Indeed, the differentiation between species was so complete that it raises the possibility that the few individuals plotted in the factor space of the other species may have been misidentified. Summer and winter collections of each species were also distinguished, although the sole summer location where both species were collected (3PS4) was one that was isolated in discriminant space from all other summer samples.

Stock mixture analysis was used to determine the stock origin (in terms of summer reference samples) of each of the winter samples. Based on the elements that entered into the DFA, five elements were selected for entry into the mixture analysis: Li, Mn, Sr, Ba, and K. The accuracy of the resulting mixture estimates could not be directly measured. However, a jackknifed classification of each of the summer reference samples resulted in a mean accuracy of 96.5%, with no sample being classified with less than 92% accuracy.

More than half of each *S. mentella* winter sample was classified as having originated from a single summer reference sample, and in most cases, the single summer sample contributed more than 80% to the mixture (Fig. 6a). In four of the six winter samples, the summer sample that contributed most to a given winter sample was that closest and upstream (into the Gulf). Thus the mixture analysis indicated that *S. mentella* moved slightly to the southeast, towards the mouth of the Gulf, for the winter. The only samples that appeared to show a different pattern (4R51 and 4S35) were classified as having a large component from 4VN77. Although initially counterintuitive, this result may also be consistent with a winter outmigration from the Gulf; none of the summer reference samples was as far north in the Gulf as 4R51 and 4S35, suggesting that a more appropriate source group was not available from our summer sampling. There was no evidence of substantive contribution by the Scotian Shelf sample (4VS13) to any of the winter Gulf mixtures.

As was the case with *S. mentella*, all of the *S. fasciatus* winter samples were dominated by a single summer source (Fig. 6b), and once again, the source group for the winter mixtures was usually identified as a nearby summer sample. However, with this species, there was only one summer sample collected north of the Newfoundland – Cape Breton line, which is insufficient to determine the presence of any winter outmigration. The poor summer sample coverage of *S. fasciatus* may also explain the rather diverse mixture predicted for 4R53; if outmigration did occur, there were no nearby summer samples that could have served as a source, implying that the mixture analysis could only draw on incorrect summer sources for classification of this sample.

Discussion

The distribution of redfish in the 2002 summer surveys was broadly consistent with surveys carried out in the 1976–1993 period: most deep areas in the Gulf of St. Lawrence west of Anticosti Island contained redfish, although the distribution was patchy rather than continuous. Most of the *S. mentella* were captured at depths of 300–500 m, and most of the *S. fasciatus* were captured at depths of 200–250 m, similar to what was reported by Atkinson (1984). However, in contrast to summer surveys before 1994, *Sebastes* spp. were most concentrated in the Laurentian Channel and its

approaches, rather than in the Gulf (Atkinson 1984; Morin et al. 1994; Gascon 2003). Presumably, the scarcity of redfish in the Gulf is due to the population collapse and subsequent fishery closure of Gulf of St. Lawrence (Management Unit 1) redfish (Department of Fisheries and Oceans (DFO) 2004). The winter distribution of *Sebastes* was not mapped as part of this project but has been well documented in previous summaries of winter research vessel surveys and fishing fleet distributions (Atkinson 1987; Morin et al. 1994; Gascon 2003). In all cases and in all years, redfish were concentrated in the southern Gulf of St. Lawrence – northern Laurentian Channel area during the winter, with relatively low numbers further west within the Gulf of St. Lawrence.

Does the winter concentration of *Sebastes* spp. in the Laurentian Channel and its approaches represent a simple movement out of the Gulf of St. Lawrence for overwintering, or is the winter concentration the focus of movement from all surrounding areas into one optimal overwintering ground? The stock mixture analyses provided clear evidence of southeasterly movement by *S. mentella* out of the Gulf and rejected the hypothesis that more easterly aggregations also joined the mixture. Indeed, summer *S. mentella* from the eastern edge of the Laurentian Channel (both south and north) were poorly represented in the winter samples, indicating that they overwintered somewhere else. These results are consistent with inferred movements based on research vessel surveys and fishing fleet distributions (Atkinson 1987; Morin et al. 1994; Gascon 2003). The movement demonstrated for *Sebastes* is also similar to that reported for cod (*Gadus morhua*) and other species in the Gulf of St. Lawrence, which also move out of the Gulf to overwinter (Swain et al. 1998; Campana et al. 1999; Castonguay et al. 1999). The difference between these species, though, lies in terms of evolutionary advantage: whereas cod and other species in the shallower waters of the Gulf would be exposed to a seasonal temperature range of >12 °C between summer and winter (Swain and Kramer 1995), redfish remaining in the deep waters of the Gulf would experience seasonal temperature differentials of less than 1 °C (Atkinson 1984). Therefore, temperature is unlikely to be the major cue for redfish outmigration in the winter. Food availability is a possibility, particularly as redfish vertically migrate to shallower depths on a diurnal basis, presumably to feed on euphausiids and mysids. Equally plausible is the possibility that winter outmigration occurs in response to endocrine-driven cues leading eventually to spawning, as has been observed in cod (Comeau et al. 2002). With redfish copulation occurring in late fall or early winter (Ni and Templeman 1985), overwintering aggregations may represent mating aggregations. If this is the case, the fact that few eastern Scotian Shelf (Unit 2) *S. mentella* were identified in the overwintering mixture may indicate that they constitute a population that is distinct from that in the Gulf of St. Lawrence and Laurentian Channel.

The overall absence of genetic structure observed within the Gulf of St. Lawrence *S. mentella* indicates that either there is only one spawning group or there is sufficient mixing among spawning groups to mask any genetic differentiation (Roques et al. 2001; A. Valentin, unpublished data). However, these mixing rates need not have been high; mixing on the order of 1% or less is enough to prevent genetic

differentiation (Bentzen et al. 1996). In contrast, the significant differences among otolith elemental fingerprints of the summer samples indicates that the groups remained in different environments through some portion of their lives, irrespective of their genetic origin. Although it is possible that distinct populations existed at all life history stages and that a small amount of genetic mixing occurred at the spawning stage, a more likely scenario is that distinct spawning groups of redfish contributed to a single, well-mixed larval pool in and around the Gulf of St. Lawrence. Redfish juveniles and larvae are undoubtedly more mobile than the adults, which suggests that the early life history stage is the one in which mixing occurs. As the redfish get older and settle into deeper waters, their aggregations are likely to become more structured and sedentary, mixing very little with other adult aggregations. Such a life history pattern would explain both the observed genetic homogeneity and the accumulated differences in otolith composition among groups.

Elemental fingerprints change very slowly in whole otoliths of long-lived fishes, and thus they serve as stable and accurate natural tags of groups of fish (Campana et al. 2000). Therefore, the basic limitation of the stock mixture analysis was the spacing of the summer reference samples. As with stock mixture analyses based on genetics, elemental stock mixture analyses classify an unknown sample (e.g., winter samples) in terms of proportions of each reference (summer) group. Thus it is important that all possible source groups be represented in the reference samples. The summer reference samples were reasonably well spaced for *S. mentella*, so the movement of most of the winter samples could be tracked with reasonable precision. An exception was the most westerly of the winter samples; if they originated further to the west, as was the case with the other winter samples, our analysis would have classified that sample incorrectly, owing to the absence of any reference group further to the west. A similar limitation was in effect for the classification of the *S. fasciatus* winter samples; the summer reference samples were widely spaced in the Gulf, implying that any movements of winter samples could only be detected at similar or larger scales.

Our conclusion that deepwater *Sebastes* undertake annual migrations, perhaps in the context of reproduction, seems plausible, but tracking studies on deepwater species are scarce (Starr et al. 2000). Virtually all studies on the distribution of adult *Sebastes* in the Atlantic have been confounded by difficulties in distinguishing among species and thus have been focused on the zoogeography of the congeneric species rather than within-species movements (Misra 1985; Stransky and MacLellan 2005; Valentin et al. 2006). Nevertheless, broad categories of deepwater fish migrations have become increasingly well documented. Diel vertical migrations in response to the day–night cycle are well established among deep-sea fishes (Butler et al. 2001; Gauthier and Rose 2002), as are ontogenetic migrations towards deeper water as the fish grows (Jacobson et al. 2001; Allain et al. 2003). However, the large-scale seasonal migrations so commonly observed in pelagic fishes have not been reported in deep-sea fishes (Beamish et al. 2005). For example, orange roughy (*Hoplostethus atlanticus*) are often associated with specific seamounts and do not venture far from their settling location (Smith et al. 2002). Edmonds et al. (1991) also reported minimal move-

ments by deepwater aggregations of orange roughy. In contrast, smaller-scale migrations associated with reproduction and (or) feeding have been reported both for deep-sea angler (*Lophius budegassa*) (Duarte et al. 2001) and hoki (*Macruronus novaezelandidae*) (Kuo and Tanaka 1984). In the latter case, the scale of the migration (50–500 km) was on the same scale as was seen in our study on *Sebastes* spp.

The *S. mentella* collected from the Saguenay Fjord were characterized by elemental fingerprints that were completely unlike any of the other summer or winter samples. This fact indicates that the Saguenay redfish must have spent a portion of their lives separated from other redfish in the Gulf. Although it is not possible to determine from whole-otolith composition exactly how long different groups may have remained isolated from each other, the very distinct nature of the Saguenay fingerprints suggests a large portion of their lives must have been spent in isolation from the other groups. Microsatellite DNA assays indicate that the Saguenay redfish are genetically indistinguishable from *S. mentella* in the Gulf of St. Lawrence (Roques et al. 2002; A. Valentin, unpublished data). Therefore, Saguenay redfish appear to represent a population sink: a recruitment pulse of Gulf redfish that settled away from the bulk of the population and have since grown up in isolation from other redfish.

The interspecies difference in elemental fingerprints of *S. mentella* and *S. fasciatus* probably reflects an interspecies difference in life history and habitat more than an intrinsic difference in trace element incorporation into the otolith. Otolith composition is largely a product of the environment, both physical and chemical, as modified by growth rate and physiology (Campana 1999). It is unlikely that the water chemistry differed appreciably between the depths occupied by the two redfish species, even though *S. fasciatus* is found somewhat closer to shore. However, the temperature environment presumably differed, with *S. fasciatus* being found in shallower, warmer water (Atkinson 1984; Gascon 2003). The fact that *S. mentella* grows larger and, presumably, has a different growth rate would also contribute to differences in the elemental fingerprint. Environmental and physiological causes of the differences in otolith elemental fingerprints between *Sebastes* species are also consistent with the findings of Stransky et al. (2005), who reported significant differences in otolith elemental fingerprints between *S. mentella* and *S. marinus* collected at the same location.

The implications of our findings extend to the fisheries management of *Sebastes* spp. in both the Gulf of St. Lawrence and the Laurentian Channel areas. The current management of redfish in these areas assumes the presence of two populations based largely on biological characteristics and distribution: a population in the Gulf of St. Lawrence (Unit 1, NAFO divisions 4RST (January–December) and 3Pn4Vn (January–May)) and a population in the Laurentian Channel (Unit 2, NAFO divisions 3Ps4VsWfgj (January–December) and 3Pn4Vn (June–December)). These two populations are managed as if they overlap in a mixing area in 3Pn and 4Vn but are segregated by season (Atkinson 1987). Our results strongly support the interpretation that the 3Pn4Vn region is occupied by Laurentian Channel redfish (Unit 2) in the summer and by overwintering Gulf (Unit 1) redfish in the winter. There are also indications that southeasterly movements of redfish occur throughout the Gulf and

Laurentian Channel regions between summer and winter. Our results indicated that the southeasterly movement from the Gulf into the 3Pn area extended to at least the 3Ps border. This suggests that the mixing area may be more extensive than what is currently defined by the management units, which leaves open the possibility that overwintering Gulf (Unit 1) redfish could be fished as part of the Unit 2 quota. Because Unit 1 redfish are now under a fishing moratorium (DFO 2004), this mismatch between management areas and population mixing areas may be exacerbating its current low population numbers. With the likelihood that both the timing of migrations and the extent of the mixing area are variable from year to year, additional management measures (seasonal and (or) area closures) could be required as a precautionary measure for Unit 1 redfish, at least during the moratorium. More broadly, the limited movement of redfish observed in our study would suggest that large-scale management areas for redfish may be at risk of locally overfishing what are essentially semi-isolated redfish aggregations, even if they share a genetic origin. If future work confirms the limited movement of redfish in other areas, optimal management may require smaller management areas than now exist.

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